McGill University

GEOLOGICAL SIGNIFICANCE OF BORING SPONGES ON BARBADOS REEFS

by

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ABSTRACT

The boring sponge fauna of Barbados reefs includes 15 clionid species, 3 Siphonodictyon species, one species each of Spheciospongia, Alectona, Acarnus, and an unidentified species. Clionids are more abundant and diverse than Siphonodictyon species.

Boring sponge populations on a fringing reef and deeper bank reef differ significantly. Boring sponges are uniformly distributed in the bank reef crest environment (13-20 m) but the sponge population in this bank crest environment is distinct from that in the fore-reef slope of the bank reef. Species abundance and diversity of boring sponges is greater in massive corals than in branching corals. Levels of abundance and diversity in coralgal substrate on the fringing reef are similar to those found in massive corals on the fringing reef. Lowest abundance and diversity were recorded in coral rubble from the swash zone.

Sponge borings generally occupy a narrow subsurface zone in the non-living basal regions of coral colonies. Four main categories of sponge borings were recognized. Sponge boring strategy appears to be genetically controlled since the same basic borehole morphology is produced in different coral species. Variations in skeletal density in corals affect the pattern of development of borings.

The volume removed from coral samples by sponge boring ranges from 0-29%. Coral colonies on the fringing reef are less extensively bored than those on the bank reef crest which are in turn less extensively bored than those on the deeper outer slope of the bank reef. M. cavernosa is most extensively bored followed by A. agaricites, M. annularis and either P. astreoides or S. siderea. The extent of sponge boring in different coral species depends mainly on the extent of exposed base and on the balance between coral growth rate and sponge boring rate. Skeletal density may also influence the extent of boring.

Rates of boring by sponges range from 102-756 $g/m^2/a$ in massive corals. Rates are higher on the bank reef crest than on the fringing reef and are highest on the bank sides. The average boring rate obtained by measuring weight loss in blocks of unbored coral which had been attached to sponge-infested substrate for known lengths of time is 752 mg per square centimetre

of sponge tissue per year. Sponges account annually for the erosion of more than 1/6 of the calcium carbonate secreted on the fringing reef.

Expansion of coral reefs results from the interplay between coral and algal growth and physical and biological erosion. Sponge boring appears to be the most important form of bioerosion. In shallow waters physical erosion is the dominant destructive process. As water depth increases and calcification rates decrease bioerosion by sponges becomes more important.

RÉSUMÉ

La faune d'éponges perforantes des récifs de la Barbade comprend 15 espèces de clionides, 3 espèces de Siphonodictyon, une de Spheciospongia, une d'Alectona, une d'Acarnus, et une espèce non-identifiée. Les clionides sont plus abondantes et plus diverses que les espèces de Siphonodictyon.

Les populations d'éponges perforantes de récif frangeant et de banc récifal, plus profond, diffèrent de façon significative. Dans un banc récifal, les éponges perforantes sont distribuées uniformément sur la crête (13-20 m), mais avec une population d'éponges distincte de celle de la pente frontale du banc. L'abondance et la diversité des espèces d'éponges perforantes sont plus grandes dans les coraux massifs que dans les coraux ramifiés. Dans un récif frangeant, les niveaux d'abondance et de diversité dans les substratums coralguaires sont similaires à ceux observés dans les coraux massifs. Les plus basses abondance et diversité furent enregistrées dans les débris coralliens des zones les plus agitées.

Les perforations d'éponge occupent généralement une faible épaisseur des régions basales, non-vivantes, des colonies de corail. Quatre catégories principales de perforations ont été identifiées. L'activité perforatrice semble impliquer un certain contrôle génétique, car l'essential de la morphologie d'une perforation se retrouve dans des espèces de corail différentes. Des variations dans la densité du squelette des coraux affectent le pattern de développement des perforations.

Le volume de matériel enlevé par perforation d'éponges dans des échantillons de coraux varie de 0 à 29%. Les colonies de coraux de récif frangeant sont moins intensivement perforées que celles de la crête de banc récifal, ces dernières étant toutefois moins intensivement perforées que les colonies des régions les plus profondes des pentes du banc. M. cavernosa est l'espèce la plus perforée, suivie de A. agaricites, M. annularis et l'une ou l'autre de P. astreoides ou S. siderea. L'importance de la perforation dans les différentes espèces de corail dépend principalement de l'importance de l'exposition de la base et de la différence entre le taux de croissance du corail et le taux de perforation. La densité du squelette peut aussi influencer l'importance de la perforation.

Les taux de perforation par éponges varient de 102 à 756 g/m^2/a dans

les coraux massifs. Les taux sont plus élevés sur une crête de banc récifal que dans un récif frangeant et sont les plus élevés sur les flancs du banc. Le taux moyen de perforation obtenu en mesurant la perte de poids de blocs de corail non-perforé attachés à des substratums infestés d'éponge pour des longueurs données de temps est de 752 mg par centimètre carré de tissus d'éponge par année. Les éponges contribuent annuellement à l'érosion de plus du 1/6 du carbonate de calcium sécrété dans le récif frangeant.

L'expansion des récifs coralliens résulte de l'interaction entre la croissance corallienne et alguaire et l'érosion physique et biologique. La perforation par des éponges semble être la forme la plus importante de bio-érosion. En eaux peu profondes, l'érosion physique est le processus de destruction dominant. Avec l'augmentation de profondeur et la diminution des taux de calcification, la bio-érosion par les éponges devient plus importante.

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INTRODUCTION

Boring sponges exploit a wide range of carbonate substrates in tropical and temperate waters of the world ocean. In tropical regions, limestone coasts and coral reef environments provide a favourable habitat for boring sponges because of the abundance of carbonate substrate into which they can penetrate. Sponges belonging to the families Clionidae, Adociidae and Spirastrellidae are an important component of the boring fauna of coral reefs. Although ubiquitous they are inconspicuous members of the reef community since they are cryptic in habit and live in cavities which they excavate beneath the substrate surface.

In recent years reef ecologists have directed their attention more and more towards the biological mechanisms of erosion in reef environments. Recognition of the extent of biogenic destruction of coral reefs is one of the most significant developments in the understanding of reef dynamics. Boring sponges are important agents of reef erosion. Boring takes place in all hard tissue which has been abandoned by the growing tissue of frame-building organisms. Boring activity is of sedimentologic and structural significance. Calcium carbonate chips which are released during the boring process contribute to the silt fraction of reef sediments. Coarse debris is formed when substrate, weakened by boring, collapses. The coarser material accumulates in channels and depressions within the reef framework. The fine particles are transported into quieter depositional environments in deeper waters off the reef front. The removal of material from the reef frame decreases its structural stability and results in modification of the shape of the frame since protruding parts which are highly bored are susceptible to break-off. The attachment areas of coral colonies are weakened by boring

until they become unstable and are detached during storms or under the influence of gravity.

Bourne (1893) pointed out that undermining by boring sponges was partly responsible for the break-off of young colonies of the coral Fungia from their attachment points. Gardiner (1903) noted the importance of the boring sponge Cliona in weakening coral skeletons for the attack of other boring organisms. The important role played by boring sponges in weakening coral reef framework and aiding marine erosion in shallow water was recognized by Bertram (1936) at Al Ghardaqa in the Red Sea, by Otter (1937) at Low Isles on the Great Barrier Reef and by Ginsburg (1957) in South Florida. Goreau and Hartman (1963) showed that boring sponge activity is responsible for weakening reef framework and supplying coarse coral rubble to the deep fore-reef on the fore-reef slope in Discovery Bay, north Jamaica. They also suggested that sponge-generated sediment contributes significantly to the fine fraction of reef sediments. This was later confirmed by Futterer (1966) who calculated that sponge produced particles can constitute 2 to 3% of the total sediment in reefs in the Persian Gulf and Northern Adriatic Sea and up to 30% at Fanning Island, and by Moore et al. (1976) who found that sponge particles can amount to more than 5% of the total volume of island slope sediments off Discovery Bay. Warme and McCrevey (1974) found clionid sponges were an important component of the boring fauna from shallow depths to depths of over 100 m in Yucatan and Jamaica. Hein and Risk (1975) found that boring sponges (and boring polychaetes) removed the greatest amount of coral skeleton from massive reef corals on patch reefs in the Florida reef tract. Of the borers present in colonies of Montastrea annularis on Hens and Chickens patch reef in the Florida reef tract, boring sponges again appeared to be most important in hard tissue destruction (Hudson, 1977). Bak (1976) found that sponges

were the most common borers in corals on Curaçao reefs. The importance of boring sponges in reef erosion and sediment production is emphasized by Hartman (1977) and Warme (1977).

Appreciation of the real significance of boring sponges in carbonate erosion and sediment production followed the work of Neumann (1966) who estimated that the sponge Cliona lampa was capable of eroding between 23 and 25 $kg/m^2/a$ from the subtidal portion of calcarenite cliffs which surround Harrington Sound, Bermuda. Ruetzler (1975) arrived at a more conservative estimate of 256 $g/m^2/a$ for the erosion rate of boring sponges in nearshore patch reefs and rock bottoms in Bermuda and Spurr (1975) obtained a figure of 14 $kg/m^2/a$ for the erosion rate of boring sponges on the reefs of Discovery Bay, Jamaica. In Curaçao, erosion rates by Cliona peponaca ranged from 2.6 to 3.3 $kg/m^2/a$ (Bak, 1976). On the coral reefs of St. Croix and Jamaica, rates of erosion by clionids can approach 7 $kg/m^2/a$ (Moore and Shedd, 1977).

During a previous investigation in Barbados (MacGeachy and Stearn, 1976) the relative importance of different groups of borers was assessed using X-radiography in Montastrea annularis. Boring sponges accounted for the removal of 90% or more of the total coral skeleton removed by boring organisms from coral samples. Comparable high levels of sponge boring in other corals examined suggested that sponges account for this high percentage in most reef corals. These results (and the results of other studies which revealed the sedimentologic and structural significance of boring sponges in other reef environments) generated interest in this group and prompted further more detailed study of their geological significance on Barbados reefs.

The main aims of the study are:

1. to identify, describe and define the distribution of Barbados boring sponges. (Some comparative work was also done on the sponge faunas of Carriacou in the Grenadines and Curaçao in the Netherlands Antilles.)
2. to document borehole morphology and determine the controls on sponge boring strategy.
3. to compare the amount of sponge boring in the principal reef-building corals in Barbados and to determine the factors controlling the amount of sponge boring in different coral species.
4. to determine sponge boring rates and to estimate the total amount of erosion by sponges over the entire reef surface.

This study was part of a larger project on the calcium carbonate budget of the Bellairs fringing reef (Stearn et al., 1977; Scoffin et al., /in press/) and one of the main objectives was to determine erosion rates, by borers, which could be directly compared with productivity data. Since boring sponges account for 90% or more of the total boring in coral heads their erosion rate closely approximates the total figure for all borers. Whereas Stearn et al. (1977) concentrated on the inshore Bellairs fringing reef this study covered both the fringing reef and part of a deeper water offshore reef. Since no productivity data is available from the deep reef a similar comparison of growth and erosion can not be made.

Study Site Description

Fieldwork was carried out from May to September in 1975 and 1976 in the region offshore from the Bellairs Research Institute on the west coast of Barbados. The bathymetry and ecological zonation of this area have been

described by Stearn et al. (1977) and are shown in Figs. 1 and 2. The two main reefs present are an inshore fringing reef, called the Bellairs reef since it lies immediately offshore from the Bellairs Institute, and a deeper water offshore reef.

The Bellairs reef is divided into a northern and southern lobe by a triangular sand area (Plate 1A). Prolific coral growth occurs in the more seaward coalesced spur and spur and groove zones (Plate 1B). The dominant coral species present and their percentage coverage are Porites porites (12%), Porites astreoides (8%), Agaricia agaricites (6%), Montastrea annularis (5%) and Siderastrea siderea (3%). In the reef crest zone corals are sporadically distributed and most of the reef surface is covered by coralline algae (41%). The swash zone is an area of sand and coral rubble accumulation.

The deeper reef, which is referred to in this report as the bank reef, is part of a ridge which parallels the west coast of the island over most of its length. Macintyre (1967) suggests that this ridge and a deeper second ridge which is of a similar form are remnant barrier reefs which formed during a low stand of sea level in Pleistocene times and were drowned by rising sea level. The ridge crest in the region offshore from Bellairs is around 100 m wide and lies at a depth of 15 m. A thriving community of massive reef corals, soft corals and sponges covers the top and sides of the ridge. This community has been described by Ott (1975). The principal coral species present and their percentage coverage are Montastrea annularis (5%), Montastrea cavernosa (4.5%), Siderastrea siderea (4%), Porites astreoides (2%), Stephanocoenia michelinii (2%), Diploria strigosa (1.7%), Colpophyllia natans (1.5%) and Agaricia agaricites (1.3%). Sponges (Agelas, Callyspongia, Xestospongia, Hymeniacidon, Verongia, Ircinia, Hemectyon) cover around 3.3% of the bottom and gorgonids (Pseudopterogorgia, Plexaurella, Plexaura,

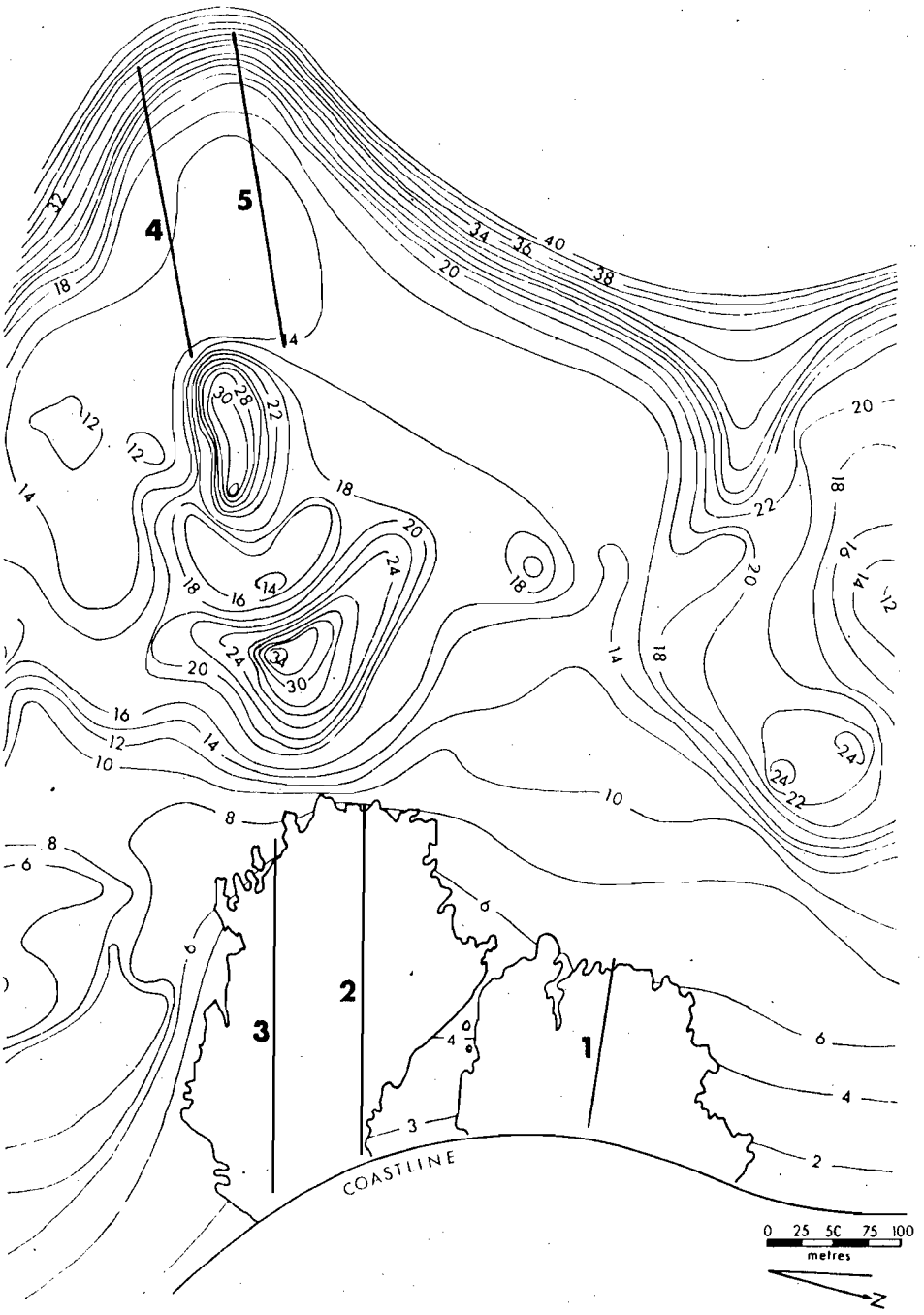

Figure 1: Bathymetry in the area offshore from the Bellairs Research Institute, Barbados. Contour interval 2 m. (from Stearn et al., 1977) Location of transects 1-5 indicated.

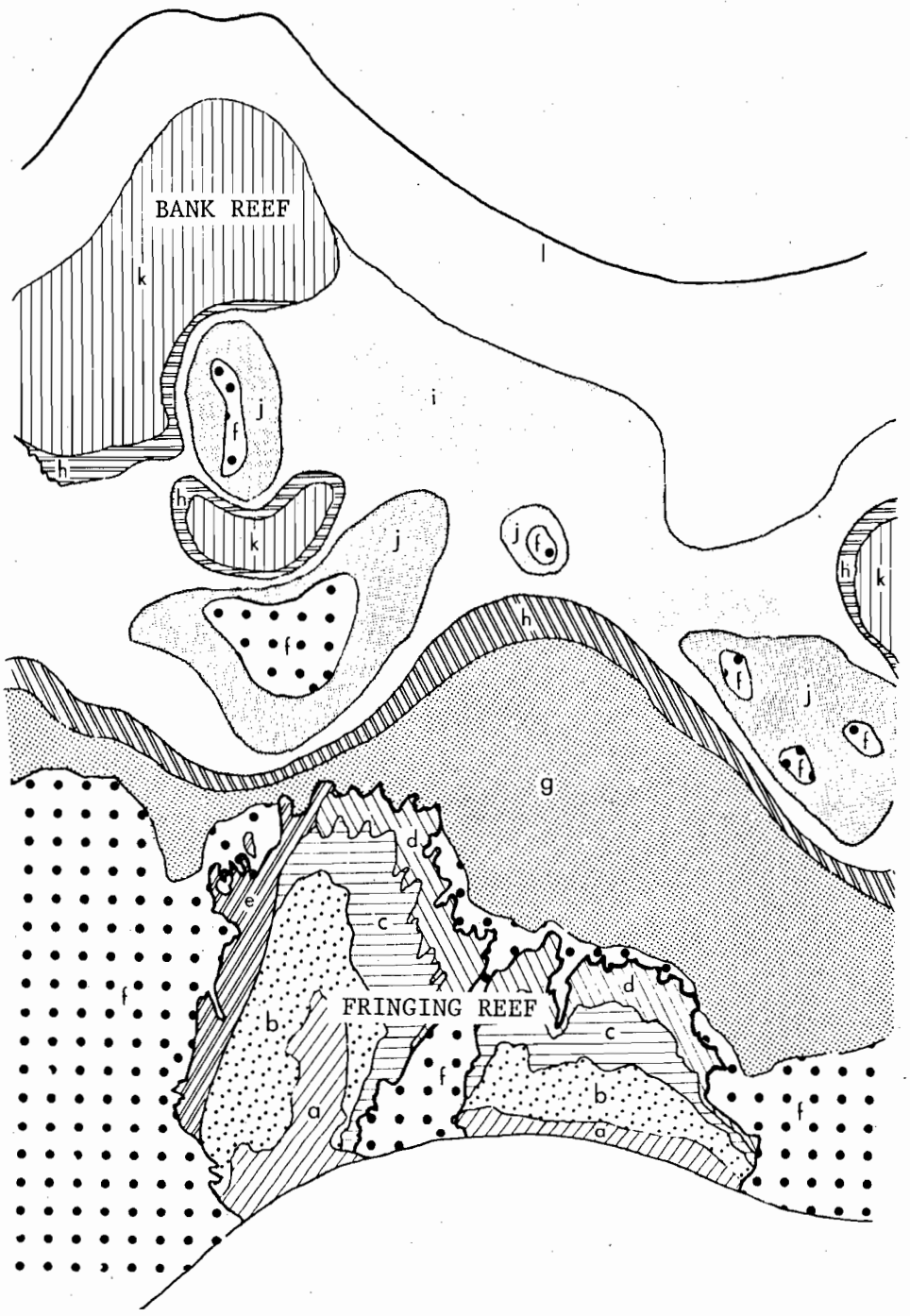

Figure 2: Ecological zones and dominant substrate types in the area offshore from the Bellairs Research Institute. Zones are: (a) swash zone, (b) crest zone, (c) coalesced spurs zone, (d) spurs and grooves zone, (e) Porites porites zone, (f) sand zones, (g) rubble zone, (h) Madracis mirabilis zone, (i) Acropora cervicornis zone, (j) mushroom-coral zone (become platy in deeper parts), (k) dome-coral zone, (l) platy-coral zone. (from Stearn et al., 1977)

Gorgonia, Eunicea) about 2%. Coral coverage on the top of the bank reef (Plate 1C) averages 30%. The bank top is defined as the region above 20 m since at this depth there is an increase in the slope. Approximately 7% of the bottom is covered by other zoobenthic organisms and the remaining 63% by dead coral, sand and a small amount of coral rubble.

The seaward flank of the bank reef slopes at an angle of around 30 degrees. Coral coverage in this area is higher (up to 40%) than on the bank top. Growth extends on the slope to depths of between 35 and 40 m and most species develop platy growth forms. Thin platy colonies of Agaricia lamarcki form a narrow zone between 30 and 35 m. Antipatharians are common in the deeper parts of the slope. At the lower limit of coral growth there is a break in slope. Beyond this point the bottom slopes off at an angle of around 15 degrees and is covered with sediment shed from the reef above. A second ridge is present at a depth of 70 m.

The slope of the shoreward (inner) flank of the bank reef is not as uniform as that of the seaward flank. A 30 m deep subcircular depression (one of three which occur in the region between the fringing and bank reefs) which lies just shoreward of the bank gives rise to a steeply dipping (45 degrees) inner slope which supports platy coral growth similar to that of the outer slope. The inner slope is gentler to the north and south of this depression and is colonized by stands of Madracis mirabilis and Acropora cervicornis. Much of the sea floor between the fringing and bank reefs is covered by these two species. The three depressions which are present in this area lie within the A. cervicornis zone. The walls of these holes are colonized by massive reef corals and all are floored by fine sediment. The depressions are probably sink holes which formed during a low stand of sea-level in late Pleistocene time.

Terminology

The term 'bioerosion' (Neumann, 1966) is used to describe the destruction and removal of hard calcareous substrate by the direct action of organisms. The terms 'boring' and 'excavating' are used in the geological context to describe penetration of hard calcareous substrates by sponges.

The general structure and physiology of boring sponges is described by Goreau and Hartman (1963). The terminology given by Ruetzler (1974, p. 5) is followed throughout this report.

Most boring sponges form cavities which are located a short distance beneath the substrate surface. The cavity is connected to the substrate surface by narrow tunnels called papillary canals. The canals terminate in roughly circular openings, called papillary perforations, on the substrate surface. Some species do not form canals and the papillary perforations lead directly into the underlying cavities. Neighbouring sponge chambers are often connected by small pores, called foramina, which are located in the separating wall.

There are two types of sponge tissue: the choanosome which contains choanocyte chambers and the ectosome which does not contain choanocyte chambers. The choanosome partly or completely fills the chambers within the substrate. Small roughly circular patches of ectosome, called papillae, protrude from papillary perforations in the substrate surface. These bear ostia (inhalent openings) and/or an osculum (exhalent opening).

METHODS

1. Sampling

The fringing and bank reefs were chosen as the principal study sites. The location of line transects on these reefs is shown in Fig. 1. Systematic sampling of massive and branching corals, cor-algal substrate and coral rubble was carried out on the transects. Massive corals were sampled on transect 3 on the fringing reef and on transects 4 and 5 on the bank reef. Massive corals were collected randomly on the north lobe of the fringing reef and on the inner flank of the bank reef in the vicinity of transect 4. Porites porites and coral rubble were sampled on all three fringing reef transects and cor-algal substrate was sampled on transects 1 and 2. Acropora cervicornis and Madracis mirabilis were also collected from random sites.

Since collection and processing of samples was time-consuming it was not possible to sample any more than one fringing reef and a small section of the bank reef. The Bellairs reef is typical of the fringing reefs of the west coast of Barbados and the results obtained from this reef should be applicable to other fringing reefs in the vicinity. The part of the bank reef chosen for study is typical of the bank reef offshore from Bellairs. Since time permitted only two transect surveys across this reef, closely spaced transect locations were purposely chosen to allow a check on the accuracy of the sampling.

1.1 Massive Corals: The principal reef building corals on the fringing and bank reefs were studied in most detail. On the fringing reef these corals are Montastrea annularis, Porites astreoides, Siderastrea siderea and Agaricia agaricites. On the bank reef they are Montastrea annularis,

Montastrea cavernosa, Siderastrea siderea and Porites astreoides. Several other common bank reef species were sampled. These are Stephanocoenia michelinii, Diploria strigosa and labyrinthiformis, Colpophyllia natans and Agaricia agaricites.

Specimens were collected at regular intervals along transects 3, 4 and 5. Colonies were broken loose from the substrate using a hammer and chisel. The colony lying closest to the 10 m mark on the transect line was sampled. Colonies collected ranged in diameter from 5 to 30 cm. The upper limit, for colony size which could be handled, of 30 cm was set by the diameter of the saw blade which was used to cut slabs for X-radiography. Larger colonies could not be cut and also proved difficult to remove and handle underwater.

After cutting slabs for X-radiography from colonies the remaining portions of the colonies were split into small fragments. Tissue samples of all boring sponge species present in the slabs or in the coral fragments were extracted and spicule preparations made (method described in foreword to Appendix A). Species identification was based mainly on spicule complement, tissue colour and borehole morphology. The location, form and extent of the different boreholes made by the sponge species present were examined and recorded.

1.2 Branching Corals: Branching corals cover large areas of the seafloor in the study area. The three principal types are Porites porites, Acropora cervicornis and Madracis mirabilis. P. porites is most common on the fringing reef on the top of spurs in the spur and groove zone but also occurs in patches in deeper water off the reef front. A particularly extensive P. porites 'meadow' occurs in the southern part of the south lobe of the Bellairs reef. M. mirabilis occurs sporadically on the sides of spurs on

the fringing reef. It is more common in the area between the bank and fringing reefs where it forms narrow bands which border the more extensive A. cervicornis beds. These beds cover most of the sea floor between the bank and fringing reefs.

P. porites samples were collected at 10 m intervals on transects 1, 2 and 3. At each sample site all of the P. porites colonies in a ¼ metre square area were collected to a depth of about 20 cm. Below this depth sea water does not circulate freely and branches contained no occupied sponge borings. Random samples of M. mirabilis and A. cervicornis colonies were collected. The dead basal parts of branches were split up into small fragments and all boring sponges present identified as described above.

1.3 Cor-algal Reef Rock: A large part of the fringing reef surface consists of dead coral rock, much of which is covered by the encrustations of coralline algae. A survey was made to determine the nature and extent of sponge boring in this type of substrate.

Protruding knobs of partly or totally encrusted reef rock (measuring up to 20 cm x 20 cm x 20 cm) were broken off with a hammer and chisel at 10 m intervals along transects 1 and 2 on the fringing reef. Each piece was brought back to the laboratory and carefully broken up into small fragments. All boring sponges present were recorded and the type and extent of their excavations noted.

1.4 Coral Rubble: The shallowest zone of the Barbados fringing reefs is the swash zone. No corals grow here and the bottom is covered by coral rubble and sand. The coral rubble was examined to determine firstly if sponges occurred at this depth in this type of substrate, and if so what species are present, and secondly to establish an upper limit for the depth

range of boring sponges on Barbados reefs.

Loose blocks of coral rubble were collected at regular intervals along transects 1, 2 and 3 in the swash zone of both the northern and southern lobes of the Bellairs reef. Since the swash zone of the southern lobe is wider more rubble fragments were taken from this area. Coral rubble extends from the low water mark to the beginning of the reef crest zone 20 to 30 m offshore.

The blocks collected were broken up into small fragments using a hammer and chisel and all boring sponges present identified. Records were made of the morphology and location of all sponge borings.

2. Radiography

A previous investigation (MacGeachy and Stearn, 1976), using X-radiography to quantify sponge boring in M. annularis, the principal frame-building coral on Barbados reefs, showed that colonies from the fringing reef, bank top and bank sides are bored to different extents. Colonies from the bank sides display higher levels of boring than those on the bank top which, in turn, are more extensively bored than those on the fringing reef. Preliminary field observations made during this study revealed that other important massive coral species also exhibit different levels of sponge boring. The extent of sponge boring in several of the more important massive coral species was investigated to assess the relative importance of sponge boring in different coral species and to determine the principal factors controlling the amount of sponge boring in different reef corals. Rates of boring in each of the principal massive reef corals were also derived from radiographs.

To save time, in slabbing specimens for X-ray work, and money, in

freight charges for shipping slabbed corals back to the X-ray laboratory, a method was devised for quantifying sponge boring in coral specimens from small representative samples of each colony. The method is based on the one used by Stearn et al. (1977) to measure calcium carbonate productivity in coral specimens. Only those colonies which are roughly symmetrical about the growth axis can be treated using this method and an effort was made during sampling to collect colonies which were as symmetrical as possible. Most of the colonies collected from the fringing reef and bank reef top were roughly symmetrical. Asymmetrical colonies, such as the platy colonies from the sloping sides of the bank reef, had to be slabbed completely and shipped back to the laboratory.

Each coral specimen is cut along the growth axis in two planes approximately dividing it into four roughly symmetrical quarters. Slabs (9 to 10 mm thick) are cut parallel to these planes to produce two representative cross-sections. The location and extent of sponge infestation in each slab are recorded. After removing coral tissue by blasting with a high pressure jet of water the slabs are bleached overnight to remove sponge tissue and any additional organic matter. Radiographs of each slab are made using a Picker Minishot industrial instrument and Kodak 'Industrex' AA2 film. Different exposures are used for different coral species. For M. annularis an exposure time of 10 s and voltage of 45 kV was used, for M. cavernosa, P. astreoides and A. agaricites 10 s and 50 kV and for S. siderea 5 s and 65 kV. The skeletal structure of the coral and the pattern of attack on this structure by borers are clearly visible in the radiographs (Plates 2, 3 and 4). Annual growth bands, from which age estimates can be made, are prominent in radiographs of M. annularis, S. siderea and P. astreoides. In radiographs of

M. cavernosa and A. agaricites growth bands are not as clearly defined.

The percentage of the volume of each coral specimen which had been removed by boring was estimated from the radiographs. Each radiograph was overlain by an acetate sheet and placed on a light table. Sponge borings and sponge-bored areas were traced around with black ink. The assumption is made that the bored areas on the cross-sections are representative of the total boring in the sample. As the entire outer margin of colonies is usually uniformly bored by sponges the assumption is reasonable. The bored area and total area (fresh + bored areas) can be converted to volumes by rotating the cross-sections about the growth axis. (For a detailed explanation of methodology see Stearn et al. (1977). The operation has been programmed for a Wang desk computer -- modified version of Stearn et al. program.)

To obtain the actual volume of coral skeleton removed by boring sponges from the bored volume the percentage of skeleton removed per unit volume of slab in bored areas must first be estimated. The method used to obtain this figure is described in MacGeachy and Stearn (1976). It involves use of a photocell circuit to measure the average light transmission through bored and unbored areas. The proportion between the average readings on the unbored and bored parts gives the percentage of coral skeleton removed. The volume affected by boring is converted to actual bored volume of coral skeleton removed by multiplying by this percentage figure. The proportion between this amount and the volume of the specimen gives the total percentage of the coral specimen removed by boring.

For asymmetrical specimens such as the platy growth forms found in deeper water the whole corallum is cut into slabs parallel to the growth axis,

the bored and unbored areas are calculated for each slab from radiographs using a planimeter, these are converted to volumes by multiplying by slab thickness and bored volume (%) is estimated as outlined above.

A general rate of boring which is based on the average rate at which sponges penetrated a coral specimen during its life span can be obtained from the age and the volume removed from the coral.

3. Boring Rate Experiments

Boring rates were also directly measured using experiments based on weight loss from test blocks of unbored coral which were attached to blocks of coral infested by Cliona delitrix. Boring rates of C. delitrix were determined in several different coral species.

C. delitrix forms patches which partly or completely cover the living surface of coral colonies on the bank reef (Plates A3A, A3B: Appendix A). Borings penetrate up to 5 cm into the coral surface and greatly weaken the underlying skeleton. This sponge is amenable to boring rate studies since blocks can be cut from infested coralla underwater using a hacksaw.

Unbored substrate blocks (5 cm x 5 cm x 3 cm) were cut from the central parts of several different coral species of different skeletal structure and density. The corals used were M. annularis, M. cavernosa, S. siderea, D. labyrinthiformis and C. natans. The blocks were dried to a constant weight in an oven at 110°C. After weighing they were attached underwater, using plastic coated wire, to the blocks which had been cut from sponge-infested colonies. Each set of blocks was labelled and anchored on the reef (Plate 1D) in the bank top environment for periods ranging from 121 to 415 days. The initial contact area of the sponge (usually the entire upper surface of the

block) and the area affected by new sponge growth (parts of the base and sides) were outlined on tracing paper and measured using a planimeter. Calcareous encrusters were carefully removed by scraping and the block immersed overnight in full strength commercial sodium hypochloride to remove sponge tissue. (Control experiments done with preweighed blocks confirmed that the bleaching did not affect the weight of the block.) After blasting with a high pressure jet of water to remove spicules and any other debris the blocks were rinsed and again dried to a constant weight.

RESULTS

1. GENERAL DISTRIBUTION AND ABUNDANCE

1.1 Boring Sponge Fauna

Table 1 lists all of the boring sponge species encountered during the study. A general description of the systematics and distribution of each species and of the procedures used in identification is given in Appendix A. Table 2 lists general characteristics such as appearance of ectosome and choanosome and nature of excavations and includes notes on the relative abundance and distribution of each species. It is intended as an aid to field identification of the Barbados species.

During the course of the study additional work was done in Carriacou in the Grenadines, Lesser Antilles and in Curaçao in the Netherlands Antilles. The boring sponges recorded in these two areas are indicated in Table 1. Only limited sampling was carried out and the species lists are probably incomplete. A more detailed study of the type conducted in Barbados would doubtless have revealed more species.

All of the species listed except Siphonodictyon coralliphagum forma obruta are new records for Barbados, Carriacou and Curaçao. Cliona mucronata, Cliona ensifera, Cliona ?rovignensis, Cliona amplicavata, Cliona flavifodina, Cliona paucispina and Acarnus sp. are new records for the West Indies and Cliona spp. 1 and 2, Thoosa spp. 1, 2 and 3, species X and Siphonodictyon sp. are possible new species.

1.2 Comparison With Other Areas in the Western Atlantic

Recent work by Pang (1971) is the first comprehensive study done on the systematics of boring sponges in the Caribbean, although other work is in

Table 1: Sponge species present on Barbados reefs

Order HADROMERIDA

Family CLIONIDAE:

⊕ Cliona vermifera Hancock, 1867
O Cliona ensifera Sollas, 1878
O Cliona mucronata Sollas, 1878
O Cliona schmidti (Ridley), 1881
⊕ Cliona caribbaea Carter, 1882
O Cliona ?rovignensis Volz, 1939
⊕ Cliona lampa Laubenfels, 1950, forma occulta (Ruetzler, 1974)
O Cliona lampa Laubenfels, 1950, form 4
+ Cliona delitrix Pang, 1971, form 1
⊕ Cliona delitrix Pang, 1971, form 2
⊕ Cliona amplicavata Ruetzler, 1974
O Cliona flavifodina Ruetzler, 1974
Cliona paucispina Ruetzler, 1974
⊕ Cliona sp. 1 (unidentified species)
Cliona sp. 2 (unidentified species)
O Thoosa sp. 1 (unidentified species)
Thoosa sp. 2 (unidentified species)

Family SPIRASTRELLIDAE:

⊕ Spheciospongia sp.

Order HAPLOSCLERIDA

Family ADOCIIDAE:

Siphonodictyon cachacrouense Ruetzler, 1971
⊕ Siphonodictyon coralliphagum Ruetzler, 1971, forma obruta (Ruetzler, 1971)
⊕ Siphonodictyon coralliphagum Ruetzler, 1971, form 5
O Siphonodictyon sp. form 1
Siphonodictyon sp. form 2

Order POECILOSCLERIDA

Family ACARNIDAE:

Acarnus sp.

(Order and Family uncertain)

O Alectona jamaicensis Pang, 1971
O species X

O present in Curaçao
\+ present in Carriacou
C. lampa Laubenfels, 1950 forma lampa Ruetzler, 1974 is present in both Curaçao and Carriacou.
S. coralliphagum forma typica and another Thoosa species (Thoosa sp. 3) occur in Curaçao.

TABLE 2: General Characteristics of Barbados Boring Sponges

Sponge species	Ectosome (epilithic)	Choanosome and borehole characteristics	Relative abundance and distribution	General notes
C. vermifera	conspicuous papillae bright reddish-orange circular-oval (irregular) 0.5-1.5 mm (1.0 mm) up to 2.0 x 1.5 mm shaded surfaces mainly	reddish-orange/orange partly filled chamber network spheroid-ovoid (irreg.) 1.0-4.0 mm (2.0 mm) 1.5 x 1.0-5.0 x 3.0 mm (3.0 x 2.0 mm)	fairly common common occurrence in coral rubble in swash zone	distinctive tissue colour and consistency
C. ensifera	inconspicuous papillae yellow circular 0.5-1.5 mm (1.0 mm)	brownish-yellow completely filled single chambers ovoid 6x4-16x7 mm (10x6 mm)	fairly common most abundant on fringing reef	distinctive spiculation
C. mucronata	inconspicuous papillae reddish-orange circular 0.5-1.0 mm (0.8 mm)	orange completely filled chamber network spheroid-ovoid 1.0-2.5 mm (1.5 mm)	very common occurs throughout entire depth range	very distinctive small sword-shaped tylo-styles
C. schmidti	very conspicuous purple papillae circular 0.5-1.8 mm (1.0 mm)	purple partly filled network, confluent spheroid-ovoid (irreg.) 2.0x1.5-5.0x3.0 mm	rare occurs in depths of 3-32 m	easily recog-nized by the purple coloura-tion of the tissue
C. caribbaea	conspicuous papillae greyish-brown circular-oval (irregular) 0.5-3.0 mm (1.5 mm) often confluent exposed surfaces	yellow partly filled irregular chambers 3.0x1.5-7.0x3.0 mm confluent	very common ubiquitous in depths of up to 20 m particularly abundant on fringing reef	easily recog-nized by its large greyish-brown papillae

Table 2: Continued

Sponge species	Ectosome (epilithic)	Choanosome and borehole characteristics	Relative abundance and distribution	General notes
C. ?rovignensis	inconspicuous papillae light yellow circular 0.5-1.5 mm (1.0 mm)	greyish/olive yellow soft, mucous completely filled single chambers spheroid-ovoid (irreg.) 5x3-8x7 mm (7x4 mm)	common abundant in depths below 20 m	distinctive tissue colour and consistency
C. lampa	inconspicuous papillae reddish-orange circular 0.2-0.8 mm (0.5 mm) shaded surfaces	reddish/brownish orange completely filled 1. network, spheroid 0.5-1.5 mm (1.0 mm) 2. single chambers spheroid, 1.5-3.0 mm ovoid, up to 4x2.5 mm	common abundant in depths of less than 1 m and greater than 25 m	easily overlooked since papillae are very small
C. delitrix form 1	very conspicuous encrustation reddish-orange prominent oscules small white zoanthids	brownish-orange completely filled chamber network, lacy cylindrical chambers 2.5-5.0 mm diam. 3-23 mm in length	common occurs in depths of 13-40 m on bank reef	distinctive: partly or completely covers live surface of coral colonies with layer of reddish-orange tissue over which small white zoanthids are dotted
C. delitrix form 2	very conspicuous reddish-orange papillae circular-oval 1.5-5.0 mm (2.0 mm) 3x2-5x4 mm (4x3 mm)	brownish-orange completely filled single chambers ovoid 6x4-25x22 mm (13x8 mm)	common more abundant on fringing reef	easily recognized by its large red papillae

Table 2: Continued

Sponge species	Ectosome (epilithic)	Choanosome and borehole characteristics	Relative abundance and distribution	General notes
C. amplicavata	conspicuous yellow papillae circular 1.0-2.0 mm (1.5 mm)	yellow, soft, mucous completely filled single chambers ovoid 7x4-16x5 mm (10x4 mm)	rare only occurs on fringing reef	resembles C. ensifera but can be distinguished by yellow tissue colour and larger more prominent papillae
C. flavifodina	conspicuous papillae yellow circular 1.0-4.0 mm (2.5 mm)	dark yellow, tough completely filled irregular cavity 6x4-26x16 mm (14x8 mm)	rare common occurrence in cor-algal substrate on fringing reef	resembles C. amplicavata - can be distinguished by larger papillae, irregular shaped boreholes and tough tissue
C. paucispina	conspicuous encrustation brown	light brown fills existing spaces no chamber formation enlarges existing spaces	rare only occurs in shallow subtidal areas	easily recognized by its encrusting habit
Cliona sp. 1	inconspicuous papillae orange-red circular 0.5-1.5 mm (1.0 mm)	reddish-orange/orange completely filled chamber network spheroid-ovoid 1.5-2.5 mm (2.0 mm)	common occurs in depths of 2-26 m	can be confused with C. mucronata: the two species can be distinguished by examining spicules
Cliona sp. 2	inconspicuous papillae pale yellow circular 0.2-1.0 mm (0.5 mm)	light brown completely filled chamber network spheroid-ovoid 1.0-3.0 mm (2.0 mm) 1.5x1.0-4.5x2.5 mm (2.5x1.5 mm)	fairly common most abundant in cor-algal substrate on fringing reef	papillae are easily overlooked the extensive chamber network is very distinctive

Table 2: Continued

Sponge species	Ectosome (epilithic)	Choanosome and borehole characteristics	Relative abundance and distribution	General notes
Thoosa spp. 1 and 2	inconspicuous papillae brownish-yellow circular 0.2-0.8 mm (0.4 mm)	brownish-yellow, tough completely filled spheroid-ovoid 1.5-3.5 mm (2.0 mm) 1.5x1.0-4.0x2.5 mm	both species are rare both species are common in cor-algal substrate on fringing reef	distinctive spiculation
Spheciospongia sp.	conspicuous papillae and perforated ectosomal membranes greyish-brown/black pap: 2-3 mm diam. memb: 7-9 mm diam. 6x4-28x11 mm	yellow-olive brown, tough, lines walls tunnels up to 12 cm long 5-12 mm (10 mm) diam. 9x7-16x10 mm (13x9 mm)	common occurs in depths of 2-40 m	easily recognized by its distinctive ectosomal structures and borings
Siphonodictyon cachacrouense	conspicuous greyish-brown, bristly conical mounds 20-35 mm (30 mm) diam. 10-20 mm (15 mm) height on live surface or enc. base	brownish-orange soft, mucous completely filled single chambers spheroid up to 30 mm diam.	rare occurs only on bank reef	easily recognized by its distinctive ectosomal structures
Siphonodictyon coralliphagum forma obruta	conspicuous ectosomal structures, white or yellow oscular: open tubes 1.0-4.0 mm (1.8 mm) diam. 2.0-6.0 mm (4.6 mm) long ostial: closed tubes 1.0-3.0 mm (1.7 mm) diam. 1.2-6.0 mm (3.3 mm) long on encrusted surfaces	greyish-orange soft, mucous completely filled single chambers spheroid-ovoid 4-10 mm diam. 5x3-18x14 mm (10x7 mm)	very common occurs in depths of less than 1 m to 26 m	easily recognized by its white or yellow ectosomal structures which protrude from encrusted basal parts of coral colonies

Table 2: Continued

Sponge species	Ectosome (epilithic)	Choanosome and borehole characteristics	Relative abundance and distribution	General notes
Siphonodictyon coralliphagum form 5 and Siphonodictyon sp. form 2	inconspicuous ectosomal structures, white oscular: open tubes 0.5-1.5 mm (0.8 mm) diam. 1.0-2.5 mm (1.2 mm) long ostial: mounds 0.5-1.5 mm (0.9 mm) diam. 1.0-3.5 mm (1.8 mm) high on encrusted surfaces	greyish-orange soft, mucous completely filled chamber network spheroid-ovoid 1.0-2.5 mm (2.0 mm) diam.	both forms are common both occur in depths of 2-26 m	ectosomal structures are easily overlooked, easily recognized by distinctive boring pattern
Siphonodictyon sp. form 1	conspicuous ectosomal structures, white form and dimensions similar to S. coralliphagum forma obruta	sim. to obruta	common abundant on bank reef, rarely occurs on fringing reef	distinctive spiculation
Acarnus sp.	conspicuous encrustation red	red no chamber formation	?	distinctive spiculation
Alectona jamaicensis	inconspicuous papillae light yellow circular less than 1 mm diam.	brownish-orange, tough completely filled single chambers spheroid or ovoid 3-5 mm diam. 4x3-7x5 mm	rare occurs in depths of 3-30 m	distinctive spiculation
Species X	inconspicuous papillae pale yellow circular 0.2-0.8 mm (0.5 mm)	pale yellow completely filled chamber network spheroid 0.5-2.0 mm (1.0 mm)	fairly common abundant on bank reef, rarely occurs on fringing reef	easily overlooked: papillae are small, chambers are small and tissue colour blends with coral substrate

progress in Belize (Ruetzler, personal communication). Early records of new boring sponge species were based on specimens collected from shallow water by schnorkel diving, from deeper water by dredging or from dry specimens extracted from shell collections. Previous reports of boring sponge species in the Caribbean are reviewed by Pang (1971).

SCUBA made it possible to conduct detailed sampling over a large depth range (0-50 m) and to obtain detailed information on the systematics and distribution of boring sponge populations on reefs. Pang (1971) described 7 new species of boring sponge from the reefs off Discovery Bay, Jamaica and increased the number of species recorded from Jamaica from 2 to 13. Ten of those are Cliona species (C. schmidti, C. vermifera, C. janitrix, C. lampa, C. caribbaea, C. delitrix, C. peponaca, C. langae, C. laticavicola, C. aprica), while one is a spirastrellid (Anthosigmella varians). The remaining two are Siphonodictyon brevitubulatum and Alectona jamaicensis.

The boring sponge fauna of Barbados reefs differs considerably, in composition and diversity, from the Jamaican fauna. The most marked differences are in the clionid and Siphonodictyon components. Both genera are more diverse in Barbados. Only five clionid species are common to the two areas. These are C. schmidti, C. vermifera, C. lampa, C. caribbaea and a new species C. delitrix which Pang described. C. aprica, the most abundant clionid in Jamaica (Spurr, 1975) was not recorded in Barbados. None of the 3 Siphonodictyon species which occur in Barbados was recorded by Pang (1971) or by Ruetzler (1971) in Jamaica. S. coralliphagum forma typica was described from Jamaica by Ruetzler (1971) and was observed in Jamaica by the writer.

The boring sponge fauna of Barbados resembles that of Bermuda (Ruetzler, 1974) more than that of Jamaica. Six of the 7 clionid species described from

Bermuda occur in Barbados. Three of these, C. flavifodina, C. paucispina and C. amplicavata were new species described by Reutzler. (C. flavifodina and C. amplicavata were also recorded in Curaçao.) A Spheciospongia sp. also occurs in Bermuda.

Acarnus and Cliona schmidti have been described from the Brazilian coast by Boury-Esnault (1973).

1.3 Relative Abundance of Boring Sponges in Different Substrates

Although many species are found in more than one substrate type, differences in their relative abundance in the different substrates occur. The results of each of the sampling programs which were conducted are described below.

1.31 Massive Corals: All of the boring sponge species except C. paucispina were present in massive reef corals. Tables B1 to B19 (Appendix B) show the sponge species present in specimens of each coral species sampled on the fringing and bank reefs. Sample locations and depths are indicated. Table 3 is a composite table derived from the above tables and lists the frequency of occurrence of each sponge species in bank and fringing reef massive* coral samples.

Boring sponges are ubiquitous in the study areas and almost all of the corals sampled (with the exception of four S. siderea, two P. astreoides and two A. agaricites colonies on the fringing reef) were bored to some extent by species from one or more of the boring sponge families shown in Table 1. Clionids are the most abundant and diverse group with 14 species and 61.2% of

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*Several specimens of A. lamarcki were collected. Colonies of this species are not massive but platy.

TABLE 3: Frequency of Occurrence of Each Sponge Species in Bank and Fringing Reef Coral Samples

Transect	Coral Sample	N	Sponge Species																		
			Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
3(FR)	M. annularis	15	5	5	4	4	0	2	1	0	1	1	6	3	1	1	0	0	0	3	0
	S. siderea	12	2	0	1	1	0	2	0	0	1	0	1	3	0	0	0	0	0	2	0
	P. astreoides	14	2	2	5	4	0	2	0	0	0	1	3	5	1	0	0	0	0	4	0
	A. agaricites	14	4	0	4	0	2	1	0	0	0	1	0	3	0	1	0	0	1	0	1
*	S. siderea	6	0	0	3	0	1	1	3	2	0	0	1	0	1	0	0	0	0	2	0
	P. astreoides	7	2	1	6	0	0	0	2	0	0	0	1	1	0	0	0	0	2	0	1
	Total (FR)		15	8	23	9	3	8	6	2	2	3	12	15	3	2	0	0	3	11	2
4(BR)	M. annularis	19	4	8	3	0	3	1	1	0	1	2	7	2	4	2	7	0	1	4	0
	M. cavernosa	15	9	5	3	0	0	1	0	0	0	0	2	6	5	1	4	1	0	3	1
	S. siderea	13	0	5	5	2	2	2	1	0	0	0	6	7	3	1	2	0	0	3	0
	P. astreoides	24	3	2	14	3	0	2	0	0	1	0	6	10	9	3	0	0	0	4	0
	Diploria spp.	2	0	0	0	0	1	2	0	0	0	0	0	2	0	1	0	0	0	0	0
	A. agaricites	8	2	5	1	0	1	1	0	0	1	0	0	3	2	0	1	0	0	1	0

Table 3: Continued

Transect	Coral Sample	N	Sponge Species																		
			Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
5(BR)	M. annularis	17	7	8	4	2	1	0	1	0	0	1	3	3	5	6	4	0	0	2	0
	M. cavernosa	13	8	2	1	0	1	0	0	0	0	2	1	5	2	5	1	1	0	1	0
	S. siderea	13	4	4	6	1	0	0	4	0	0	0	5	7	2	1	0	0	0	3	0
	P. astreoides	12	1	1	5	0	0	1	1	0	0	1	5	2	3	1	0	0	1	3	0
	S. michelinii	10	4	3	2	0	0	2	0	0	0	0	0	3	1	1	0	0	1	1	0
	Diploria spp.	8	4	3	1	0	2	2	0	0	0	0	2	2	1	2	1	0	0	1	0
	C. natans	4	3	2	1	1	0	0	1	0	0	0	0	3	0	2	0	0	0	0	0
	A. agaricites	8	2	1	0	1	2	1	0	0	1	0	0	2	1	3	0	0	0	1	0
	A. lamarcki	3	3	1	1	1	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0
Total (BR)			54	50	47	11	13	15	10	0	4	6	38	58	38	29	20	3	3	27	1
Total (BR + FR)			69	58	70	20	16	23	16	2	6	9	50	73	41	31	20	3	6	38	3

N - number of specimens
FR - fringing reef

* randomly collected samples from north lobe of Bellairs reef
BR - bank reef

Cm - Cliona mucronata
Cc - Cliona caribbaea
Cd - Cliona delitrix form 2
Cv - Cliona vermifera
Cl - Cliona lampa
Ce - Cliona ensifera
Ca - Cliona amplicavata
Cs - Cliona schmidti
Cr - Cliona ?rovignensis
Cf - Cliona flavifodina
Cl - Cliona sp. 1
C2 - Cliona sp. 2
X - species X
T - Thoosa spp. 1 and 2
AJ - A. jamaicensis
Sp - Spheciospongia sp.
S1 - S. coralliphagum forma obruta
S2 - Siphonodictyon sp. form 1
S3 - S. coralliphagum form 5 and Siphonodictyon sp. form 2

the total occurrences. C. caribbaea and C. mucronata are most abundant (12.6 and 12.5% of total occurrences respectively), closely followed by Cliona sp.1 (10.5%). C. ?rovignensis (7.4%), C. lampa (4.1%), C. delitrix (3.6%), C. vermifera (2.9%) and C. ensifera (2.9%) are relatively abundant and Cliona sp. 2 (1.6%), C. schmidti (1.1%) and Thoosa sp. 1 and 2 (1.1%) least abundant. C. flavifodina (0.5%) and C. amplicavata (0.4%) are rare occurrences.

Different clionid species are commonly found in the same coral head and some sponge species or groups of species appear to be associated with a particular coral 'host'. This phenomenon will be discussed in a later section.

Siphonodictyon species are less diverse (3 species) but are also abundant. They account for 27.8% of the total occurrences. S. coralliphagum forma obruta is more abundant (13.2%) than Siphonodictyon sp. (5.6%). Both are found at times in the same coral head. S. coralliphagum form 5 and Siphonodictyon sp. form 2 both produce the same type of distinctive boring pattern and account for 9% of the total occurrences. S. cachacrouense is rare in the study area (3 occurrences) and was not recorded in any of the corals sampled.

The spirastrellid, Spheciospongia sp., is common (6.9% of total occurrences) and often coexists in the same coral head with Cliona and Siphonodictyon species. The unidentified species X accounts for 3.6% of the total occurrences. Alectona jamaicensis is rare and accounts for only 0.5% of the total occurrences.

1.32 Branching Corals: The diversity of sponge species in branching corals is less than in massive corals. Ten out of the 21 species which occur in massive corals were found in branching corals. These species are Cliona delitrix form 2, C. caribbaea, C. ensifera, C. amplicavata, C. mucronata,

C. lampa, C. ?rovignensis, S. coralliphagum forma obruta, Spheciospongia sp. and A. jamaicensis.

The greatest variety of different species was found in P. porites. The species present in P. porites samples on transects 1, 2 and 3 are shown in Table B20 (Appendix B). The number of occurrences of each species in colonies in each sample was recorded and the percentage abundance of each species estimated. C. caribbaea, C. delitrix form 2 and C. ensifera are the three most abundant species accounting for 35%, 23.5% and 20% of the total occurrences. C. amplicavata (7%), S. coralliphagum forma obruta (6%) and Spheciospongia sp. (5%) are relatively abundant and C. mucronata, C. lampa and A. jamaicensis (all 0.5%) are rare. C. ?rovignensis was not found in P. porites. Two sponge species were commonly found inhabiting the same P. porites stem. In a few stems three species were present. Clionid species coexisted most frequently and in some colonies a clionid species coexisted with Spheciospongia and/or Siphonodictyon.

Only four different species were found in A. cervicornis colonies. These are C. caribbaea, C. lampa, C. ?rovignensis and S. coralliphagum forma obruta. C. caribbaea is most abundant and was found in almost all A. cervicornis colonies examined.

C. lampa, C. ensifera, C. caribbaea and S. coralliphagum forma obruta were present in the M. mirabilis colonies sampled.

1.33 Cor-algal Reef Rock: Table B21 (Appendix B) shows the sponge species present in knobs of cor-algal reef rock which were sampled on transects 1 and 2. All of the species listed in Table 1, apart from C. schmidti, C. paucispina and A. jamaicensis, were recorded. C. caribbaea (14.6%), S. coralliphagum forma obruta (13%) and Thoosa spp. 1 and 2 (12.2%) are most abundant.

Spheciospongia sp. (8.9%), C. lampa (8.9%), Cliona sp. 2 (8.1%), C. delitrix form 2 (6.5%), C. ensifera (5.7%), C. mucronata (4.9%), Cliona sp. 1 (4.1%) and C. flavifodina (4.1%) are relatively abundant and C. vermifera (2.4%), C. amplicavata (2.4%), Siphonodictyon sp. (1.7%), species X (1.7%) and C. ?rovignensis (0.8%) are rare occurrences.

C. caribbaea and S. coralliphagum forma obruta, the most common sponges in cor-algal reef rock, are also the most common species in the coral samples from the fringing reef. Spheciospongia sp. and C. delitrix form 2 are equally important in coral and reef rock samples. Important differences between the sponge populations of coral and reef rock samples include the absence of C. schmidti, the near absence of C. ?rovignensis, the presence of species X and the greater abundance of Thoosa spp. 1 and 2, Cliona sp. 2, C. lampa and C. flavifodina in cor-algal substrate. C. mucronata and Cliona sp. 1 are both less abundant in cor-algal substrate and C. ensifera, C. vermifera, C. amplicavata and Siphonodictyon sp. are equally abundant.

1.34 Coral Rubble: Boring sponges were found in all but 3 of the 16 pieces of rubble examined. Species present are C. vermifera, S. coralliphagum forma obruta, C. lampa, C. amplicavata, C. ensifera and Thoosa sp. 1. Table B22 lists the species present in coral rubble sampled on transects 1, 2 and 3. C. vermifera was present in 8 of the rubble boulders and is the commonest boring sponge found in the swash zone. S. coralliphagum forma obruta occurred in 5 boulders, C. lampa and C. amplicavata each occurred in 3 and C. ensifera and Thoosa sp. 1 were each recorded only once. C. paucispina was recorded on the underside of a piece of coral rubble in the swash zone at Graves End on the south coast of the island. This species was not observed in the study area.

Boring sponges are less abundant and diverse in this zone than in deeper reef zones. Sponges become more abundant in deeper parts of the swash zone.

1.4 Distribution of Boring Sponges in the Study Area

1.41 Comparison of Bank and Fringing Reef: Although most of the boring sponge species encountered during the course of the study do occur in both the bank and fringing reef environments several discontinuities in distribution are evident. The most obvious of these is the complete absence of species X and Alectona jamaicensis from fringing reef corals and C. amplicavata from bank reef corals. The true significance of these disparities is difficult to assess. They may be real or may be a product of the limited sampling on the fringing reef.

Although species X was not recorded in fringing reef coral samples it does occur in the cor-algal reef rock in this environment. It is extremely rare and was recorded in only 2 of the 25 blocks of reef rock which were examined. It is much more abundant on the bank reef and occurs in corals from the bank top and sides.

Since A. jamaicensis rarely occurs even on the bank reef its absence from the fringing reef may be real or, as mentioned above, a result of more limited sampling in this area.

C. amplicavata is rare but seems to prefer the shallow-water fringing reef environment where it is commonly found in P. porites. It was not found during the survey of the deeper-water transects.

The frequency of occurrence of those species which coexist in samples of M. annularis, S. siderea, P. astreoides and A. agaricites on the bank reef and fringing reef can be directly compared by normalizing either the bank or

fringing reef samples to correct for the disparity in the number of coral specimens of each species sampled for boring sponges between the two areas. If 16 specimens of M. annularis were sampled on the bank reef and 8 on the fringing reef the numbers of occurrences of boring sponges on the fringing reef were multiplied by the factor 16/8 = 2 for comparison of the two localities. When the normalized populations are compared some species are evidently more abundant on the bank reef, others more abundant on the fringing reef and a few are of equal abundance in the two environments. Both Siphonodictyon sp. and C. ?rovignensis are abundant on the bank reef but virtually absent from the fringing reef. C. vermifera and Cliona sp. 1 are more abundant on the bank reef and C. delitrix form 2, C. lampa and Cliona sp. 2 more abundant on the fringing reef. When the sponge species counts in all specimens of the four coral species are added, and the distribution of each coexisting sponge in the bank top and fringing reef coral samples is compared using a χ^2 test, a significant difference is found. (Values of χ^2 obtained in this and the following tests are listed in Table 4.) The difference appears to result from the uneven distribution of Cliona sp. 1, species X, C. delitrix form 2, C. ?rovignensis, C. vermifera, C. lampa and Siphonodictyon sp.

The total number of sponge occurrences (irrespective of sponge species) in the bank top and fringing reef samples of each coral type can be obtained by summing the frequency of occurrences of each sponge species within each particular coral species sample. The number of species present in each coral type of the bank reef sample can be compared to the number present in the fringing reef sample. Bank and fringing reef samples of the corals M. annularis and P. astreoides contain comparable numbers of boring sponges whereas

TABLE 4: Results of Chi-Square Tests

Comparison of boring sponge distributions in coral samples (individual or grouped) from:	χ^2comp.	χ^2tab. α = 95	df
a) fringing reef and bank top			
Ma, Pa, Ss, Aa	85.5	30.1	19
Ma	12.8	19.7	11
Pa	12.4	19.7	11
Ss	51.1	19.7	11
Aa	33.8	19.7	11
b) the bank top sections of transects 4 and 5			
Ma, Mc, Pa, Ss, Aa	23.7	28.9	18
Ma	16.5	28.9	18
Mc	15.7	28.9	18
Ss	16.9	28.9	18
Pa	25.9	28.9	18
Aa	19.1	28.9	18
c) bank top and outside edge sections of transect 4			
Ma, Mc, Pa, Ss	41.0	28.9	18
d) bank top and outside edge sections of transect 5			
Ma, Mc, Pa, Ss	47.2	28.9	18

Ma - M. annularis
Mc - M. cavernosa
Pa - P. astreoides
Ss - S. siderea
Aa - A. agaricites

comp. = computed value
tab. = value from tables
α = level of confidence
df = degrees of freedom

S. siderea and A. agaricites samples from the bank reef contain considerably larger numbers of sponges than those of the fringing reef.

When the frequency of occurrence, in each coral species, of boring sponge species (those which coexist) in bank top and fringing reef coral samples is compared using χ^2 tests no significant difference is evident in the fauna of either the M. annularis or the P. astreoides sample but a significant difference exists in the fauna of S. siderea and A. agaricites samples. This difference reflects the uneven distribution of sponges in both S. siderea and A. agaricites in the two environments and may stem from differences in growth morphology of these two species on the bank top and fringing reef. These differences will be discussed later.

1.42 Comparison of Bank Reef Transects: When the sponge species counts from all five of the corals sampled from the bank reef are added and the distribution of sponge species in the bank top sections of transects 4 and 5 are compared using a χ^2 test, no significant difference is found at the 95% confidence level. A similar comparison, using a χ^2 test, of the distribution of sponge species in individual coral samples (M. annularis, M. cavernosa, S. siderea, P. astreoides and A. agaricites) on the bank top sections of transects 4 and 5 also revealed no significant difference showing that sponges are evenly distributed within the bank top study area.

When sponge species counts in M. annularis, M. cavernosa, S. siderea and P. astreoides samples from the bank top and outside edge sections of transects 4 and 5 are summed and their distribution in these two environments compared, using a χ^2 test, a significant difference was found showing that the boring sponge population on the outer edge of the bank reef is distinct from that on the bank top.

1.5 Controls on Larval Settlement

Very little is known about the controls on larval settlement of boring sponges. A study by Warburton (1966), on the larval behaviour of C. celata in a glass beaker containing sea water and calcite crystals, revealed that the larvae showed two distinct activity phases: a surface swimming phase which lasted for 20 to 30 hours and a bottom creeping phase of about the same duration. They showed no reaction to periods of light and darkness and the presence of calcite blocks induced no selective settlement on calcite. Larvae settled just as frequently on the glass bottom of the beaker. Warburton postulated that, in nature, identification of suitable substrates may take place by chemotactic response to surface microbial communities.

No experimental work on sponge larvae was carried out during this study but observations made on the distribution of papillae and borings suggest that certain species are influenced, during larval settlement, by ambient light. Some species show a preference for either the exposed upper surface or shaded undersurface of cor-algal reef knobs and rubble fragments. Others show no particular preference and occur in both exposed and shaded areas.

C. caribbaea papillae are always found on the upper surface or in exposed marginal regions of knobs and seldom occur on the undersides. The strong preference of this species for well-lit reef surfaces is clearly demonstrated in dead branches of A. cervicornis where papillae occur only on the upper surfaces and not at all on the lower surfaces (Plate 5A). The light dependence of this species is due to the presence in its tissues of unicellular photosynthetic algae (Ruetzler, 1974). The decrease in abundance of this species at depths below 20 m is presumably due to the decrease in light intensity with depth. Certain other species such as the encrusting

form (form 1) of C. delitrix and S. cachacrouense show a preference for exposed surfaces of live coral colonies.

Spheciospongia sp. apertures and C. lampa and C. vermifera papillae are more common on the shaded sides and undersides of knobs. C. delitrix papillae occur more commonly in shaded areas but are also present on exposed surfaces. C. vermifera, S. coralliphagum forma obruta, C. lampa and C. amplicavata occur mainly in the undersurface and sides of rubble fragments but are also occasionally present beneath the exposed upper surface. The greater incidence of sponge papillae on shaded sides and undersides suggests that the larvae of most sponges settle in shaded areas which are also generally more sheltered. These conditions may also be provided on the exposed surface in non-encrusted areas which are covered by filamentous algae. The fact that some sponge borings (particularly those of C. vermifera) are commonly located in the walls of vacated bivalve and sipunculid boreholes is further evidence that some larvae either seek protected areas for settlement or survive preferentially in such settlement areas. A study of boring in scallop shells from Newfoundland waters (Evans, 1969) showed that the sponge C. vastifica settled almost exclusively on the lower shaded, and presumably more protected, valve. Hartman (1958) found that larvae of C. celata settled on oyster shells in preference to clam shells and suggested that irregularities on the oyster shell may provide sheltered locations in which the larvae can find protection from water currents during the initial critical periods of metamorphosis and borehole establishment. The high incidence of sponge papillae on shaded, more sheltered reef surfaces may in fact be not so much a response to light intensity as to this effect. A study of the effect of various types of physical conditions on larval settlement would be required to determine

which of these two factors is responsible.

1.6 Factors Controlling Sponge Distribution

Possible factors which influence the distribution of boring sponges over reefs are substrate availability, food availability, light intensity, sedimentation and current regime (Reiswig, personal communication). The abundance of suitable substrates in reef environments precludes substrate availability as a limiting factor. The diet of demosponges consists mainly of particulate organic matter which is microscopically unresolvable (Reiswig, 1971). This food source is uniformly distributed throughout the water column over the reef surface (Reiswig, personal communication) and would not be expected to influence sponge distribution. Light intensity undoubtedly affects the distribution of species like C. caribbaea which possess symbiotic algae. The zooxanthellae-bearing species, C. aprica and C. langae, on Jamaican reefs, like C. caribbaea on Barbados reefs, show a preference for well-lit environments (Pang, 1971).

Reiswig (1971) noted that demosponges can not tolerate heavy sedimentation. Storm-generated turbidity and sedimentation result in a reduction, or occasionally a complete cessation, of water pumping due to clogging of incurrent passages by fine suspended sediment. The paucity of boring sponges in shallower parts of the swash zone in Barbados may be due to the greater wave-surge and sediment mobility in this region. Sediment scouring here may inhibit sponge settlement or make it difficult for sponges which do settle to survive. Rubble fragments containing sponge borings may be periodically overturned or buried and sponge papillae blocked by sediment particles. The presence of C. vermifera in the shallow subtidal parts of the swash zone

suggests that this species is adapted to life in areas of greater wave-surge and turbulence.

Water currents undoubtedly play an important role in larval dispersal. If Warburton's (1966) laboratory data on the activity pattern of sponge larvae are applicable to natural populations, and sponge larvae in nature do exhibit an initial free swimming phase, the extent of larval dispersal within a reef environment will depend on the current regime prevailing at the time of larval release. The Barbados bank reef is often affected by strong currents. These currents are tidal-generated (Peck, personal communication) and generally flow either offshore across the bank or in a north-south direction along the bank. Sponge larvae, which move by flagellar activity, are not efficient swimmers and are not capable of swimming against currents. If larval release occurs at a time when strong currents are flowing over the reef the larvae will be widely distributed possibly travelling up to several miles before settling. These conditions would result in the randomly distributed sponge population which occurs on the bank reef. If larval release occurs under calm conditions larvae would not travel far. They are likely to exhibit a random swim pattern which would result in settlement near the parent colony. Within small localized areas on the bank reef many neighbouring colonies were found to be infested by a particular sponge species. Several sponge species exhibited this 'clumped' distribution but it was most clearly demonstrated by C. delitrix form 1. Small groups of closely spaced colonies, infested by this sponge, occurred in certain areas of the bank reef. These were separated by areas in which there were few or no C. delitrix-infested colonies. This 'clumped' distribution which is superimposed on the general random distribution pattern probably results from settlement

near the parent colony.

A study of predation, by various invertebrates, on boring sponges in oyster beds in Beaufort, North Carolina (Guida, 1976) showed that several echinoid, gastropod and crustacean species are important spongiovores which could possibly affect sponge distribution. Since reports of sponge predation, by invertebrate groups in Barbados, are lacking it is not possible to predict the importance of predation in regulating the distribution of boring sponges. It seems unlikely however that predation is important since there are only a few possible predators on Barbados reefs.

1.7 Depth Zonation

There appears to be no clearly defined depth zonation of sponge species on Barbados reefs. Although most boring sponge species present in the study area are fairly evenly distributed over the bank and fringing reefs certain species are more predominant in particular depth zones. C. vermifera and C. lampa occur throughout the depth range but are more abundant at the extremes. C. lampa occurs most commonly at depths greater than 20 m on the inside edge of the bank and, like C. vermifera, is also abundant in depths of less than 1 m in the swash zone. S. cachacrouense occurs only on the bank reef and Siphonodictyon sp. and C. ?rovignensis are restricted mainly to the bank reef. S. cachacrouense and Siphonodictyon sp. occur mainly between 15 and 20 m on the bank top and C. ?rovignensis at depths of 20 m or more on the sides of the bank reef. C. caribbaea, the zooxanthellae-bearing species, occurs mainly in depths of less than 20 m and is most abundant in the shallow waters of the fringing reef. The few occurrences of Alectona jamaicensis on the bank reef were in water depths of around 15 m and species X was encountered in the 15-30 m depth range.

1.8 Substrate Specificity

Observations made during the fieldwork provided no evidence of actual substrate specificity in which a particular sponge species occurred exclusively in one particular coral 'host'. All of the sponge species present were encountered in several different coral types. Certain species did however exhibit a preference for a particular coral species.

The most striking association is that which exists between A. cervicornis and C. caribbaea. Almost all of the A. cervicornis colonies examined were infested by C. caribbaea. The same association was evident in A. cervicornis beds on the south coast of Curaçao. Other species which commonly occur in association with C. caribbaea in A. cervicornis branches are C. ?rovignensis and S. coralliphagum forma obruta.

P. porites is usually inhabited by either C. caribbaea or C. delitrix form 2. These two species never coexisted in P. porites and appear to be mutually exclusive; the presence of one may inhibit settlement of the other. Other species were frequently associated with C. caribbaea and C. delitrix form 2 in P. porites branches. The spirastrellid, Spheciospongia sp., often coexisted with C. caribbaea. C. delitrix form 2 occurred frequently with C. ensifera and in some colonies with C. amplicavata and S. coralliphagum forma obruta.

A recurring suite of sponge species is present in several massive coral species. M. annularis and M. cavernosa commonly contained a Siphonodictyon species, C. mucronata or Cliona sp. 1 and C. caribbaea or C. delitrix form 2. C. ensifera is common in S. siderea colonies and often coexists with C. caribbaea and a Siphonodictyon species. C. caribbaea, Spheciospongia sp. and a Siphonodictyon species occur most frequently in P. astreoides.

C. mucronata and Cliona sp. 1 are rare in P. astreoides but are common in association with a Siphonodictyon species, and occasionally C. caribbaea, in A. agaricites. C. mucronata occurs most frequently in platy colonies of A. lamarcki from the outer edge of the bank reef.

2. RELATIONSHIP OF BORING SPONGES TO THEIR SUBSTRATE

2.1 Location of Borings

Sponge borings in all of the substrates examined are generally located just beneath the substrate surface. The only borings which are inhabited by live sponge are those which are in direct communication with the circulating waters of the reef. Those which are sealed off from the external environment by overgrowth of encrusting organisms, growth of adjacent coral colonies or by sedimentation are vacant and may be partly or completely infilled by sediment.

In live massive coral colonies borings normally occupy a narrow subsurface layer in the base of colonies but occasionally penetrate further into coralla. Certain species form branching tunnels (Spheciospongia sp.) or cavity networks (Cliona sp. 2) which ramify through the entire corallum. In branching corals borings generally occupy the central axis of the dead basal parts of branches. Much of the base of coral colonies is usually covered by calcareous encrusting organisms (coralline algae, Gypsina, Millepora, bryozoans, encrusting corals such as Agaricia agaricites and Madracis decactis) and encrusting sponges. Some areas are colonized by filamentous algae. Sponge borings occur beneath both encrusted and non-encrusted surfaces and often occupy the skeletons of thick encrusters.

Although boring sponges most commonly inhabit the non-living lower regions of coral colonies some species are also found on the living coral surface. Two Siphonodictyon species, S. cachacrouense and S. coralliphagum forma typica, and two clionid species, C. delitrix and C. caribbaea, occur locally on the live surface of massive coral colonies.

Ruetzler (1971) has suggested that Siphonodictyon species may be capable of establishing on the live surface of coral colonies. S. cachacrouense and S. coralliphagum forma typica can be easily recognized since each has conspicuous ectosomal structures which protrude from the surface of infested colonies. These processes are surrounded by living coral tissue and lead through canals into cavities in the underlying coral skeleton. The ectosomal processes of S. cachacrouense appear as conical mounds of brown bristly tissue a few centimetres in diameter and up to 2 cm in height. Those of S. coralliphagum forma typica appear as deep yellow cylindrical (often chimney-like) protrusions which are up to 3.5 cm in diameter and up to 4 cm in length (Ruetzler, 1971).

It is difficult to establish whether S. cachacrouense and S. coralliphagum forma typica actually settle amongst the live coral polyps, settle on dead patches (such as those made by grazers) on the live surface or settle on the dead base and invade the living parts of the colony in later stages of growth. Ruetzler (1971) believes that settlement takes place amongst the living polyps. He suggests that Siphonodictyon larvae are capable of settling on the living surface since they are protected by large amounts of mucus. Mucus secretion from the larvae (and later mucus expulsion through the oscules) apparently kills surrounding coral polyps and allows the sponge to establish on the living surface of the colony. These suggestions are

supported by an observation made during this study. Many of the ectosomal structures which were closely examined were surrounded by a narrow (5-10 mm) band of dead coral which was usually covered by filamentous algae. The living polyps in this zone had apparently been killed, possibly by mucus expulsion through the oscules.

C. delitrix has two different morphological forms: a non-encrusting form (form 2) characterized by groups of large red papillae which show no tendency to fuse and an encrusting form (form 1) which results from fusion of papillae. The encrusting form affects the live surface of many coral species on the bank reef. Papillar fusion forms a continuous layer of reddish-orange ectosomal tissue which partly or completely covers the live surface of coralla, beneath which excavations extend into the underlying coral skeleton. The patches of ectosomal tissue are surrounded by a 1-2 cm wide band of dead coral. This band is often encrusted by filamentous algae and occasionally is colonized by calcareous algae. (Encrusting sponge had settled on one band.) C. delitrix apparently kills surrounding coral tissue, spreads onto and starts to bore into the dead area. Individual papillae of this sponge on or near the tissue-covered corallum surface cause recession of the coral tissue in their immediate vicinity. The presence of individual papillae of C. caribbaea near the live surface of coral colonies also causes recession of live tissue. In Curaçao large S. siderea colonies were commonly totally encrusted by C. caribbaea. Papillar fusion was not complete (individual papillae could still be discerned) and a continuous layer of ectosome was not formed. This encrusting habit was not observed on Barbados reefs.

Unlike the Siphonodictyon species the two clionids do not appear to be capable of actually settling on the live surface of corals. In substrates

bored by these species papillae and encrustations appeared to have been established from beneath the live surface or on a dead patch on the live surface. Only the Siphonodictyon species appear to be capable of settling on live coral surfaces.

The presence of bands of dead coral around the edges of C. delitrix overgrowths and ectosomal structures of Siphonodictyon species on the live surface of coral colonies, and of bare zones, caused by tissue recession, around C. delitrix and C. caribbaea papillae, suggests that these sponges release toxic substances which can kill coral tissue. Jackson and Buss (1975) contend that the presence of zones of dead coral skeleton around the sponge edge provides strong circumstantial evidence that sponge allelochemical interactions are involved. They suggest that mucus secretion may provide a mechanism for concentrating allelochemicals in the immediate vicinity of the sponge without excessive dilution by currents.

Cor-algal reef rock is heterogeneous. It is composed mainly of dead skeletons of frame-building corals such as P. astreoides, A. palmata, M. annularis, S. siderea and P. porites and the hydrozoan Millepora (complanata and squarrosa mainly) which are locally bound together by various calcareous encrusters and sponges. Calcareous algae are the most important encrusters and form crusts, 1 to 10 mm thick, over the surface of the coral remnants. Other encrusters include Gypsina, Homotrema, Millepora, bryozoans, encrusting corals such as Agaricia agaricites and Favia fragrum and sponges. These occur mainly on the shaded protected surfaces and as linings on the walls of internal cavities. Non-encrusted surfaces are covered by mats of filamentous algae and are commonly grazed by the echinoid Diadema antillarum. The concave or indented nature of many of these surfaces is due to the erosive

activity of this echinoid. Some cor-algal knobs, especially those composed largely of P. porites, are bound together by sponges. The structure of the original coral framework in most cor-algal knobs is commonly almost completely obliterated by boring, internal sedimentation and cementation.

The excavations of most of the sponges present in cor-algal substrate are located in the peripheral 1 or 2 cm of the substrate surface and only penetrate into the interior where access is gained through a vacated borehole. The spirastrellid, Spheciospongia sp., forms long branching tunnels and is the only sponge which penetrates far (up to 12 cm) into cor-algal substrate. Where a thick calcareous algal crust is present species like Thoosa spp. 1 and 2, C. lampa, Cliona spp. 1 and 2 and C. mucronata, all of which form a network of small chambers, are usually restricted to the surface and seldom penetrate the underlying coral skeleton. C. caribbaea borings are commonly found in the underlying coral skeleton. Papillary canals which penetrate the algal crust and connect the sponge chambers to the surface papillae are probably established from below. Parts of the chambers of other species are in the algal crust and parts are in the underlying coral skeleton.

Coral rubble is composed principally of heads and fragments of A. palmata, M. annularis, S. siderea and other of the major frame-building corals on the fringing reef. Large flat fragments of former fronds of A. palmata are most abundant. The upper surface and lower surface (if not buried in sand) of rubble fragments are heavily encrusted. Filamentous and fleshy algae and coralline algae grow on the exposed upper surfaces. The dense growth of filamentous algae produces a thick turf which traps and binds sand grains. Encrustation on the shaded lower surfaces is similar to that found on the base of coral colonies or undersurfaces of cor-algal blocks.

Sponge borings are again located mainly in peripheral parts of coral rubble fragments. The extent of infestation increases with increasing depth in the swash zone. Rubble from just below the low water line rarely contains live sponge and borings which do occur are not well developed. In shallow parts of the swash zone other boring organisms are more important in erosion than sponges. Sipunculid worms (Phascolosoma antillarum, Phascolosoma perlucens and Paraspidosiphon spp.) are especially abundant in flat fragments of A. palmata. P. antillarum forms large boreholes and removes considerable quantities of coral substrate. The other species form smaller boreholes and are not as important in substrate degradation. Small bivalves of the genera Lithophaga and Petricola are also present in rubble fragments.

The papillae of many of the sponge species present in the different substrate types are small and inconspicuous and are visible only on close examination of the substrate surface. Only the spirastrellid, Spheciospongia sp., which possesses large distinctive apertures, and clionids such as C. delitrix and C. caribbaea which have large prominent papillae, can easily be recognized. In coral rubble papillae are conspicuous only on the basal surface. On the upper surface they are usually hidden by algal turf and adherent sand particles.

2.2 Borehole Morphology

Sponge borings range in shape from well-defined discrete chambers or chamber networks to ill-defined irregular spaces and tunnel systems. Most borings can be placed in one of four different categories. These are:

1) single spheroid to ovoid chambers

2) networks of small interconnected well-defined or poorly defined

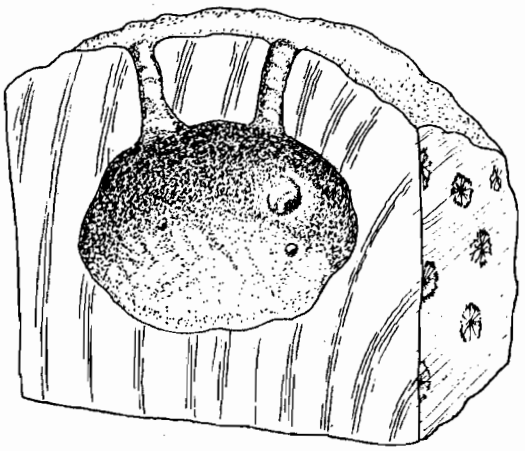
spheroid to ovoid chambers

3) irregularly shaped cavities

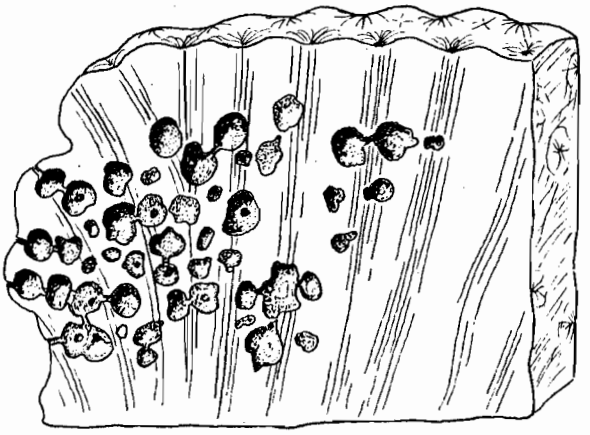
4) tunnels

The main borehole types are illustrated in Fig. 3. A description of the boreholes formed by each of the different sponge species appears in Appendix A. The term 'gallery' which was originally used to describe branching camerate sponge borings of the type found in shells is avoided since it does not adequately describe the range of form of sponge borings found in corals.

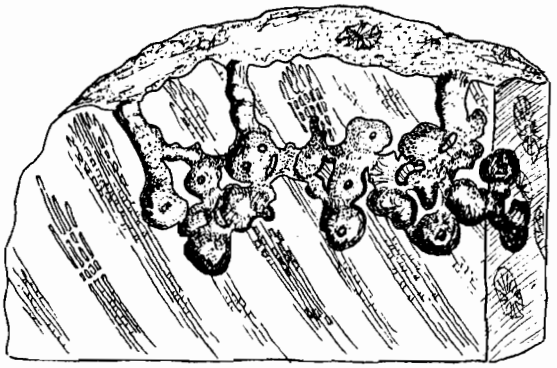
Clionids show the greatest range of borehole morphology. C. ensifera, C. ?rovignensis, C. delitrix form 2 and C. amplicavata borings fall into category 1. The chambers formed by these species are usually roughly ovoid and are connected to the substrate surface by several papillary canals (Plates A1B, A1G, A2C: Appendix A). Chambers may occur singly or in groups of 2 or 3 in which individual chambers are connected by small tunnels. Chambers range in diameter from 10 to 30 mm and may be partly or completely filled with sponge tissue. The commonest type of clionid borings are those of category 2. C. vermifera, C. mucronata, C. lampa, Cliona sp. 1, Cliona sp. 2, species X and Thoosa spp. 1 and 2 form networks of small (1-5 mm diam.), well-defined, roughly spheroid chambers which give the substrate a honeycombed appearance. This is the typical clionid boring pattern. In borings of C. schmidti, C. caribbaea and the encrusting form of C. delitrix (form 1), chamber definition is poorer since the interconnecting walls are partly removed. These borings are commonly ragged and have a delicate lace-like appearance (Plates A1D, A1F, A3D: Appendix A). The extent of infestation of category 2 species varies with species. Chamber formation begins a few millimetres beneath the substrate surface and usually extends up to 20 mm



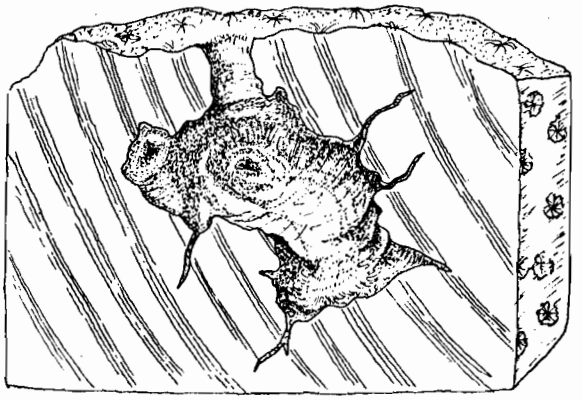
1. Single chamber



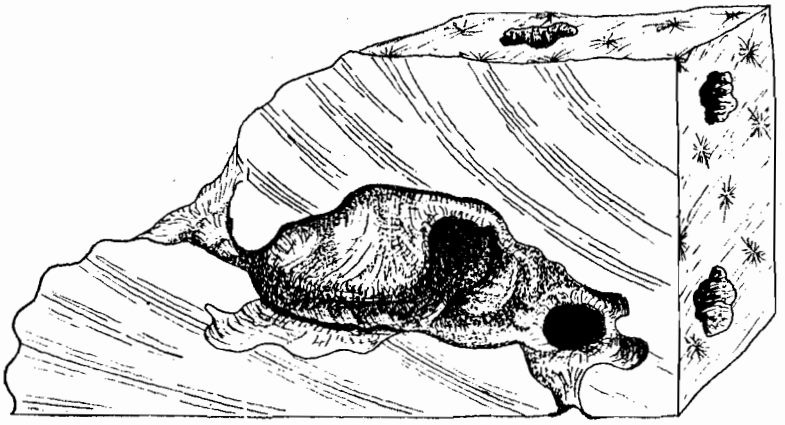
2. Network of interconnected well-defined chambers



3. Network of interconnected poorly defined chambers



4. Irregularly shaped cavity



5. Tunnel system

FIG. 3: SPONGE BOREHOLE MORPHOLOGIES

into the substrate. Cliona sp. 2, species X and C. delitrix form 1 produce more extensive networks (Plates 7D-H, A3D). The apparent control over the boring strategy of some category 2 species by the structure of the coral substrate will be discussed later. C. flavifodina forms irregularly shaped cavities (Plate A2D) which fall into category 3. In porous substrates such as Porites spp. the cavities formed by some clionids (especially C. caribbaea) may also be irregular and ragged in shape and are grouped with category 3 types. Acarnus sp. and C. paucispina do not fall into any of the above categories since they encrust the substrate and bore directly into its surface. These species do not form discrete chambers but seem to enlarge existing spaces within the substrate.

Siphonodictyon boreholes are mainly of category 1 type. All three species form roughly spheroid to ovoid chambers (10-50 mm in largest diameter) which are linked to the substrate surface by cylindrical papillary canals. Siphonodictyon sp. and S. coralliphagum (form 5) also develop chamber networks of category 2 type. This type of boring strategy has not been previously reported in any Siphonodictyon species. Individual chambers are small (up to 3 mm in diameter), roughly circular and are connected to adjacent chambers by small foramina. They are similar to clionid networks and extend from a few millimetres to 15 to 20 mm into the substrate.

Alectona jamaicensis forms single roughly spheroid or ovoid chambers of category 1 type. They reach 10-15 mm in largest diameter and are connected to the substrate surface by papillary canals.

The spirastrellid, Spheciospongia sp., forms branching tunnel systems (category 4) which ramify through the substrate.

2.3 Factors Controlling Sponge Boring Strategies

The boring mechanism of sponges has been extensively studied. Literature on the subject is reviewed by Goreau and Hartman (1963) and Pomponi (1977). Recent studies done on the ultrastructure of borings and sponge cells using light microscopy (Cobb, 1969) and transmission and scanning electron microscopy (Ruetzler and Rieger, 1973; Cobb, 1975; Pomponi, 1976, 1977) have brought about significant progress in our understanding of the boring mechanism. Boring sponges of the families Clionidae, Spirastrellidae and Adociidae bore using a similar mechanism (Ruetzler and Rieger, 1973) which involves both chemical and mechanical processes. Small (40-60 microns) characteristically shaped chips of calcium carbonate (Plates 8A, 8B) are removed from the bored surface leaving a distinctive pitted surface texture (Plate 9E). Specialized cells are responsible for etching the chips from the substrate. Etching activity, which is localized at the area of contact between the cell edge (Cobb, 1969) or cellular processes (Ruetzler, 1973) and the carbonate substrate, forms slit-like crevices and dislodges chips. Freed chips are removed from the bored substrate surface by simple displacement by new etching cells (which move in to replace exhausted etching cells) and are forced into the exhalent canal system and expelled through the oscules. Exhausted etching cells are either phagocytized or removed with the chips. The chemical nature of the etching agent is not known but the dissolution process is believed to occur in stages (Cobb, 1975) since concentric microterraces are observed on the walls of many pits (Plate 9E). Ruetzler and Rieger (1973) have estimated that only 2-3% of the eroded carbonate goes into solution.

Various techniques can be used to examine sponge boring strategies in

carbonate substrates. The finer structural features of borings are best resolved using scanning electron microscopy. Bored substrates can be examined directly, or can be examined indirectly using casts of borings made by vacuum impregnating bored substrate with epoxy resin then dissolving the carbonate. The high magnification, three-dimensional image of borings which is produced clearly reveals the microtopography of the pitted surface of the bored substrate and provides data on the size range of pits and chips and on the details of the etching process. Different sponge species (Clionidae, Spirastrellidae and Adociidae) produce different size ranges of pits and chips (Ruetzler and Rieger, 1973; Pomponi, 1977). The variation in size is more dependent on the point of origin of the chip and on the microtopography of the substrate than on the species and the nature of the substrate (mineralogy, structural homogeneity). Small chips are removed during new tunnel formation and larger chips are freed during enlargement of existing chambers and tunnels (Ruetzler and Rieger, 1973; Ward and Risk, 1977).

Few studies have been done on the factors controlling patterns of sponge penetration in carbonate substrates. Pomponi (1976) notes that the orientation of aragonite crystals in the bored substrate may influence the boring pattern. Ward and Risk (1977) examined the boring strategy of Cliona vermifera in Montastrea annularis, using X-radiography and scanning electron microscopy, and showed that it was based on exploration for and exploitation of areas of low skeletal density. X-radiography provides a most effective means of examining penetration patterns. Radiography was first used to study borings in shells (Evans, 1969; Bromley, 1970) but has recently been applied successfully to studies of boring in massive corals which have been cut into thin slabs (Hein and Risk, 1975; MacGeachy and Stearn, 1976; Hudson, 1977).

X-ray negatives clearly reveal the growth structure of the coral and the pattern of attack on this structure by sponges. Data on the finer details of the boring process and on larger scale patterns of penetration can also be obtained from thin sections of bored substrates.

A variety of bored substrates was examined during this study, using the above techniques, to determine the relative influence of genetic and substrate controls on boring pattern.

2.31 Substrate type: Boring sponge species encountered during this study inhabit a wide variety of different coral species. Since there is considerable variation in growth structure between different coral species this might be expected to affect sponge boring strategies and produce similar variation in the morphology of the borings produced. To determine the effect of substrate type on borehole morphology the borings of several of the more common sponge species were examined.

Plates 5C-F, 6, 7A-F show several different coral substrates, each of which is bored by one of the following species: a network-forming Siphonodictyon species (S. coralliphagum form 5 or Siphonodictyon sp. form 2), C. caribbaea, C. mucronata, Cliona sp. 1 and species X. All of these species except C. caribbaea produce a network of interconnecting chambers that is similar in pattern and size range in all of the substrates examined. Chambers formed by C. mucronata and Cliona sp. 1 are more ovoid in shape and more widely spaced (separating walls between individual chambers are thicker) than those of the network-forming Siphonodictyon species. The boring patterns of C. mucronata and Cliona sp. 1 are similar but can be distinguished since Cliona sp. 1 produces a smaller size range of chambers. Cliona sp. 1 is the only network-forming species which was found in a Porites porites

colony (Plate 8D). The same borehole morphology is developed as is developed in massive corals: small interconnecting chambers which are connected to the substrate surface by narrow canals are formed. Chambers produced by species X are of smaller dimensions than those of the other network-forming species.

C. delitrix form 1 exhibits the same boring pattern in all of the coral surfaces examined. The sponge penetrates parallel to the direction of growth of the corallites and forms cylindrical chambers which are usually located in endothecal areas (Plate A3D). Chambers are not well-defined since the separating walls are partly removed and perforated by large foramina.

C. caribbaea boreholes are always poorly defined. They have the same characteristic irregular outline and ragged appearance in all substrates examined (Plates 5C-F).

Some species produce very distinctive borings. The typical large spheroid to ovoid chambers formed by Siphonodictyon species (Plates A4B-D: Appendix A) are very characteristic as are the tunnel systems of spirastrellids and the irregular cavities of C. flavifodina. Different borehole morphologies are produced by species such as C. delitrix and C. lampa which have more than one growth form. The boring pattern produced by each growth form is distinctive.

Comparison of the borings of a particular sponge species in different substrates shows that the basic form of the boring pattern developed in each substrate is the same. This supports genetic control of borehole morphology. The fact that the patterns produced by different species are morphologically diagnostic is important palaeontologically since identification of sponges can be based on boring pattern morphology in fossil substrates. Borings

present in corals in Pleistocene reef terraces in Barbados can be readily identified to the genus level and often to the species level by comparison with borehole morphologies of presently living species.

Although the borehole morphology developed in different substrates is consistent the skeletal structure of the coral does affect the fine details of development of the borings. The most marked effect is that produced by variations in skeletal density associated with the pattern of development of the corallites.

2.32 Influence of Coral Growth Structure on Boring Pattern: The form of the coralla of colonial coral species depends mainly on the mode of asexual development of the colony (Wells, 1967). The principal coral species examined during this study differ in the spacing of their corallites.

The corallum of S. siderea is cerioid. Individual corallites are roughly polygonal in cross-section and are contiguous. Corallite walls are united to form a common boundary between adjacent corallites. In P. astreoides the corallites are also closely united without coenosteum. The coralla of M. cavernosa, M. annularis and A. agaricites are plocoid. Individual corallites are cylindrical in shape and are united by coenosteum (costae and exothecal dissepiments). Three areas of different skeletal density can be distinguished in M. cavernosa and M. annularis. The corallite wall or theca is the most dense area. The endothecal area (comprising septa and endodissepiments) and the exothecal area (coenosteum) are both less dense areas. The exothecal area is denser than the endothecal area due presumably to the closer spacing and greater thickness of skeletal elements. (In A. agaricites the thecal and exothecal areas can not be easily differentiated.) Differences in skeletal density apparently affect sponge boring. Borings of

some species are confined to the less dense endothecal area, other species occupy the denser zone formed by the thecal and exothecal areas. Preferential boring in the denser zone is more common in M. cavernosa where the exothecal-thecal zone is sufficiently wide (2-8 mm) to accommodate sponge chambers. It is less commonly seen in M. annularis where the dense zone is narrower (1-3 mm).

The effect of variations in skeletal density in the growth structure of M. annularis on the boring strategy of Cliona vermifera was noted by Ward and Risk (1977). Chamber formation by C. vermifera took place in the less dense endothecal areas. Pioneering filaments of sponge tissue penetrated the denser thecal and exothecal area and initiated new chamber development in an adjacent endothecal area. This produces a characteristic string-of-beads pattern of the type described by Bromley (1970). This pattern of development which appears to be based on exploration for and exploitation of zones of least density (Ward and Risk, 1977) was observed during this study in M. annularis specimens bored by C. vermifera.

Other sponge species encountered during this study used a similar boring strategy in M. annularis. A preference for the endothecal areas was shown by C. delitrix form 1 and the network-forming Siphonodictyon species (S. coralliphagum form 5 and Siphonodictyon sp. form 2). These species form strings of chambers in the endothecal areas by removal of endodissepiments and septa. Thin tabular dissepiments which are not removed during boring form transverse partitions between individual chambers. Chambers are basically cylindrical in shape since they occupy the whole or part of the endothecal region. Siphonodictyon locally forms long cylindrical tunnels in M. annularis by removal of all of the endothecal skeletal elements (Plate 8C). A similar boring

pattern was shown by an unidentified clionid species in a Dichocoenia colony from Curaçao reefs (Plate 5B).

Since excavating in the endothecal areas of Montastrea specimens, where the skeletal structure is less dense, undoubtedly requires less energy than excavating the more dense exothecal-thecal areas this type of boring strategy might be expected to be used by sponges exploiting all Montastrea species. The opposite strategy was however observed frequently in M. cavernosa and some M. annularis colonies bored by network-forming species. C. mucronata, Cliona sp. 2 and species X, which form similar honeycomb networks of small interconnecting chambers, were commonly observed to form chambers which were confined to the denser exothecal-thecal areas (Plates 6B; 7G, H; 7D-F). Sponge chambers in A. agaricites colonies were located more commonly in the denser areas (Plate 6D). Plate 9F is a photomicrograph of boring, by an unidentified species, which is confined to the exothecal area.

In P. astreoides and S. siderea there is no marked control on chamber location. Since neither of these species develop coenosteum their structure is more homogeneous than that of Montastrea species. Individual sponge chambers are either centred in endothecal areas or span the region between corallites (P. astreoides lacks thecal walls) and occupy parts of adjacent endothecal areas.

2.33 Influence of Growth Banding on Boring Direction: Growth banding appears on positive prints of X-ray negatives of coral slices as well-defined eccentric light and dark bands (Plate 2). The banding is due to cyclic variations in skeletal density and has been shown to be annual in nature (Buddemeier et al., 1974). Dark areas correspond to areas of high skeletal density and light areas to areas of low skeletal density. These variations

in skeletal density appear to have a directional influence on sponge penetration.

Plate 4A shows a P. astreoides colony in which chamber development of the sponge Siphonodictyon sp. form 2 closely follows the trend of the growth bands. Narrow conduits formed by advancing strands of sponge tissue extend along the growth bands ahead of the advancing chambers. These tunnels represent the earliest stages of boring and chamber development takes place at regular intervals along their length. Plate 4B shows an X-radiograph of a S. siderea colony containing numerous small borings which roughly parallel the direction of the growth bands. Scanning electron microscopic examination of the walls of these borings shows they have the characteristic scalloped texture produced by boring sponges.

Since the growth banding is indistinct in each of the radiographs the position of the borings in the high or low density bands cannot be located with confidence. The close alignment of borings and growth bands in both corals does however strongly suggest that the growth bands exert directional control over sponge boring.

Another factor which may influence the location of sponge borings is the spatial relationship which exists in coral colonies between the location of sponge boreholes and the surface of the coral. Borings containing live sponge tissue occupy a subsurface zone which is a constant depth beneath the coral surface. In the two corals described above the only borings which were occupied by live tissue were those directly beneath the coral surface. Bored zones deeper in the corallum were vacant and undoubtedly were formed by previous generations of sponges during earlier stages of growth of the coral colony. No means of testing the relative importance of these two possible

effects could be devised.

2.34 Control over Direction of 'Pioneering Filaments': The main mass of sponge tissue in borings sends out tissue offshoots which penetrate into the surrounding substrate. These offshoots appear as thin strands of sponge tissue and presumably function as pioneering filaments (Ward and Risk, 1977) which travel some distance away from the main borehole then initiate new chamber development. They form narrow conduits in the substrate; some are of uniform diameter (usually less than 1 mm), others taper towards their extremities. Plate 5G shows several fine tissue strands radiating out into the substrate surrounding a Siphonodictyon borehole which is in an early stage of development. The cavity is located beneath the live coral surface in the upper part of the corallum of a M. annularis colony. The main mass of the sponge, from which the tissue strands grew, is located in larger boreholes in the basal parts of the corallum.

The direction of travel of many of these 'pioneering filaments' appears to be influenced by the growth structure of the coral substrate. Strands follow either the corallites or the direction of the growth bands. Filamentous offshoots were commonly observed extending out into the substrate around C. caribbaea and C. delitrix borings in directions parallel to the corallites or growth banding. Plate 5H shows strands of Siphonodictyon tissue following the direction of the growth banding in a M. annularis colony. Strands of tissue associated with C. caribbaea and C. delitrix borings in the base of coral colonies commonly extend parallel to the growth banding just beneath the coral surface into the region beneath the live tissue-covered surface (Plates 8E, F). Strands locally change direction and advance up corallites to the surface where they apparently establish new papillae.

2.35 Effect of other borings: Utilization of vacated boreholes of macro-boring organisms such as worms and bivalves by sponges, as access routes to the interior of coralla, occurs locally. The common occurrence of borings of C. vermifera in the walls of vacated bivalve boreholes has already been mentioned. Sponge penetration was also locally observed taking place along sabellid borings.

Microborings produced by filamentous endolithic algae are abundant in coral skeletons, and sponges, during initial penetration, may make use of pathways provided by these microborers.

3. RATES OF BORING BY SPONGES

3.1 Rates Obtained from New Substrate Colonization Experiments

Little is known at present about the rate of boring of most boring organisms (worms, bivalves, barnacles) due to the problems involved in obtaining data. Rates inferred from bored fouling blocks are subject to error since the time of initial settlement can not be established precisely. Since borers are not visible, direct measurements of boring rates can only be made using X-radiography (Evans, 1969). This method is limited since it can only be applied to thin substrates such as shells and flat pieces of limestone or coral. Methods based on measurement of weight loss from bored substrates are probably most effective and easiest to carry out but are difficult to apply to most borers since the decrement incurred by a single boring organism is small and likely to be masked by encrustation on the bored substrate.

Boring sponges are amenable to the weight loss method since they are capable of removing a measureable amount of calcium carbonate in a few days.

Boring rates can be obtained by either measuring weight losses in substrate blocks which have been attached to sponge bearing substrate for known lengths of time, or by measuring the weight loss from substrates which already contain sponge. Neumann's (1966) erosion rates of 23-25 $kg/m^2/a$, for C. lampa in Bermuda, were determined by measuring weight loss in limestone blocks of known surface area which had been attached to sponge-infested blocks for up to 100 days. Ruetzler's (1975) estimate of 256 $g/m^2/a$ was obtained using similar experiments of longer duration (10-12 months) with C. lampa in Bermuda and C. aprica in Belize. Bak's (1976) erosion rate estimates of 2.6-3.3 $kg/m^2/a$ for C. peponaca in Curaçao were also based on weight loss in coral slabs which had been attached to sponge-infested slabs for a period of one year. Spurr's (1975) figure of 14 $kg/m^2/a$ for the erosion rate of sponges on Discovery Bay reefs was based on weight loss from calcareous substrates (coral fragments and rubble) containing known species of sponge.

Studies in which unbored substrate blocks are used show that boring rates are initially high and become steady after about 6 months. The high initial rates result from the stimulation of the new substrate and lack of competition (Ruetzler, 1975) and reflect the rapid rate at which the sponge attacks new substrate. The steady rate which is attained once the stimulation effect has ceased more truly represents the actual excavating capacity of the sponge. To obtain realistic estimates of boring rates from experiments in which fresh substrates are used, long term experiments of 12 months or more should be conducted (Ruetzler, 1974). Studies using substrates which already contain boring sponges probably provide more reliable boring rate estimates. However since these experiments are only practical using fragments of branching or platy corals, or shells, which are totally infested and

not growing or being encrusted the rates obtained may not be representative of boring rates on the reef as a whole (rates in the branching and platy corals may be different from rates in the massive corals which dominate most reef communities).

Boring rate experiments with C. delitrix form 1 were started in July and August and in December of 1975. Of the 34 experiments started in July and August, 32 were allowed to run for periods ranging from 363 to 415 days and 2 were sampled during December to monitor the weight loss after a 4 to 5 month period. The 12 experiments started in December were run for 253 days. Experiments started in July and August were more successful than those started in December. Twenty-one of the 34 July-August test substrate blocks were attacked by sponge from the attached infested substrate whereas only 4 of the 12 December substrate blocks showed evidence of new sponge growth. Although all of the block pairs were initially tightly wired together, in 10 of the 21 unsuccessful experiments the sponge infested substrate had become detached from the test block. In the other 11, although the blocks were still attached after the duration of the experiment, there was no sign of new sponge growth in the test block.

Test substrates used were M. annularis, S. siderea, P. astreoides, D. labyrinthiformis and C. natans. The highest success rate was obtained in experiments in which S. siderea blocks were used. In 11 of the 17 experiments started in July and August and 3 of the 4 experiments started in December the sponge attacked the S. siderea blocks. Experiments using M. annularis and P. astreoides started in July and August were more successful than those started in December. New sponge growth occurred in 6 of the 9 July-August M. annularis blocks and in 3 of the 4 P. astreoides blocks. Only

1 of the 4 December M. annularis blocks and none of the 4 December P. astreoides blocks was attacked. /Of the December experiments only the 4 S. siderea experiments were set up by the author (due to an ear infection which prevented the author from diving). The high failure rate in the M. annularis and P. astreoides experiments, which were set up by dive partners, is believed to be due to the blocks not being securely attached./ Of the 2 experiments using D. labyrinthiformis one block was bored. No new sponge growth was evident in either of the 2 C. natans blocks. An additional 5 test substrate blocks, through which a central hole was drilled, were attached to the surface of C. delitrix-infested colonies using galvanized nails. Although some growth of the parent colony occurred around the sides of the block no penetration occurred in any of the blocks.

Table 5 lists the results of the boring rate experiments conducted with C. delitrix over periods ranging from 121 to 415 days. The average rate of removal of carbonate is determined in each test substrate block by dividing the weight loss from the block by the length of time the block was in contact with sponge-infested substrate. Boring rates in $g/m^2/a$ are obtained by relating these figures to the surface area of the substrate block covered by sponge tissue (initial contact area plus area of new sponge growth). In blocks sampled after a 6 month period this area closely approximates the initial contact area since the sponge has not yet bored through the test block and established new ectosomal patches or papillae. In blocks sampled after a 12 month period the area of sponge cover is greater since ectosomal tissue from the attached sponge block has spread onto the sides of the test block and sponge tissue has penetrated the contact area on the upper surface of the test block, bored through the test block, and established ectosomal patches

TABLE 5: Results of Boring Rate Experiments using *Cliona delitrix*

A. Experiments of 1 year duration or longer

Experiment	Duration	Weight			Area		Weight removed	
	days	Original g	Final g	Loss g	Contact cm^2	Final cm^2	mg/cm^2	$mg/cm^2/a$
Ss-1	415	123.85	84.76	39.09	24.4	57.5	680	598
2	414	37.00	24.00	13.00	18.4	27.3	476	419
3	414	40.24	23.87	16.37	11.6	22.0	744	655
4	414	26.54	16.79	9.75	8.8	15.5	629	556
5	414	23.86	13.97	9.89	6.0	7.2	1374	1209
6	408	112.50	84.51	27.99	19.8	44.6	628	563
7	408	116.71	94.75	21.96	13.5	28.2	780	700
8	378	67.47	59.20	8.27	11.7	12.9	641	621
9	378	106.19	86.39	19.80	6.7	24.8	798	773
10	368	123.54	90.65	32.89	17.1	31.6	1041	1035
							Mean = 713 SD = 238	
Ma-1	378	87.10	79.79	7.31	5.3	5.3	1379	1335
2	378	86.34	60.54	25.80	19.6	34.1	757	732
3	378	85.63	72.53	13.10	16.7	18.3	716	693
4	357	66.34	51.07	15.27	14.6	23.7	644	660
5	357	71.09	59.41	11.68	12.2	18.4	635	651
6	357	72.04	51.31	20.73	16.7	29.2	710	728
							Mean = 800 SD = 264	
Pa-1	363	117.52	87.89	29.63	13.9	25.4	1168	1178
2	363	113.93	70.44	43.49	22.6	57.8	727	733
3	363	88.57	77.90	10.67	17.5	23.9	445	449
							Mean = 787 SD = 367	

SD = Standard Deviation

Overall Mean = 752 $mg/cm^2/a$ (SD = 254)

TABLE 5: Continued

B. Experiments of less than 1 year duration

Experiment	Duration	Weight			Area		Weight removed
	days	Original g	Final g	Loss g	Contact cm^2	Final cm^2	mg/cm^2
Ss-1	253	94.14	88.88	5.26	14.2	14.2	370
2	253	97.62	94.71	2.91	8.0	8.0	364
3	253	104.55	96.08	8.47	11.4	11.4	742
4	159	101.10	92.74	8.36	21.1	25.6	326
Ma-1	253	87.31	53.02	34.29	20.3	25.6	1339
Dl-1	121	129.00	114.94	14.06	15.2	16.4	857

Ss - S. siderea
Ma - M. annularis
Pa - P. astreoides
Dl - D. labyrinthiformis

and papillae on the base and sides of the block (Plates 9A and B). Plates 9D and 9C show the effects of sponge penetration, from the attached infested substrates, on originally unbored blocks of S. siderea after 6 and 12 month periods.

The average rate of removal of calcium carbonate in the 363 to 415 day experiments is 752 mg per square centimetre sponge tissue per year. A wide range of removal rates is found in each of the three substrate types used. The average figures for S. siderea, M. annularis and P. astreoides blocks (363-415 day experiments) are 713, 800 and 787 mg/cm^2/a respectively. Because successful M. annularis and P. astreoides experiments were small in number, and the range of values overlap, the boring rates in the different substrates are statistically insignificant. More experiments would be required to establish whether the boring rate of C. delitrix is affected by substrate type. Experiments with C. lampa (Neumann, 1966) in different types of carbonate substrate show that although porous substrates are invaded more rapidly and are more deeply penetrated than compact substrates the rate of removal of calcium carbonate is the same.

The boring rates obtained during this study are slightly higher than those found by Ruetzler (1975) for C. lampa and C. aprica in Bermuda and Belize. If the average biomass (mg dry weight) of these clionids per unit surface area (cm^2) of their papillar fields or encrustations and the average biomass of all boring sponges per unit area (m^2) of reef surface are known the boring rate figure can be converted from per unit area sponge tissue to per unit area reef surface. Ruetzler's figure of 256 g/m^2/a for the erosion rate of sponges in near-shore patch reefs and rock bottoms in Bermuda was determined in this way. Since no data on boring sponge biomass is available

from Barbados reefs sponge erosion rates per unit area of reef surface can not be determined by this method. However if the biomass of boring sponges in Barbados inshore regions is assumed to be similar to that in Bermudan inshore regions, an erosion rate of 278 $g/m^2/a$ is obtained (average boring rate of 752 $mg/cm^2/a$ from 363-415 day experiments used). This figure is similar to 302 $g/m^2/a$, the average boring rate in coral species and cor-algal substrate on the Bellairs reef determined by radiography.

3.2 Boring Rates from Radiography

The average rate at which boring sponges penetrated a particular massive coral specimen during its life span was calculated from the bored volume and age of specimens determined from radiographs. The bored volume can be converted to weight loss using the average bulk density of each species. Densities of all of the principal massive corals except M. cavernosa were determined by Stearn et al. (1977). They are 1.41 for M. annularis, 1.61 for S. siderea, 1.40 for P. astreoides and 1.87 for A. agaricites. The average density of M. cavernosa was determined in specimens from the bank top and outside edge. Blocks measuring 3 cm by 3 cm were cut from the unbored parts of the slabs of each specimen. The average density of each colony was calculated from the volume and weight of these blocks. Colonies from the outer edge of the bank reef are more dense (1.68 g/cm^3) than those from the bank top (1.5 g/cm^3). The weight removed per square metre per year was obtained by dividing the weight removed per year by the planimetric area of each colony. Tables B24 to 32, Appendix B, list the age, volume bored, area and weight removed per square metre per year in specimens of each of the massive coral species sampled on the fringing reef and bank reef. The average rates

of removal in coral samples from the fringing reef, bank top and bank sides are shown in Table 6.

Rates of boring are higher on the bank reef than on the fringing reef. The highest rates were recorded in A. agaricites on the bank reef. Rates of boring in M. cavernosa, S. siderea and P. astreoides from the outer edge of the bank reef are higher than on the bank top. P. astreoides colonies from the inner edge of the bank reef display lower rates of boring than P. astreoides colonies from the bank top and M. annularis colonies from both the inner and outer edges exhibit lower rates than M. annularis colonies from the bank top.

Colonies collected from the bank top are dome-shaped; those collected from the bank sides are both dome-shaped and platy. Boring rates are in general more uniform in coral samples comprising dome-shaped colonies. The M. annularis sample from the inner and outer edges and the P. astreoides sample from the inner edge, both of which consist predominantly of platy colonies, show a wider range of boring rates. In the M. annularis sample several colonies are more extensively bored than those on the bank top but a large number are less extensively bored (Plate 10A). The differences are due to differences in the extent of encrustation of the undersides of colonies. Non-encrusted colonies exhibit greater infestation and higher boring rates than encrusted colonies, in which the base is more protected. The presence of platy colonies which are not extensively bored results in the lower average boring rates for M. annularis samples from the bank sides. The lowest average boring rate was recorded in the P. astreoides sample from the inner edge of the bank (Plate 10B). These platy colonies are not extensively encrusted and the low boring rates cannot be attributed to protection of the

TABLE 6: Boring Rates ($g/m^2/a$) in Massive Corals from Fringing and Bank Reefs

Coral species	Fringing reef	Bank reef		
		Outside	Top	Inside
Montastrea annularis	480	567	590	552
Montastrea cavernosa	NS	608	585	NS
Siderastrea siderea	102	512	427	NS
Porites astreoides	202	285	257	148
Agaricia agaricites	320	NS	756	NS

NS - not sampled

undersides by encrustation. Possible reasons for the low rates in these colonies will be discussed later.

3.3 Boring Rates in Porites porites and Cor-algal Substrate

Although a large area of the Bellairs fringing reef is covered by massive corals of the species sampled during this study, an even larger area is covered by dead coral and coralline algae and by the branching coral P. porites. Rates of boring were determined in these two additional substrate types.

Boring rates in P. porites can not be determined using the method that was used for massive corals since P. porites is a branching form which can not be easily slabbed for X-ray analysis. However, most of the important boring sponge species which attack this coral excavate cylindrical chambers in the axes of branches and simple direct measurements of the segments of the branches can be used to assess the volume of branches and the volume removed from branches by boring. The method involved cutting up all of the branches present in each P. porites sample into unbranched lengths with a set of shears. The lengths and diameters of each of the segments were measured to obtain the total volume of the coral sample. The lengths were broken into segments about 1 cm long and classified as to whether they contained boring sponge that was dead, boring sponge that was alive, or were unbored. For the samples that were bored, the length of the segments, and the diameter of the borings at each end were measured. The diameters of the bored axial holes at each end of the stems were averaged, halved to give the radius, squared, and multiplied by the length of the segment and π to give the volume bored for each stem of coral. From this and the total of the volume of the coral

collected, the volume bored was calculated. This volume can be converted to weight and to weight bored per square metre by using the specific gravity of the coral and the size of the area collected. Since age estimates /based on growth rate data obtained by Lewis et al. (1969)/ can be made for P. porites samples, the weight bored per square metre per year can be obtained. The calculations yielded an average boring rate of 200 $g/m^2/a$.

Another method was also devised for determining rates of boring in cor-algal substrate since it was not possible to establish the age of cor-algal substrate specimens. The method is based on a comparison with boring in the algal-encrusted dead bases of M. annularis colonies in which the extent of boring was similar to that found in cor-algal substrate. By considering the dead bases as representative of the algal-encrusted and dead coral surfaces of the reef a rate of boring was obtained for cor-algal reef surfaces. Fourteen colonies of M. annularis from the fringing reef were considered.

The surface area of the base of colonies is calculated from serial sections of the corals and the weight removed per year determined from radiographs as outlined above. If the area of the base is divided into the weight removed per year, rates of removal per square metre can be determined (Table 7). The average rate of boring obtained is 507 $g/m^2/a$. Examination of Table 7 shows that the range of values is large and that the rate of removal of skeleton is not obviously related to the area of the dead base. This is probably due to different levels of encrustation.

3.4 Factors Controlling Rates of Sponge Boring

Studies of sponge boring rates (Neumann, 1966; Ruetzler, 1975; Spurr, 1975) indicate that boring activity is dependent on substrate availability,

TABLE 7: Sponge Boring Rates in Dead Bases of *Montastrea annularis* Colonies

Coral specimen location MA:T3	Dead base surface area $m^2 \cdot 10^{-4}$	Weight removed	
		g/a	$g/m^2/a$
120	91	3.98	436
130	30	3.55	1177
140	113	9.57	846
150	337	4.48	133
160	85	3.79	443
170	55	4.65	843
180	563	11.20	199
190	106	4.58	431
200	266	25.62	963
210	68	2.75	405
220	65	1.69	259
230	171	10.12	591
240	132	2.71	144
250	156	3.47	222

Average weight removed = 507 $g/m^2/a$ (SD = 331)

biological interactions such as competition and predation, and environmental factors which influence growth and reproduction.

The influence of environmental factors on the boring rate of Cliona lampa in Bermuda have been investigated by Ruetzler (1975). High light intensity, strong currents, mechanical stimuli (such as may be triggered in nature by scraping organisms) and possibly low temperature all appear to stimulate the boring activity of this species. This explains the widespread occurrence of this species in well-lit shallow-water habitats which are exposed to strong water movements. Spurr (1975) relates differences in boring rates of sponges in different reef zones in Discovery Bay, Jamaica to the degree of sediment stress, light intensity, substrate availability and possibly to water currents which supply nutrients. Differences in excavation rates between individual species may be related to differences in ostial and oscular papillae diameters and to the presence of symbiotic zooxanthellae. (Filter feeding efficiency is partly determined by the efficiency of the pumping system which, in turn, is partly dependent upon the diameter of the papillae.) Species with large papillae and probably faster pumping rates can take in larger food particles and greater quantities of nutrients. These may thus be able to channel proportionally more energy into growth and reproduction. Since these species have strong exhalent currents they could be expected to remove sediment from their surface and could cope better with high sediment stress. The faster boring rate of species which possess symbiotic algae may be due to the transfer of some product of algal metabolism to the sponge.

An investigation of the boring rate of C. aprica in different reef zones in Jamaica (Spurr, 1975) showed that the boring rate of this species changes

significantly with depth. Rates are lowest in the shallow waters of the reef crest (3 m) and become higher on the fore-reef terrace (14-15 m). They reach a maximum at a depth of 20 m on the fore-reef escarpment and decrease at greater depths. (C. aprica may react differently to environmental conditions than other clionids since it contains symbiotic zooxanthellae. The maximum boring rate which is attained at 20 m suggests an optimum light intensity is reached at this depth. Sponges which contain no zooxanthellae may not show such a marked change in boring rate with depth.) Boring rates of C. caribbaea in Barbados might be expected to show a similar pattern to that of C. aprica since C. caribbaea, like C. aprica, contains symbiotic zooxanthellae. It is also the most abundant boring sponge on the reefs and is found throughout the entire depth range.

No comparative data on boring rates in different environments were obtained from the experiments with C. delitrix in Barbados since the experiments were only carried out on the bank top where C. delitrix-infested colonies are common. Data from the radiography study do however reveal that boring rates on Barbados reefs show a similar pattern of change with depth as those in Jamaica. The general trend towards higher boring rates of the boring sponge population at greater depth in the M. cavernosa, S. siderea and P. astreoides populations is similar to that found by Spurr in Discovery Bay. Rates are higher on the bank reef top than on the fringing reef and are highest on the bank sides. The comparable variation in rates in the two areas is not surprising since the environments present on the west coast of Barbados and north coast of Jamaica are similar. The Barbados bank reef top and sides are closely comparable in depth, physical conditions and bottom communities to the Jamaican fore-reef terrace and fore-reef escarpment. The

reef crest environments in the two areas are comparable in depth range and physical conditions but have different coral communities.

3.5 Factors Controlling the Extent of Sponge Boring in Massive Reef Corals

Table 8 shows the range, mean and standard deviation of values of volume bored in M. annularis, S. siderea, P. astreoides and A. agaricites colonies from the bank and fringing reefs and M. cavernosa colonies from the bank reef. The mean values of volume bored in coral samples collected from each of the different environments sampled are summarized in Fig. 4. A general depth profile of the study area is included in this diagram to show the sampling sites. Three main points emerge from the diagram:

1) A. agaricites, M. annularis, S. siderea and P. astreoides are bored to different extents in the two reef communities. A. agaricites is most extensively bored, followed by M. annularis. On the bank reef P. astreoides is least bored and S. siderea shows levels of boring intermediate between M. annularis and P. astreoides on the bank top and outside edge. On the fringing reef P. astreoides exhibits intermediate levels of boring and S. siderea is least bored.
2) Fringing reef colonies of each coral species are less extensively bored than bank reef colonies.
3) Colonies from the outside edge of the bank reef are more extensively bored than those from the bank top. M. cavernosa colonies are most extensively bored. M. annularis colonies from the inside edge are more extensively bored than M. annularis colonies from the bank top whereas P. astreoides colonies from the inside edge are less extensively bored than those on the bank top.

TABLE 8: Volume Bored (%) in Coral Samples from Bank and Fringing Reefs

Coral species	Fringing reef				Bank reef			
	Range	Mean	SD	N	Range	Mean	SD	N
Montastrea annularis	0.8 - 8.9	4.4	2.7	14	outside 6.1 - 20.3	12.3	4.7	9
					inside 3.2 - 22.6	10.5	7.7	6
					top 2.5 - 18.4	9.4	4.5	16
Porites astreoides	0 - 11.6	3.3	3.9	13	outside 1.3 - 20.4	7.4	6.7	8
					inside 0.5 - 11.0	3.8	3.8	8
					top 0 - 15.7	4.7	4.1	17
Siderastrea siderea	0 - 5.3	1.3	1.7	12	outside 6.3 - 18.9	10.9	4.3	6
					top 1.1 - 16.5	6.7	4.8	17
Montastrea cavernosa	not sampled				outside 11.6 - 24.6	17.3	5.9	6
					top 4.5 - 29.3	15.4	7.0	16
Agaricia agaricites	0 - 17.8	6.8	6.7	12	top 2.3 - 24.8	13.6	7.1	15

N = number of specimens

SD = standard deviation

the substrate has been entirely encrusted.

Many of the platy colonies on the sides of the bank reef are heavily encrusted. Sponges and bryozoans are the dominant encrusters; coralline algae are less important. Boring sponges are scarce in these colonies and it appears that the spread of encrusters was efficient enough to exclude sponge infestation. Since grazers find it difficult to gain access to the basal surface of these colonies few grazed areas suitable for sponge settlement will be produced.

3.513 damage: Areas of dead substrate suitable for boring sponge larval settlement can be produced on the live surface of corals or encrusters in various ways. Predators such as fish, gastropods, and polychaetes form scars on the live surface of corals and fish and echinoids form scars on encrusting organisms on the base of coral colonies. The bare skeleton of the coral or encruster is exposed in these scars and is usually rapidly colonized by filamentous algae. Sponges can settle and start to bore into these areas if the sponge larvae settle before the coral or encruster regenerates and grows back over the damaged area.

Grazing fish in their search for epilithic and endolithic algae attack corals and form rasp and scrape marks on their surfaces. Some feed exclusively on coral polyps, some feed on filamentous and calcareous algal coated substrates and others feed on both live coral and algal-encrusted substrates. The extent of damage to the coral varies considerably. Polyp-feeding fish form small nicks and cause little damage to the underlying skeleton but larger fish, especially scarids, form large rasp marks on the surface of the skeleton and can denude large areas of tissue-covered or encrusted surfaces.

M. annularis and P. astreoides colonies in which large areas of living

tissue had been removed by grazing fish were commonly observed in deeper parts of the Bellairs reef front (Frydl, 1977). The damaged areas which had been recently grazed were colonized by filamentous algae. Those which had been exposed longer were encrusted by coralline algae or other calcareous encrusters and in some scars the coral had partly or completely regenerated and overgrown the original scar. New sponge borings were present in several of the grazed areas covered with filamentous algae. This indicates that sponges make use of the grazed areas for settlement and provides additional evidence of the preference of sponge larvae for non-encrusted substrate.

The gastropod Coralliophila abbreviata feeds on M. annularis on the Bellairs reef (Ott and Lewis, 1972) and removes small patches of tissue at the boundary between the dead skeleton and living tissue. Since no regeneration occurs in grazed areas on the coral periphery the bare patches created may provide suitable settlement areas for boring sponges. The echinoid Diadema antillarum grazes on reef surfaces covered with filamentous and calcareous algae. Numerous rasp marks are made on coralline algae on the base of coral colonies but since these are small and quickly healed by regeneration (Hawkins, personal communication) it is unlikely that much new substrate, on which boring sponges can settle, is created.

Experiments done in Curaçao (Bak, 1977) showed that boring sponges are the second most abundant colonizing organisms on artificially damaged areas of live corals (filamentous algae are most abundant). Fresh lesions, made by the investigator, on the live surface of corals were colonized by filamentous algae within a few days and by boring sponges within two weeks. The damage inflicted on corals was designed to simulate the effects of different coral predators. One type of lesion was made by removing only the coral tissue,

the other by removing coral tissue and the underlying superficial skeletal elements. The first type of damage corresponds to the effects of gastropods and some polyp-feeding fishes which suck off coral polyps without damaging the underlying skeleton, the other type corresponds to the effects of most of the larger grazing fishes which scrape away the skeleton beneath the tissue.

The presence of boring sponges other than Siphonodictyon spp. and C. delitrix form 1 on the live surface of only a few of the colonies sampled suggests that boring sponges do not often establish successfully on the living surface of even damaged colonies. Most scars produced by grazers are small and probably heal before, or soon after, sponges settle. Boring sponges which have colonized scars can be overgrown and killed (Bak, 1977).

Data from Barbados reefs (Frydl, 1977) show that parrotfish are important erosive agents. Grazing scars, produced mainly by large individuals of Sparisoma viride, are particularly common on M. annularis and occur frequently on P. astreoides, S. siderea and P. porites and occasionally on A. agaricites, M. cavernosa and M. mirabilis. Diadema antillarum is locally important as a coral predator on Curaçao reefs (Bak and van Eys, 1975) but has not been observed feeding on coral tissue on Barbados reefs (Hawkins, personal communication). Since the erosional effects of other coral predators seem to be limited, parrotfish are probably most important in the provision of new substrate for secondary colonizers.

3.52 The Balance Between Coral Growth Rate and Sponge Boring Rate: Although no data on calcification rates of coral species on the bank reef are available the average linear extension rates, measured from growth banding on X-radiographs of slabbed coral specimens, give an indication of the relative

rates of calcification of bank reef and fringing reef colonies. The average linear extension rates of A. agaricites, P. astreoides and S. siderea on the fringing reef are 5 mm, 5.5 mm and 4.8 mm respectively and on the bank top 5 mm, 5 mm and 4.8 mm. These figures suggest that calcification rates of the three species are comparable on the fringing reef and bank top. The lower average extension rates of 4.2 mm and 3.4 mm in colonies of P. astreoides from the outer and inner edges of the bank reef and 3.9 mm in colonies of S. siderea from the outer edge of the bank suggest that calcification rates in these species decrease on the bank sides.

A general decrease in extension rates is found in the M. annularis samples from the fringing reef, bank top and bank sides. The average annual increment of fringing reef colonies is 12.5 mm, 6.0 mm in bank top colonies and 3.8 mm in colonies from the bank sides. This trend indicates that calcification rates of M. annularis decrease with depth. This is supported by data on calcification rates of M. annularis from Jamaica (Dustan, 1975) and St. Croix (Baker and Weber, 1975). Although the growth morphology of M. cavernosa does not change within the depth range sampled the growth rate does change. The average linear extension rate in colonies from the outside edge of the bank reef is lower than in colonies from the bank top (4.3 mm on bank top: less than 4.0 mm on outside edge).

In those species in which the growth rate changes with depth, differences in the amount of boring between colonies from the fringing reef, bank top and bank sides can be related to changes in calcification rates with depth. The extent of boring in colonies is dependent on the balance between coral growth rate and sponge boring rate. Since the average rate at which coralla are penetrated is higher on the bank reef than on the fringing reef and highest

on the bank sides, the combination of higher penetration rates and lower calcification rates at greater depth will result in greater levels of infestation. This phenomenon is demonstrated by M. annularis. In fringing reef colonies only the outer 1 or 2 centimetres of the basal margin are bored but in colonies from the bank reef top borings penetrate farther into coralla and in platy colonies from the bank sides most of the corallum is infested (Fig. 5). The greater infestation in slower calcifying M. cavernosa, S. siderea and P. astreoides colonies from the outer edge of the bank reef is due to this effect. The platy P. astreoides colonies from the inside edge of the bank reef are the exception to this observation. They are not extensively bored by sponges which suggests that they may have developed a mechanism which inhibits sponge attack.

3.53 Skeletal Density: Of the corals examined during this study species such as M. cavernosa and A. agaricites with high skeletal density were most extensively bored and those with low skeletal density such as Colpophyllia natans were least bored. This suggests that a correlation exists between the extent of boring and skeletal density in coral species. Sponges appear to be capable of deeper penetration in denser coralla. Further study is required to explain this phenomenon.

3.6 Erosion Rate of Bellairs Reef

The total amount of $CaCO_3$ removed by boring sponges from the north lobe of the Bellairs reef can be derived since the area occupied by each of the different coral species and by algal-encrusted and dead coral substrate on this reef is known (Stearn et al., 1977). Table 9 shows the areal coverage of each substrate type and the amount of $CaCO_3$ removed by boring from beneath

TABLE 9: Weight Removed by Boring Sponges from Different Substrate Types on Bellairs Reef

Substrate	Mean weight removed $g/m^2/a$	Area m^2	Total g/a
Coralline algal encrusted substrate and dead coral	507	45162	22.90×10^6
Porites porites	200	2203	0.44×10^6
Porites astreoides	202	1469	0.30×10^6
Agaricia agaricites	320	1102	0.35×10^6
Montastrea annularis	480	918	0.44×10^6
Siderastrea siderea	102	551	0.06×10^6

Total $= 24.49 \times 10^6$ g/a

each substrate type. When the figures for bioerosion by sponges in each of the substrate types are combined they show that about 24.5 x 10^6 g/a are removed from this reef. Table 9 shows that the contribution by boring sponges in the dead coral and algal-encrusted surfaces greatly exceeds that from boring sponges in the other types of substrate. This results mainly from the large surface area of the reef covered with coralline algae.

Comparison of sponge erosion rates with rates of calcium carbonate productivity on the reef and with erosion rates of other major bioeroders allows an evaluation of the relative importance of sponge erosion and other constructive and destructive reef processes. Although sponges are the most important borers on the Bellairs reef the effect of other borers should be taken into account to determine a figure for total erosion by borers. Other groups of borers present on these reefs include bivalves, barnacles and sipunculid and polychaete worms (MacGeachy and Stearn, 1976). A total erosion figure by borers of about 27.8 g x 10^6 per year can be determined since sponges account for about 90% of the total boring in the majority of the reef substrates. The other two major bioerosive agents on the fringing reef are parrotfish and the sea-urchin Diadema antillarum. Extremely dense aggregations of this echinoid occur on the Bellairs reef and bioerosion by this organism (Stearn and Scoffin, 1977) is estimated as 163 g x 10^6 per year. Parrotfish grazing is more extensive in deeper reef areas in Barbados; on the fringing reef they account for the erosion of 1 g x 10^6 per year (Frydl and Stearn, in press). The contribution made by Diadema to reef erosion greatly exceeds that of both the boring sponges and parrotfish.

The total figure for $CaCO_3$ productivity on the north lobe of the Bellairs reef has been determined by Stearn et al. (1977) as 163 g x 10^6 per

year. Boring sponges account annually for the destruction of more than 1/6 of the hard tissue secreted on the reef and are therefore destructive agents of considerable significance. Comparison of the total production and bioerosion figures shows that bioerosion exceeds production. This suggests that the reef is being destroyed faster than it is growing. However the Diadema erosion figure may be an overestimate since an independent study by Hunter (1977) showed that up to 44% of the excreta may be reworked sand. This would lower the Diadema erosion figure to 91 g x 10^6 per year and the total bioerosion figure to 117 g x 10^6 per year.

A comparison of sponge erosion rates and rates of calcium carbonate productivity can not be made on the bank reef since no data on calcification rates of coral species on the bank reef are available. Bioerosion by sponges is undoubtedly more significant, relative to skeletogenesis, in this environment than on the fringing reef since calcification rates are in general lower.

4. EFFECT OF SPONGE BORING ON REEFS

4.1 Destructive Effects

4.11 Destabilization of Coral Colonies on Barbados Reefs by Boring Sponges: The susceptibility of corals to break-off depends on their growth structure and on the environment in which they are growing. The main stresses induced in corals are generated by water movements in the form of waves and currents (Graus et al., 1977). The magnitude of these stresses differs in different environments. The size and shape of coral colonies determine their strength and ability to withstand forces generated by water movements. Weakening by sponge boring greatly reduces this ability. The three basic growth morphologies, massive, branching and platy differ in their susceptibility to

break-off. Branching corals such as A. cervicornis, P. porites and M. mirabilis are most susceptible because of their more fragile structure and because they grow at depths in which strong water movements occur. The abundance of rubble of these three species in the study area attests to this.

The basal regions of detached branches and colonies of A. cervicornis examined in the study area were intensively bored by sponges. Boring activity weakens basal branches reducing the amount of wave surge they can withstand. Fracture is also hastened by grazers since grazing reduces the effective diameter of branches.

P. porites colonies examined during the study were commonly bored by C. delitrix, C. ensifera, C. amplicavata and Spheciospongia sp. The large cavities formed by these species occupy the central axis of branches and locally reduce their strength. Evidence obtained during dives made after a winter storm period (December, 1975) suggests that sponge boring greatly increases the susceptibility of the Porites branches to breakage. Large numbers of newly broken P. porites branches were observed in and around the P. porites zone on the southern part of the Bellairs reef. In most branches the breakage was located at the site of a sponge chamber. (Many of the cavities still contained live sponge.) Blocks of coral rubble which were thrown onto and buffeted around in the P. porites beds, by storm waves, were probably responsible for most of this damage.

The destabilizing effects of sponge boring are less evident in massive coral populations such as those which exist on the fringing reef and bank reef crest. In the shallow waters of the fringing reef most massive colonies are firmly attached to the underlying substrate. Semi-encrusting colonies of P. astreoides and A. agaricites and hemispherical colonies of S. siderea

mantle the underlying substrate and are difficult to detach. Bulbous M. annularis colonies have thick basal regions which provide strong support for the bulk of the corallum above. Levels of sponge infestation in these colonies are low due to the lack of exposed base in colonies of P. astreoides, A. agaricites and S. siderea and to the counter-balancing effect of rapid calcification in M. annularis. As a result there is little evidence of destabilization by sponges in massive corals in this environment. Coral break-off results mainly from storm wave impact.

/The destructive effects of Diadema grazing are evident in large multi-lobed colonies of M. annularis on the fringing reef. These colonies exhibit varying degrees of destruction of the type described by Lewis (1960), Scatterday (1974) and Scoffin et al. (in press). Boring sponges contribute to this destruction by weakening the peripheral coral skeleton of these colonies by making it more susceptible to disintegration by grazing Diadema./

On the bank reef crest the effects of sponge boring are more evident. Detached colonies, although not abundant, are more numerous and some of the larger colonies which are still in growth position are unstable and can be pushed over easily. Examination of the basal parts of these colonies shows they are extensively bored and locally undermined by the combined action of borers and grazers.

Massive multi-lobed colonies of M. annularis show most evidence of the effects of sponge boring. The heavier infestation in this species on the bank top (compared to the fringing reef) results from lower calcification rates coupled with possible higher boring rates in this environment. Irregular notches and scars, presumably formed by grazing fish and echinoids, occur locally in heavily bored substrate on the encrusted base of these

colonies. Sponge boring apparently weakens the coral margin to the point where it is easily disintegrated by grazers. Continued boring and grazing erodes these colonies reducing them to encrusted relics with only a few small actively growing parts left in the upper parts of the colony. These living lobes are extensively undermined by sponges and are easily detached.

M. cavernosa colonies are also extensively bored but unlike M. annularis colonies show little evidence of destabilization. Most colonies are fairly stable and only a few overturned colonies were observed. Their stability results from their mode of growth. Colonies develop a peaked mushroom shape due to peripheral growth. They have a broad base and a low centre of gravity and are inherently stable. They become firmly anchored since the periphery mantles the underlying substrate.

S. siderea, P. astreoides and A. agaricites colonies on the bank reef are less stable than their fringing reef counter-parts due to the greater area of exposed base and consequent heavier infestation. Several overturned S. siderea colonies were observed. These were all larger colonies which had become 'top-heavy'. Since only the upper surface of these colonies is living the base does not develop in proportion to the rest of the corallum. The basal regions are also weakened by borers and eroded by the combined effects of borers and grazers. Colonies apparently increase in size till a point is reached where the base can no longer support the large mass of calcium carbonate which forms the bulk of the corallum.

The presence, on the bank top, of most massive colonies, in growth position attests to the lack of strong physical forces in this environment. Periods of high wave surge caused by Atlantic storms occur on the west coast of Barbados two to five times each winter (Donn and McGuinness, 1959).

During periods of severe swells wave surge can be felt to depths of over 50 m on the bank reef (Ott, 1975) and may be strong enough on the bank top to detach the most unstable colonies. The impetus required to detach small colonies may be provided by the impact of large grazing parrotfish. The extensive sponge infestation in all detached colonies examined indicates that bioerosion by sponges is the main factor responsible for coral collapse.

Sponge boring is most effective in causing coral break-off on the sloping sides of the bank reef. The platy colonies which grow in this environment are inherently unstable since they do not have strong attachments. Many colonies are supported by thin holdfasts which are intensively bored by sponges. The high levels of infestation result from the combination of low calcification rates and possibly higher boring rates in this environment. Since these colonies grow laterally outwards from the bank sides the main mass of the corallum is rarely centred above the base. Break-off occurs when the base can no longer support the weight of the corallum. This process is hastened by the weakening effect of sponge boring and by loading by encrusting organisms which attach to the undersides of colonies. Collapsed colonies, some of which had slumped downslope, were commonly observed on the sides of the bank reef. Wave surge is negligible in these depths and corals collapse under their own weight.

4.12 Effect of Boring Sponges in Other Reef Areas: The reefs of the southwest coast of Curaçao have been described by Bak (1975). The coastal profile includes a steep cliff or shingle beach bordered seaward by a gradually sloping terrace which extends to a drop-off at 7 to 12 m. Beyond the drop-off a steeply dipping seaward slope descends to depths of 50 to 60 m. A. palmata is abundant in the nearshore zone (1-4 m). A barren zone which contains only

a few living corals occurs between depths of 3 and 4.5 m. At 4 to 5 m the number of coral colonies increases and greatest density and diversity are reached in depths of 6 to 12 m at the first drop-off. M. annularis, A. agaricites and M. mirabilis are abundant. High density and diversity continue to depths of 35 to 40 m.

During this study massive coral colonies of the species sampled in Barbados were collected from the terrace area above the drop-off, from the drop-off area and from the seaward slope. Colonies growing in the shallower parts of the terrace which are exposed to strong water movements were not extensively bored. Like corals on the fringing reef in Barbados these colonies either mantle the substrate or develop strong bases in order to survive in high energy conditions. Coral break-off in this region results principally from wave action.

A trend towards greater levels of sponge infestation with increasing depth, similar to that observed in Barbados, was seen in Curaçao. Coral colonies from the drop-off area and the upper parts of the seaward slope are more extensively bored than those from the terrace. As in Barbados this is due to greater availability of exposed base and to the decrease in calcification rates and possible increase in boring rates. This area is influenced by the destructive forces of the waves only during severe storms (Bak, 1974) and even then only colonies which have been weakened by sponge boring are detached. Sponge boring is most extensive in colonies from the deeper parts of the seaward slope where reduced light intensity results in low calcification rates. This area is rarely influenced by strong water movements and sponge bioerosion is the main destructive force.

Coral species on Curaçao reefs were found in general to be less

extensively bored than those on Barbados reefs. Boring sponge density on Curaçao reefs also appeared to be lower than on Barbados reefs.

The principal area studied in Carriacou is a steeply sloping reef off the north coast of Saline Island off the south coast of Carriacou. This area is exposed to strong winds, wave action and currents. Sponges (both free-living and boring) thrive in this environment and many coral colonies are extensively bored. Boring activity is believed to be stimulated by the strong currents.

4.13 Role of Boring Sponges in Controlling Reef Growth: Expansion (or contraction) of coral reefs results from the interplay between the growth of framebuilders and physical and biological erosion. The relative importance of the two erosional processes differs in different reef environments. Sponge boring appears to be the most important type of bioerosion.

In high energy reef environments such as the Barbados fringing reef or shallower parts of the terrace before the drop-off in Curaçao coral break-off results principally from storm-wave action. Sponge boring is important in increasing the susceptibility of less resistant branching corals to break-off in this type of environment. Massive corals are little affected because they lack an exposed base which sponges can penetrate and they calcify rapidly.

In lower energy regimes such as on the Barbados bank reef or the seaward slope in Curaçao sponge boring is more intense due to the greater availability of exposed base and to lower calcification rates and possibly higher boring rates. Physical erosion is not as strong in these depths and bioerosion becomes the principal factor limiting reef growth.

4.2 Constructive Effects

4.21 Effect of Boring Sponges on Coral Reef Morphology: Observations made during this study indicate that sponge boring has an important effect on coral reef morphology. Although sponge boring appears to be entirely destructive it also has a constructive aspect. Establishment and growth of corals is promoted in areas which could not normally be colonized. Large areas of the bank reef top, between adjacent coral clumps, are covered with loose sediment which is not suitable for coral settlement. Detachment and collapse into these areas of sponge-bored coralla from the periphery of the coral patches provides stable substrate which can be colonized by corals. This results in an increase in coral coverage.

The same process operating on the sloping sides of the bank reef can result in extension of the reef into deep water areas beyond the reef front. The bottom in these areas is covered by fine sediment which is not suitable for coral settlement. Detached colonies from the sides of the bank which slump down-slope come to rest in this sediment and provide stable substrate on which new coral growth can establish. In Jamaica extensive deep fore-reef communities consisting principally of platy colonies of Agaricia undata are believed to have established in this manner (Goreau and Hartman, 1963).

5. SEDIMENT PRODUCTION BY BORING SPONGES

Boring sponges contribute significant quantities of sediment to the silt fraction of reef sediments (Futterer, 1974; Moore et al., 1976). Hunter (1977) assessed the relative importance of boring sponges in sediment production in Barbados. Two types of sponge-produced particles were

identified in sediments from the north lobe of the Bellairs reef and the area offshore from it. The first type is the faceted chip excavated from the coral substrate by boring sponges. These chips account for between 5% and 26% (average 12%) of the less than 90 micron size fraction. The other type of grain is larger (up to 1 mm diameter) and is bounded by pitted surfaces produced by sponge boring. These grains may be formed as "islands" of substrate isolated by sponge boring and released when sponge-bored substrate is destroyed by grazing or mechanical action. They account for between 3% and 9% (average 4%) of the greater than 90 micron size fraction. No correlation was found between boring sponge activity and sedimentary facies.

Preliminary scanning electron microscopic investigations of 3 sediment samples collected during this study from the bank top showed that sponge chips accounted for an average of 18% of the silt fraction in these samples. Sediment sampling was conducted on transects 4 and 5 to depths of 40 m. These samples will be examined in a future study.

Suggestions for Further Research

1. The genus Siphonodictyon has so far received little attention. S. coralliphagum poses problems since there is considerable variation in its spicule dimensions and morphology. An attempt should be made to establish standard criteria on which definition of different forms of S. coralliphagum can be based. The network-forming Siphonodictyon species should be studied in more detail. Environmental preferences of Siphonodictyon species should be examined and the factors controlling distribution of different species investigated. Boring rate studies with Siphonodictyon species should be attempted to determine the excavating powers of Siphonodictyon species and compare them with those of clionid sponges.

2. The factors which control larval settlement of boring sponges and distribution of boring sponges in reef environments are largely unknown. Experimental work on the behaviour of boring sponge larvae in response to factors such as light, water movements and sedimentation is necessary to determine the controls on sponge location and distribution on reefs. A detailed investigation of the interaction between boring sponge larvae and live coral and boring sponge larvae and encrusting organisms should be made to establish whether sponges are capable of settling on live tissue or if they settle on dead patches.

3. Investigations made during this study show that skeletal density affects the pattern of sponge penetration and the extent of penetration. The relationship between sponge boring and skeletal density should receive more attention.

4. The filamentous tissue offshoots which penetrate substrate surrounding boreholes should be studied closely to determine their true function, how the sponge maintains itself along these narrow tunnels and their relationship to the live coral.

5. To determine erosion rates by sponges (g/m^2 reef surface/a) in reef environments from sponge boring rates (mg/cm^2 sponge tissue/a) obtained from attached block experiments, estimates of the average biomass (mg dry weight) of boring sponges per unit surface area (cm^2) of their papillar fields or ectosomal encrustations and the average biomass of all boring sponges per unit area (m^2) of reef surface are required. Procedures used to obtain boring sponge biomass estimates are outlined by Ruetzler (1975). Similar methods should be applied in Barbados to determine the biomass of boring sponges on the fringing and bank reefs in order to determine and compare erosion rates in these environments.

Determination of the density of boring sponges in different reef zones which are affected by different physical parameters may make possible a correlation between sponge abundance and physical parameters.

6. Boring rate experiments in which weight loss is monitored in sponge-infested substrates throughout the year should be attempted to determine if boring activity is constant or intermittent and variable. An attempt should be made to link sponge activity patterns to environmental factors, biological interactions or sponge physiology.

7. Rates of calcium carbonate productivity of the principal coral species should be determined on the bank reef to allow a comparison of growth and destruction by sponges in this environment.

SUMMARY

1. The boring sponge fauna of Barbados' reefs includes 15 clionid species, one spirastrellid, 3 Siphonodictyon species, one Acarnus and one Alectona species and an unidentified species. This fauna is more diverse than any so far recorded in other areas in the West Indies. Six of the clionid species and the Acarnus sp. are new records for the West Indies. Seven of the species recorded (2 Cliona species, 3 Thoosa species, 1 Siphonodictyon species and one species of unknown affinity) may be new species.

2. Boring sponges are ubiquitous on Barbados reefs and virtually all substrate which has been abandoned by the growing tissue of framebuilding organisms is bored to some extent. Species abundance and diversity of sponges differ in different types of substrate. Highest abundance and diversity levels are found in massive corals. Clionids are the most abundant and diverse group with 12 species and 61.2% of the total occurrences. Siphonodictyon species are less diverse (3 species) but are also abundant (27.8% of total occurrences). Boring sponges are less abundant and less diverse in branching corals than in massive corals. Ten out of the 21 species which occur in massive corals were found in branching corals. Abundance and diversity levels in cor-algal substrate on the fringing reef are comparable to those found in massive corals on the fringing reef. Nineteen of the 21 species which occur in massive corals also occur in cor-algal substrate. C. caribbaea and S. coralliphagum forma obruta, the most common sponges in cor-algal reef rock are also the most common species in coral samples from the fringing reef. C. caribbaea is the most abundant sponge on Barbados reefs. Lowest abundance and diversity levels were recorded in coral rubble

from the swash zone.

3. Some sponge species are more abundant on the bank reef, others more abundant on the fringing reef and a few are of equal abundance in the two environments. Siphonodictyon sp. and C. ?rovignensis are abundant on the bank reef but are virtually absent from the fringing reef. C. vermifera and Cliona sp. 1 are more abundant on the bank reef and C. delitrix form 2, C. lampa and Cliona sp. 2 are more abundant on the fringing reef. The boring sponge populations of the fringing reef and bank reef differ significantly. The difference appears to result from the uneven distribution of Cliona sp.1, species X, C. delitrix form 2, C. ?rovignensis, C. vermifera, C. lampa and Siphonodictyon sp. in the two environments.

M. annularis and P. astreoides samples from the bank and fringing reefs contain comparable numbers of boring sponges whereas S. siderea and A. agaricites samples from the bank reef contain considerably larger numbers of sponges than those of the fringing reef. The distribution of sponge species in bank top and fringing reef samples of M. annularis and P. astreoides do not differ significantly whereas the distribution of sponge species in bank top and fringing reef samples of S. siderea and A. agaricites do differ significantly. The differences may stem from differences in growth morphology of these two species on the bank top and fringing reef.

Boring sponges are uniformly distributed in the bank top environment. The sponge population on the outer edge of the bank differs significantly from that on the bank top.

4. Although a few boring sponge species are found on the live surface of corals most species inhabit the non-living basal regions. Borings generally

occupy a narrow subsurface zone although some species penetrate the interior regions of coralla. Borings range in shape from well-defined discrete chambers or chamber networks to ill-defined irregular spaces and tunnel systems. Four main types of boring are recognized: (1) single spheroid to ovoid chambers, (2) networks of small interconnected well-defined or poorly-defined spheroid to ovoid chambers, (3) irregularly shaped cavities, and (4) tunnels. Clionids show the greatest range of borehole morphology.

Boring strategy appears to be genetically determined since sponge species develop the same characteristic borehole morphology in different coral species. The pattern of development of borings is influenced by variations in skeletal density associated with the corallites and growth banding.

5. Boring rates in massive corals (determined indirectly from X-radiographs and based on the rate at which sponges penetrated a particular coral specimen during its life span) are higher on the bank reef top than on the fringing reef and are highest on the bank sides. On the fringing reef the highest rates were recorded in M. annularis, followed (in descending order) by A. agaricites, P. astreoides and S. siderea. On the bank reef the highest rates were recorded in A. agaricites followed by Montastrea species (annularis and cavernosa), S. siderea and P. astreoides. Boring rates are in general more uniform in coral samples comprising dome-shaped colonies. Samples comprising platy colonies show a wider range of boring rates because of different levels of encrustation.

An average boring rate, for C. delitrix, of 752 mg per square centimetre of sponge tissue per year was obtained by measuring weight loss in blocks of unbored coral (M. annularis, S. siderea and P. astreoides) which had been

attached to sponge-infested substrate for a known time period. Assuming this rate to be representative of sponge boring rates over the reef and assuming that the biomass of boring sponges in inshore regions in Barbados is similar to that found in Bermudan inshore waters by Ruetzler (1975) an erosion rate per unit area of reef surface of 278 $g/m^2/a$ is obtained. This figure is similar to 302 $g/m^2/a$, the average boring rate by sponges in coral species and cor-algal substrate on the Bellairs reef determined by radiography.

6. Coral colonies on the fringing reef are less extensively bored than those on the bank reef top which in turn are less extensively bored than those on the outer edge of the bank. M. cavernosa is the most extensively bored species. A. agaricites, M. annularis, S. siderea and P. astreoides are bored to different extents in the fringing reef and bank reef environments. In both environments A. agaricites is most extensively bored, followed by M. annularis. On the bank reef P. astreoides is least bored and S. siderea shows levels of boring intermediate between M. annularis and P. astreoides. On the fringing reef S. siderea is least bored and P. astreoides exhibits levels of boring intermediate between M. annularis and S. siderea.

Differences in the extent of sponge boring between different coral species are attributed mainly to differences in the amount of exposed base on colonies since sponges bore mainly in dead coral skeleton. The amount of exposed base on a colony is mainly a function of the growth morphology of the species although the actual area of dead base available for sponges to penetrate is also controlled by the extent of encrustation of the base. The extent of sponge boring in massive corals also depends on the balance between

coral growth rate and sponge boring rate. The effects of sponge boring are more pronounced in deeper water (20 m or more) where calcification rates are low.

7. The total annual production of calcium carbonate on the north lobe of the Bellairs reef is 163 g x 10^6 (Stearn et al., 1977). The total amount of calcium carbonate removed annually by boring sponges from the north lobe of the Bellairs reef is around 24.5 g x 10^6. Boring sponges account annually for the destruction of more than 1/6 of the hard tissue secreted on this reef and are therefore destructive agents of considerable significance.

8. Expansion of coral reefs results from the interplay between coral and algal growth and physical and biological erosion (notably sponge boring). The relative importance of the two erosional processes changes with depth. In shallow water control of the upward growth of the reef is mainly by physical erosion. In intermediate depths where physical forces are much reduced bioerosion becomes more important as a limiting factor. As water depth increases the influence of physical forces declines and bioerosion becomes the dominant destructive agent.

Originality of Research

This is the first comprehensive study of the geological significance of boring sponges in tropical reef environments. It is also the first work done on the systematics and distribution of boring sponges in Barbados.

The boring strategy of sponge species in coral substrate has so far received little attention. This is the first study in which boring patterns of different sponge species, in different coral substrates, have been examined to determine the controls on boring strategy.

It is the first study in which X-radiography has been used to: (1) quantify and compare the extent of sponge boring in different coral species and (2) to determine rates of boring by sponges in different coral species. The method devised for quantifying sponge boring in coral specimens from small representative samples of each colony is new. It is also the first work in which an attempt has been made to determine the factors controlling the extent of sponge boring in massive corals.

If realistic estimates of sponge boring rates in reef environments are to be obtained from attached block experiments natural coral substrates should be used as test substrates. In previous studies a variety of calcareous substrates have been used. This study is the first in which different corals have been used as the main type of substrate. Blocks of sponge-infested coral substrate have previously been obtained by removing sponge-infested coralla from their natural habitat and cutting them up under running seawater. In the present study blocks were cut from in situ infested coralla on the reef surface and were attached to test blocks and suspended in the immediate vicinity of the parent colony. With this procedure more reliable boring rate estimates should be obtained since there is minimal disturbance to the sponge.

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REFERENCES CITED

Bak, R.P.M., 1975. Ecological aspects of the distribution of reef corals in the Netherlands Antilles. Bijdragen Tot de Dierkunde, 45(2):181-190.

Bak, R.P.M., and van Eys, G., 1975. Predation of the sea urchin Diadema antillarum Philippi on living coral. Oecologia, 20:111-115.

Bak, R.P.M., 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. Netherlands J. Sea Res., 10(3):285-337.

Bak, R.P.M., Brouns, J.J.W.M., and Heys, F.M.L., 1977. Regeneration and aspects of spatial competition in the scleractinian corals Agaricia agaricites and Montastrea annularis. Proc. Third. Int. Coral Reef Symp., Miami, Florida, 1:144-148.

Baker, P.A., and Weber, J.N., 1975. Coral growth rate: variation with depth. Earth Planet. Sci. Lett., 27:57-61.

Bertram, G.C.L., 1936. Some aspects of the breakdown of coral at Ghardaqa. Proc. Zool. Soc. London, 106:1011-1026.

Bourne, G.C., 1893. On the post-embryonic development of Fungia. Sci. Trans. Roy. Soc. Dublin, ser. 2, 5:205-238.

Boury-Esnault, N., 1973. Résultats scientifiques des campagnes de la "Calypso". Fascicule X, 29, Spongiaires:263-295.

Bromley, R.G., 1970. Borings as trace fossils and Entobia cretacea Portlock, as an example. Geol. J. Special Issue 3:49-90.

Buddemeier, R.W., Maragos, J.E., and Knutson, D.W., 1974. Radiographic studies of reef coral exoskeletons: rates and patterns of coral growth. J. exp. mar. Biol. Ecol., 14:179-200.

Cobb, W.R., 1969. Penetration of calcium carbonate substrates by the boring sponge, Cliona. Amer. Zoologist, 9:783-790.

Cobb, W.R., 1975. Fine structural features of destruction of calcareous substrata by the burrowing sponge Cliona celata. Trans. Amer. Micros. Soc., 94(2):197-202.

Crocker, L.A., 1977. The ecology of the zoanthid-sponge symbiosis in Barbados. M.Sc. thesis, 113 pp., McGill Univ.

Donn, W.L., and McGuinness, W.T., 1959. Barbados storm swell. J. Geophys. Res., 64:2341-2349.

Dustan, P., 1975. Growth and form in the reef-building coral Montastrea annularis. Mar. Biol., 33:101-107.

Evans, J.W., 1969. Borers in the shell of the sea scallop, Placopecten magellanicus. Amer. Zoologist, 9:775-782.

Frydl, P., 1977. The geological effect of grazing by parrotfish (Scaridae) on a Barbados coral reef. Technical Report 77-3, McGill University: 1-136 (M.Sc. thesis).

Frydl, P., and Stearn, C.W., (in press). Rate of bioerosion by parrotfish in Barbados reef environments. J. Sed. Pet.

Futterer, D.K., 1974. Significance of the boring sponge Cliona for the origin of fine grained material of carbonate sediments. J. Sed. Pet., 44(1):79-84.

Gardiner, J.S., 1903. The origin of coral reefs as shown by the Maldives. Amer. J. Sci., 16:203-213.

Ginsburg, R.N., 1957. Early diagenesis and lithification of shallow-water carbonate sediments in south Florida. Soc. Econ. Paleontologists Mineralogists, Spec. Publ., 5:80-99.

Goreau, T.F., and Hartman, W.D., 1963. Boring sponges as controlling factors in the formation and maintenance of coral reefs. In: Mechanisms of Hard Tissue Destruction. Amer. Assoc. Adv. Sci., Publ. 75:25-54.

Graus, R.R., Chamberlain, J.A., Jr., and Boker, A.M., 1977. Structural modification of corals in relation to waves and currents. In: Reefs and related carbonates - ecology and sedimentology. Amer. Assoc. Pet. Geol., Studies in Geology 4:135-153.

Guida, V.G., 1976. Sponge predation in the oyster reef community as demonstrated with Cliona celata Grant. J. exp. mar. Biol. Ecol., 25: 109-122.

Hartman, W.D., 1958. Natural history of the marine sponges of southern New England. Peabody Mus. Nat. Hist., Yale Univ., Bull. 12:1-155.

Hartman, W.D., 1977. Sponges as reef builders and shapers. In: Reefs and related carbonates - ecology and sedimentology. Amer. Assoc. Pet. Geol., Studies in Geology 4:127-134.

Hechtel, G.J., 1965. A systematic study of the demospongiae of Port Royal, Jamaica. Peabody Mus. Nat. Hist., Bull. 20:1-103.

Hein, F.J., and Risk, M.J., 1975. Bioerosion of coral heads: inner patch reefs, Florida reef tract. Bull. Mar. Sci., 25(1):133-138.

Hudson, J.H., 1977. Long-term bioerosion rates on a Florida reef: a new method. Proc. Third Int. Coral Reef Symp., Miami, Florida, 2:491-497.

Hunter, I.G., 1977. Sediment production by Diadema antillarum on a Barbados fringing reef. Proc. Third Int. Coral Reef Symp., Miami, Florida, 2:106-109.

Jackson, J.B.C., and Buss, L., 1975. Allelopathy and spatial competition among coral reef invertebrates. Proc. Nat. Acad. Sci., 72(12):5160-5163.

Kornerup, A., and Wanscher, J.H., 1967. Methuen handbook of colour. Second edition. Methuen and Co. Ltd. 243 pp.

Laubenfels, M.W., 1955. Porifera. Treatise on Invertebrate Paleontology. Moore Ed., Part E: Archaeocyatha - Porifera, pp. E21-E122.

Lewis, J.B., 1960. The coral reefs and coral communities of Barbados, W.I. Can. J. Zool., 38:1133-1145.

Lewis, J.B., Axelsen, F., Goodbody, I., Page, C., and Chislett, G., 1968. Comparative growth rates of some reef corals in the Caribbean. Marine Sciences Manuscript Rept. 10, McGill University:1-26.

MacGeachy, J.K., and Stearn, C.W., 1976. Boring by macro-organisms in the coral Montastrea annularis on Barbados reefs. Int. Revue ges. Hydrobiol. 61(6):715-745.

Macintyre, I.G., 1967. Submerged coral reefs, west coast of Barbados, West Indies. Can. J. Earth Sci., 4:461-474.

Macintyre, I.G., 1972. Submerged reefs of eastern Caribbean. Amer. Assoc. Pet. Geol., Bull. 56(4):720-738.

Macintyre, I.G., and Smith, S.V., 1974. X-radiographic studies of skeletal development in coral colonies. Proc. Sec. Int. Coral Reef Symp., Australia, 2:277-287.

Moore, C.H., Jr., Graham, E.A., and Land, L.S., 1976. Sediment transport and dispersal across the deep fore-reef and island slope (-55 m to -305 m), Discovery Bay, Jamaica. J. Sed. Pet., 46(1):174-187.

Moore, C.H., Jr., and Shedd, W.W., 1977. Effective rates of sponge bio-erosion as a function of carbonate production. Proc. Third Int. Coral Reef Symp., Miami, Florida, 2:500-505.

Neumann, A.C., 1966. Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, Cliona lampa. Limnol. and Oceanogr., 11:92-108.

Ott, B.S., and Lewis, J.B., 1972. The importance of the gastropod Corallio-phila abbreviata (Lamarck) and the polychaete Hermodice carunculata (Pallas) as coral reef predators. Can. J. Zool., 50(12):1651-1656.

Ott, B.S., 1975. Quantitative analysis of community pattern and structure on a coral reef bank in Barbados, West Indies. Ph.D. thesis, 185 pp., McGill University, Montreal.

Otter, G.W., 1937. Rock-destroying organisms in relation to coral reefs. British Mus. Nat. Hist., Great Barrier Reef Expdn. 1928-1929, 1(12): 323-352.

Pang, R.K., 1971. The systematics and ecology of some Jamaican boring sponges. Ph.D. thesis, 191 pp., Yale University.

Pang, R.K., 1973. The systematics of some Jamaican excavating sponges (Porifera). Postilla, 161:1-75.

Pomponi, S.A., 1976. An ultrastructural study of boring sponge cells and excavated substrata. Proc. 9th Ann. SEM Symp., Part VIII, Om Johari Ed., Chicago, Illinois:569-575.

Pomponi, S.A., 1977. Excavation of calcium carbonate substrates by boring sponges: ultrastructure and cytochemistry. Ph.D. thesis, 133 pp., Univ. of Miami.

Reiswig, H.M., 1971. In situ pumping activities of tropical Demospongiae. Mar. Biol., 9(1):38-50.

Ruetzler, K., 1971. Bredin-Archbold-Smithsonian biological survey of Dominica: Burrowing sponges, genus Siphonodictyon (Bergquist), from the Caribbean. Smithson. Contr. Zool., 77:1-37.

Ruetzler, K., and Rieger, G., 1973. Sponge burrowing: Fine structure of Cliona lampa penetrating calcareous substrata. Mar. Biol., 21: 144-162.

Ruetzler, K., 1974. The burrowing sponges of Bermuda. Smithson. Contr. Zool., 165:1-32.

Ruetzler, K., 1975. The role of burrowing sponges in bioerosion. Oecologia, 19:203-216.

Scatterday, J.W., 1974. Reefs and associated coral assemblages off Bonaire, Netherlands Antilles, and their bearing on Pleistocene and Recent reef models. Proc. Sec. Int. Coral Reef Symp., Australia, 2:85-106.

Scoffin, T.P., Stearn, C.W., Boucher, D.A., Frydl, P., Hawkins, C.M., Hunter, I.G., and MacGeachy, J.K., (in press). Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part 2 - Erosion, sediments and internal structure. Bull. Mar. Sci.

Spurr, M.R., 1975. Reef bioerosion and sediment production by excavating sponges; (Families Clionidae and Adociidae). M.Sc. thesis, 126 pp., Louisiana State University.

Stearn, C.W., Scoffin, T.P., and Martindale, W., 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part 1 - Zonation and productivity. Bull. Mar. Sci., 27(3):479-510.

Stearn, C.W. and Scoffin, T.P., 1977. Calcium carbonate budget of a fringing reef, Barbados. Proc. Third Int. Coral Reef Symp., Miami, Florida, 2:471-476.

Volz, P., 1939. Die Bohrschwamme (Clioniden) der Adria. Thalassia 3(2): 1-64.

Warburton, F.E., 1966. The behaviour of sponge larvae. Ecology, 47(4): 672-674.

Ward, P., and Risk, M.J., 1977. Boring pattern of the sponge Cliona vermifera in the coral Montastrea annularis. J. Pal., 51(3):520-526.

Warme, J.E., and McCrevey, J.A., 1974. Reef borers and reef bioerosion. 7th Caribb. Geol. Conf., Guadeloupe, French Antilles. Abstracts:18.

Warme, J.E., 1977. Carbonate borers - their role in reef ecology and preservation. In: Reefs and related carbonates - ecology and sedimentology. Amer. Assoc. Pet. Geol., Studies in Geology 4:261-279.

Wells, J.W., 1967. Scleractinia. Treatise on invertebrate palaeontology. Moore Ed., Part F: Coelenterata, pp. F328-F444.


A

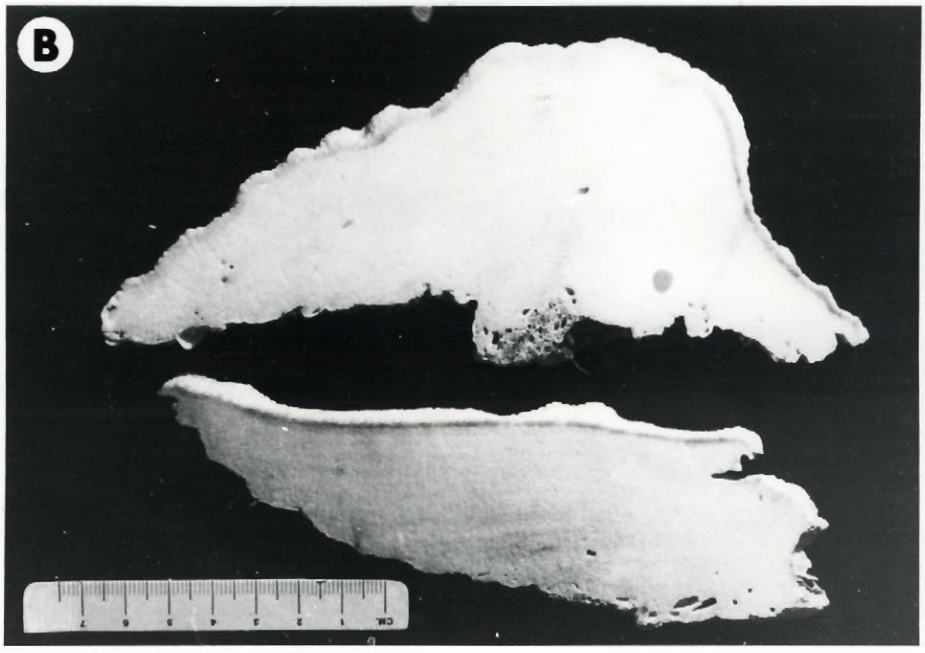

B

PLATE 1

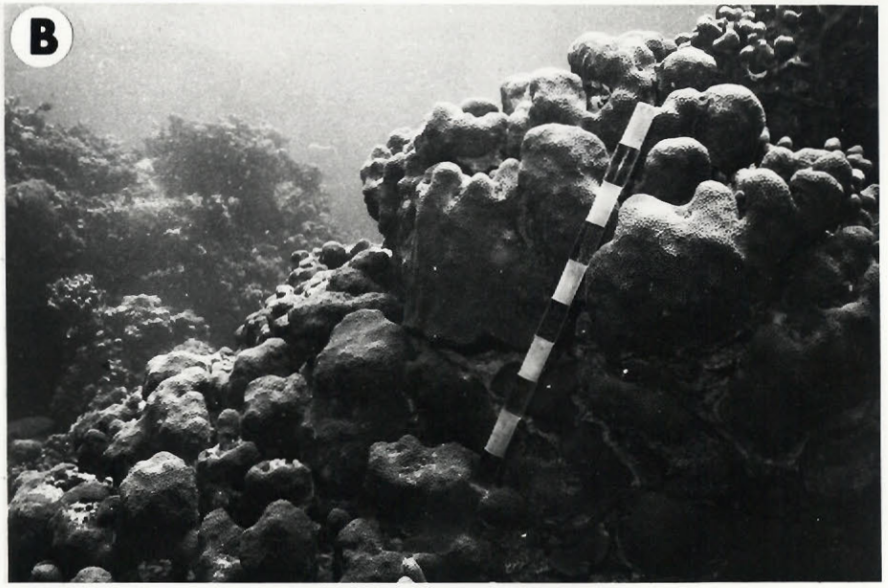
A. Aerial view of Bellairs fringing reef.

B. Multi-lobed M. annularis colony on the side of a spur in the spur and groove zone of the fringing reef. (scale = 0.5 m, depth = 4 m)

C. Mixed coral-sponge community on the bank reef crest. (mean depth - 15 m)

D. Author setting up sponge boring rate experiments on the bank reef crest. (depth = 14 m)


A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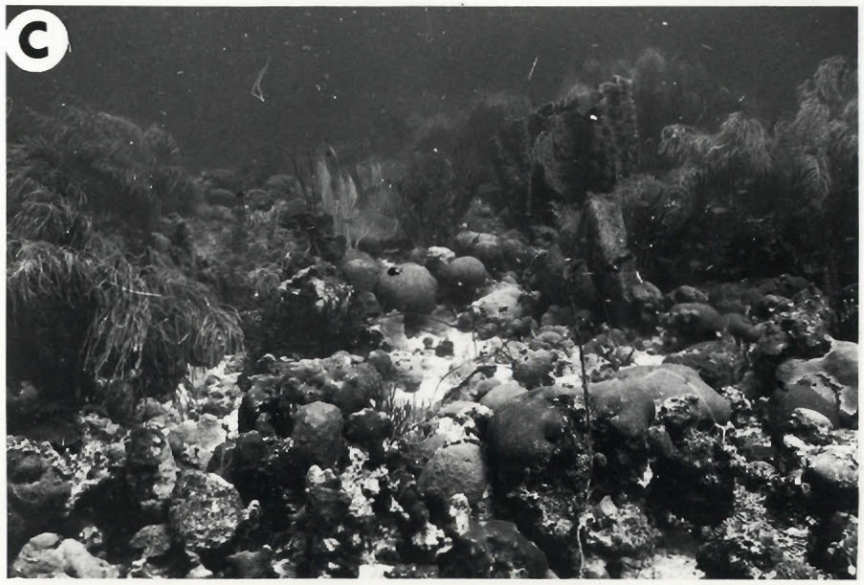

C


D

PLATE 2

X-radiograph of a M. annularis colony from a depth of 15 m on bank reef crest. Growth bands are clearly visible. Areas (a) are Siphonodictyon chambers which are connected to the substrate surface by narrow canals. Areas (b), in the marginal parts of the specimen, are Cliona chambers. (actual size)

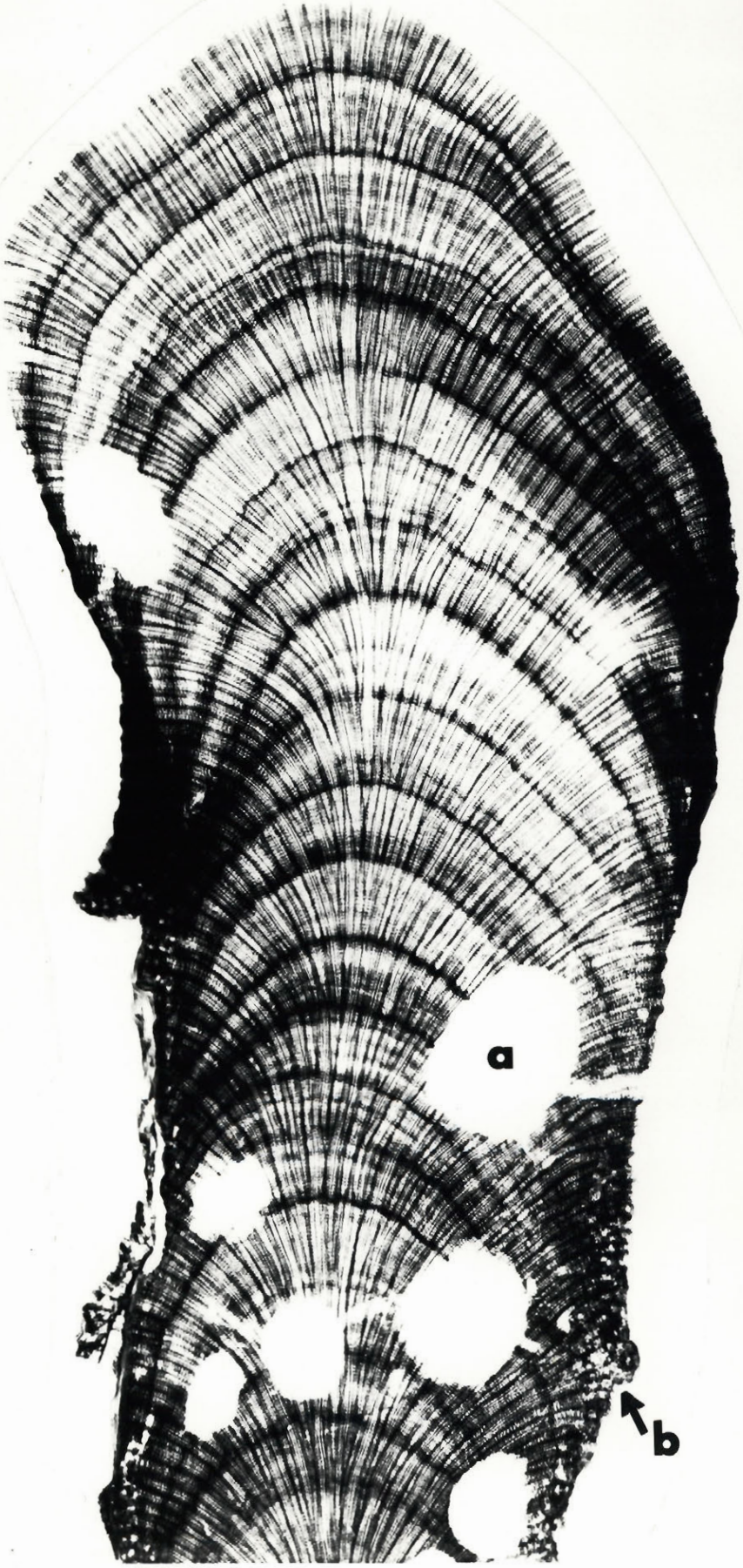

a
b

PLATE 3

X-radiograph of a M. cavernosa colony from a depth of 20 m on the bank reef. Much of the corallum is infested by the sponge Cliona. (actual size)

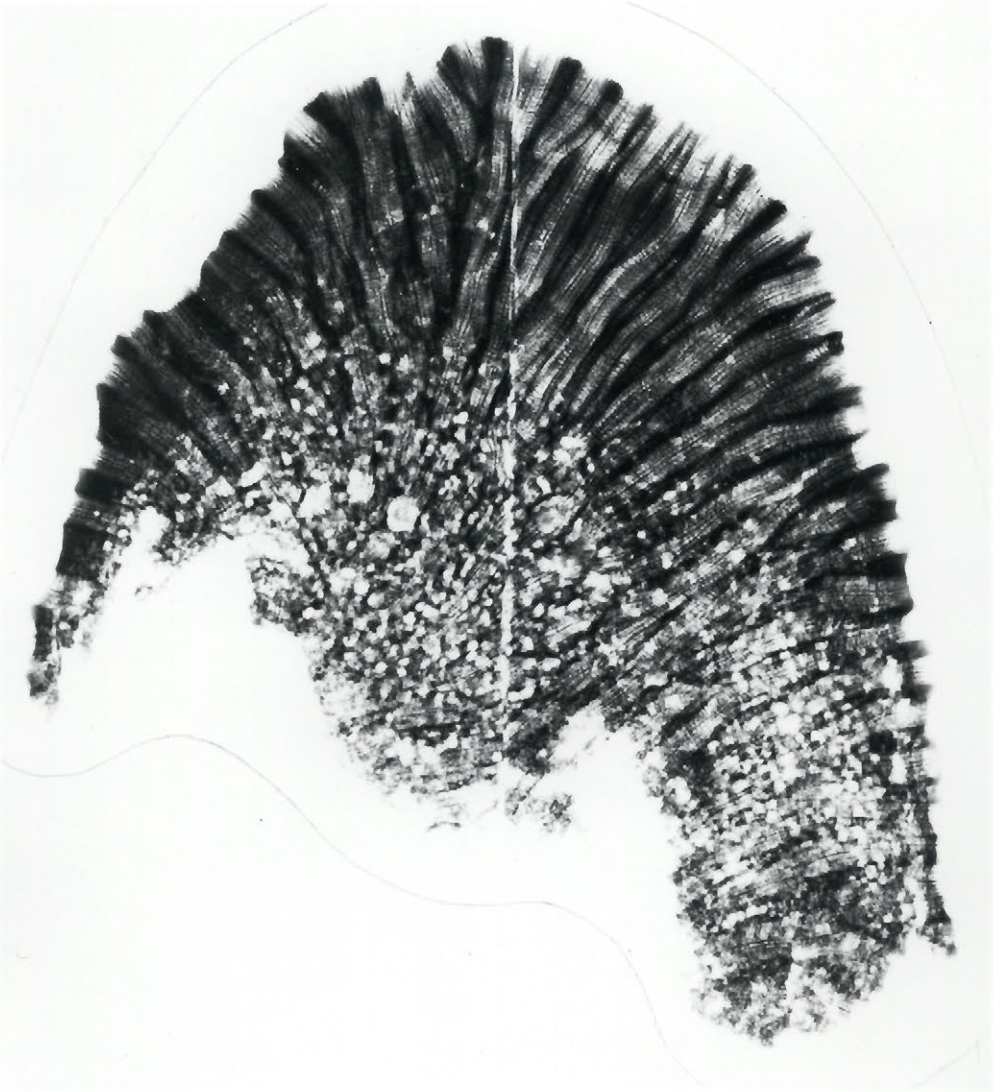
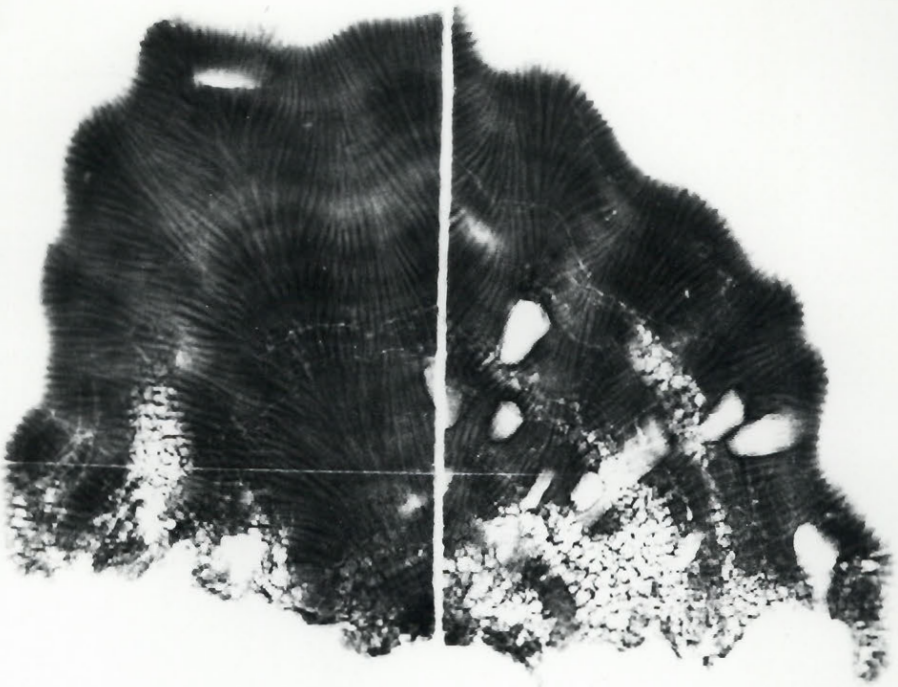


PLATE 4

A. *P. astreoides* bored by *Siphonodictyon* sp. form 2. Sponge penetration follows the trend of the growth banding. (actual size)

B. Alignment of sponge borings along the growth bands in a *S. siderea* colony. (actual size)

A



B

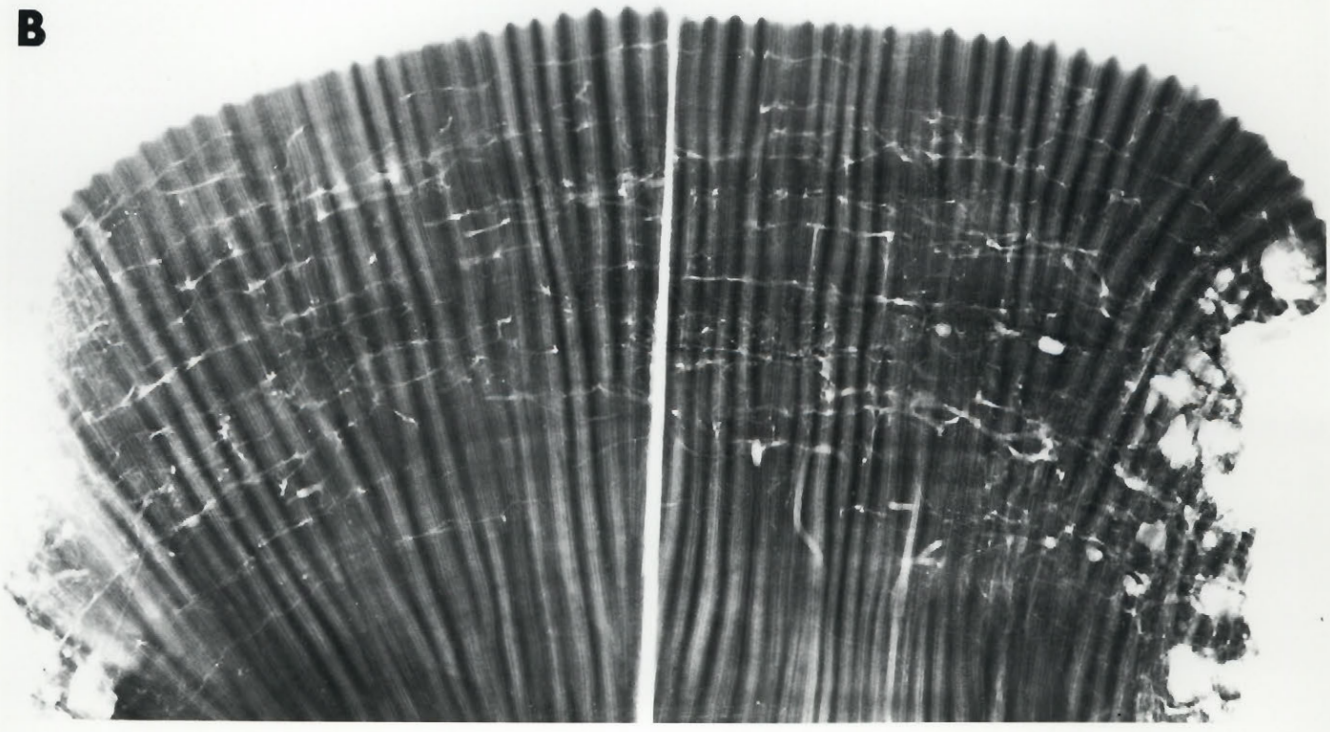


PLATE 5

A. C. caribbaea papillae on the upper side of a dead branch of A. cervicornis. (cm scale)

B. Unidentified sponge species boring in the endothecal regions in the dead base of a Dichocoenia stokesii colony. (mm scale)

C. M. annularis bored by C. caribbaea. (mm scale)

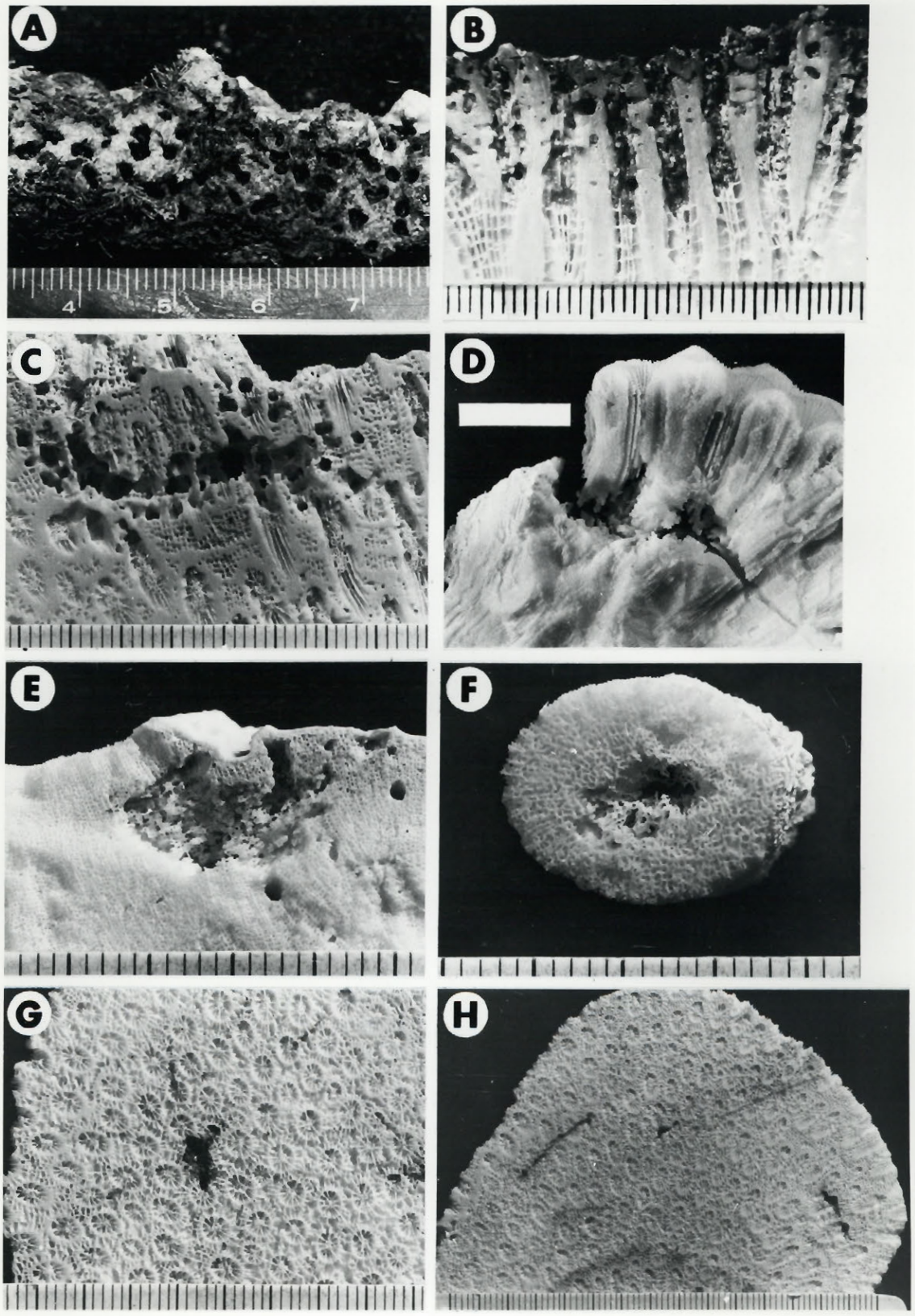
D. S. siderea bored by C. caribbaea. (bar = 1 cm)

E. P. astreoides bored by C. caribbaea. (mm scale)

F. P. porites bored by C. caribbaea. (mm scale)

G. Siphonodictyon borehole in an early stage of development in the upper part of the corallum of a M. annularis colony. Note the fine tissue strands radiating out into the coral skeleton around the borehole. (scale in mm)

H. Strands of Siphonodictyon tissue following the direction of the growth banding in a M. annularis colony. (mm scale)


A
4
5
6
7
B
C
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G
H

PLATE 6

A. *M. annularis* bored by *C. mucronata*. (mm scale)

B. *M. cavernosa* bored by *C. mucronata*. (mm scale)

C. *S. siderea* bored by *C. mucronata*. (mm scale)

D. *A. agaricites* bored by *C. mucronata*. (mm scale)

E. *M. annularis* bored by *Cliona* sp. 1. (mm scale)

F. *M. cavernosa* bored by *Cliona* sp. 1. (mm scale)

G. *S. siderea* bored by *Cliona* sp. 1. (mm scale)

H. *P. astreoides* bored by *Cliona* sp. 1. (mm scale)

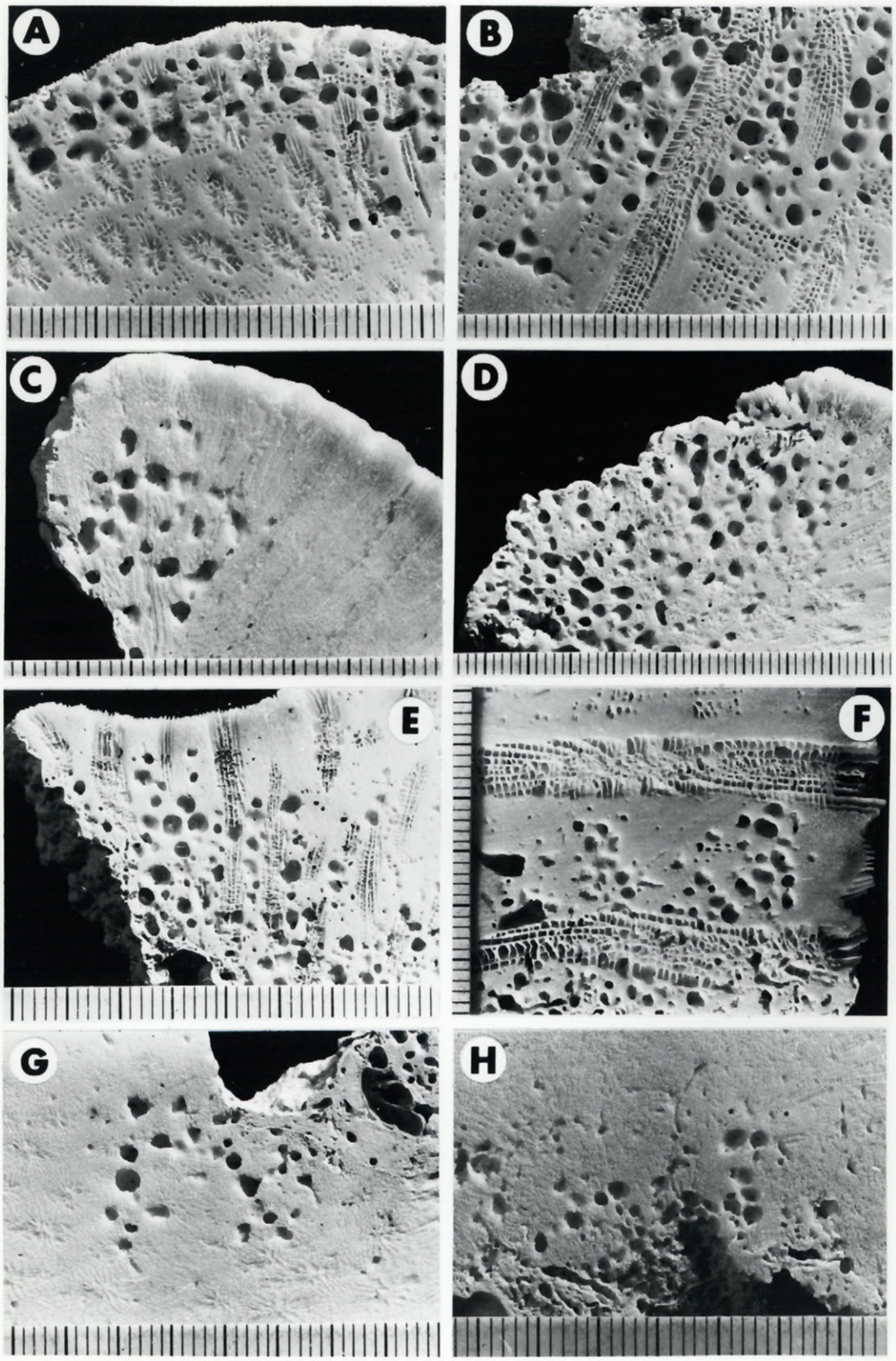
A
B
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PLATE 7

A. M. annularis bored by a network-forming Siphonodictyon species. (mm scale)

B. S. siderea bored by a network-forming Siphonodictyon species. (mm scale)

C. P. astreoides bored by a network-forming Siphonodictyon species. (mm scale)

D. M. cavernosa bored by species X. (mm scale)

E. M. annularis bored by species X. (mm scale)

F. D. labyrinthiformis bored by species X. (mm scale)

G. M. cavernosa bored by Cliona sp. 2. (mm scale)

H. M. annularis bored by Cliona sp. 2. (mm scale)

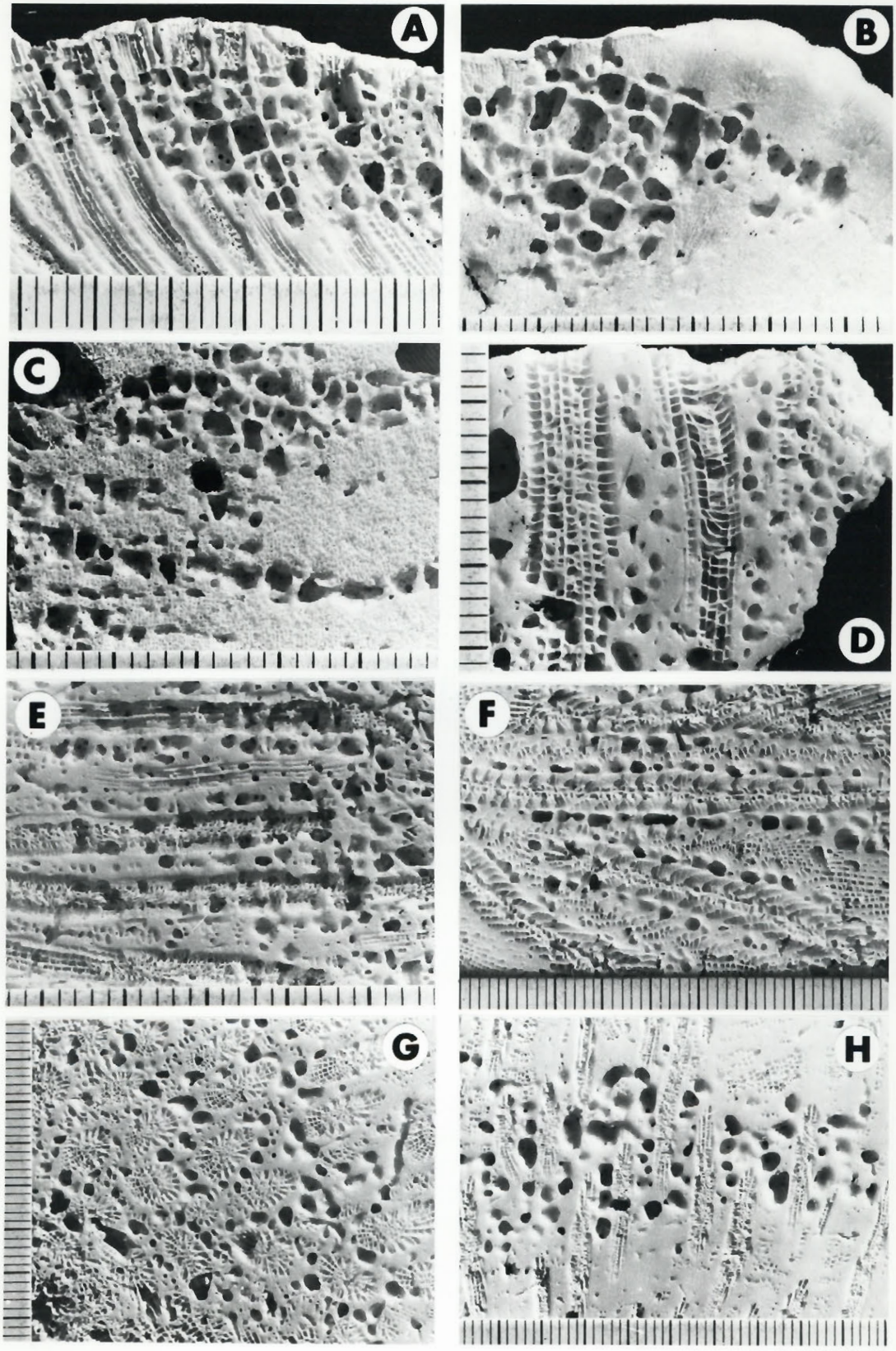

A
B
C
D
E
F
G
H

PLATE 8

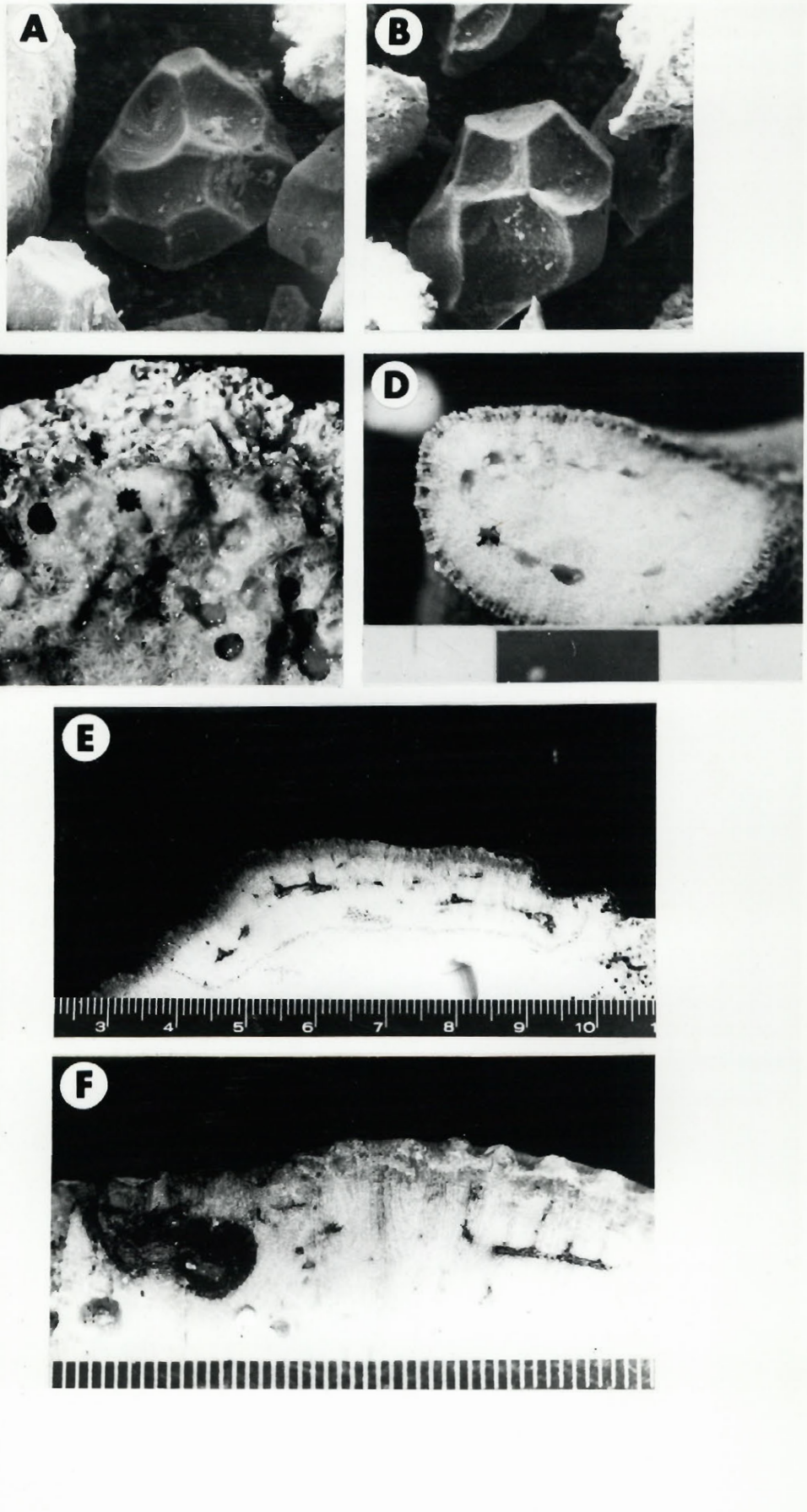
A,B. Scanning electron micrographs of chips of calcium carbonate removed by boring sponge from carbonate substrate. Chips are roughly hemispherical and have a characteristic multi-faceted appearance. (x 1000)

C. Section of the dead base of a M. annularis colony showing cross-sections of cylindrical tunnels (some filled with sponge tissue, some vacant) formed by Siphonodictyon by removal of endothecal skeletal elements. (x 2)

D. P. porites bored by Cliona sp. 1. (cm scale)

E. Tissue strands of C. caribbaea extending from boreholes in the dead base into the region beneath the live tissue-covered surface of a P. astreoides colony. (cm scale)

F. S. siderea colony bored by C. delitrix form 2. The tissue strand, which originated from the ovoid borehole beneath the dead base, has penetrated into the region beneath the live surface of the corallum. Note the fine tissue strands advancing up the corallites towards the live surface. (mm scale)


A
B
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D
E
3
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9
10
F

PLATE 9

A. Sponge boring rate experiment after 12 months. Sponge tissue from the attached block (a) has spread onto the sides of the test block (b). (½ actual size)

B. Basal surface of a test block which has been attached to C. delitrix-infested substrate for 12 months. Sponge from the attached block has bored through the test block and established oscules on the base of the test block. (actual size)

C. S. siderea test block which has been attached to C. delitrix-infested substrate for 12 months. (Sponge tissue removed by bleaching.) (mm scale)

D. Test block of S. siderea which has been attached to C. delitrix-infested substrate for 6 months. (mm scale)

E. Scanning electron micrograph of pitted surface texture of sponge bored M. annularis. Note chip which is about to be freed (lower right) and concentric microterracing within pits. (x 500)

F. Scanning electron micrograph of M. annularis skeleton in which boring is confined to exothecal areas. Thecal and endothecal areas are not removed. (x 27)

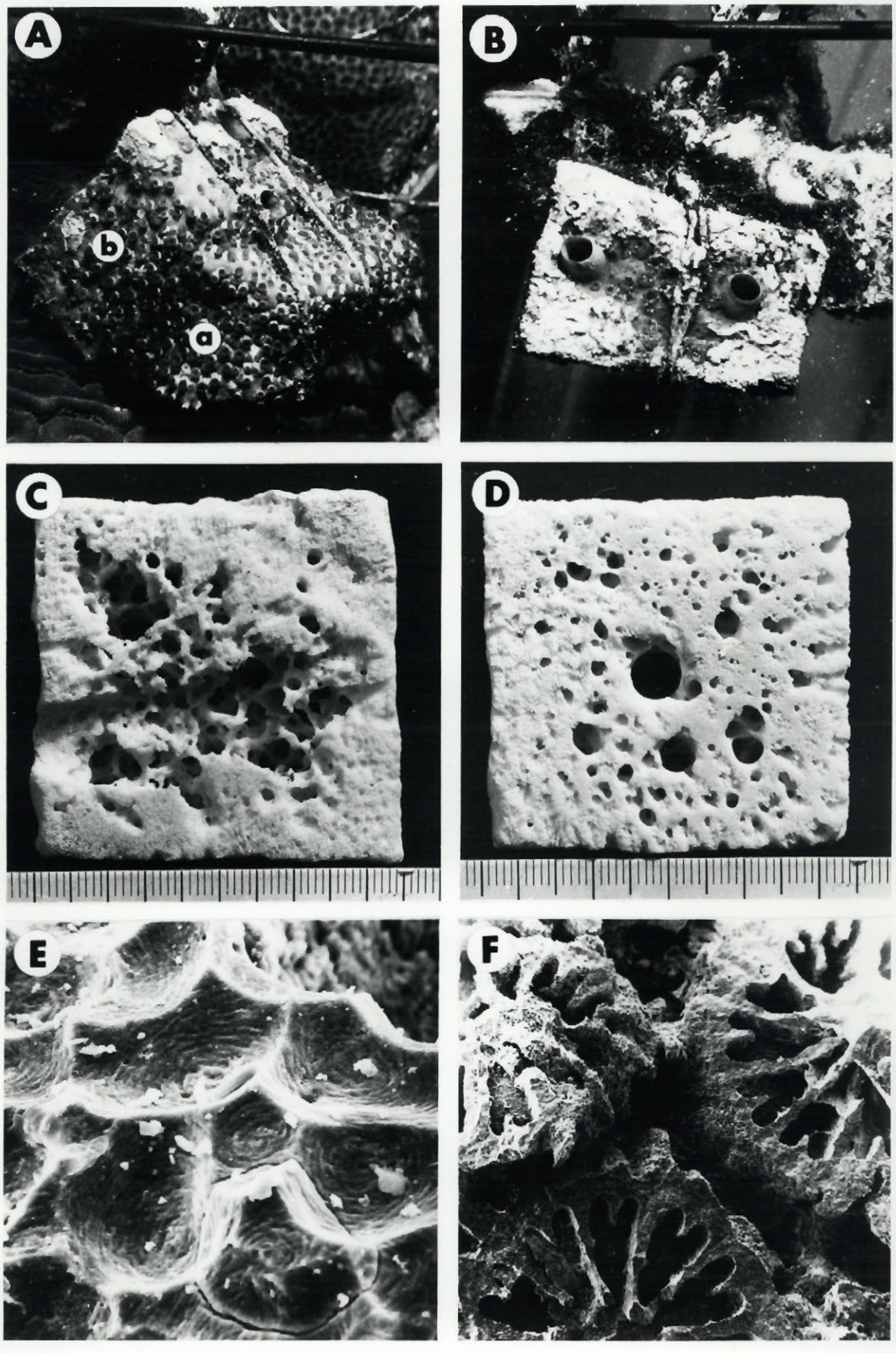
A
b
a
B
C
D
E
F

PLATE 10

A. Comparison of extensively bored (by clionid sponge) and unbored platy colonies of M. annularis from the bank sides. Encrustation on the non-living surfaces of the lower colony protected it against infestation by boring sponges.

B. Platy P. astreoides colonies, from the inner edge of the bank reef, showing very low levels of infestation by sponges.

APPENDIX A

Descriptions of Boring Sponge Species Found During Study

Foreword

Appendix A contains a description of the general systematics of the boring sponge species encountered during the study. Notes on their substrate preferences, distribution and abundance are included. The basic format used by Ruetzler (1974) is followed in this description.

Identification of sponge species was based principally on spiculation and secondarily on tissue colour and borehole morphology. Spicule terminology is given in Laubenfels (1955). Additional terminology which appears in the descriptions of clionid sponges is explained in the following discussion. Clionid sponges possess two main types of spicules: tylostyles and microscleres. Tylostyles are pin-shaped with a slender pointed 'shaft' and a prominent spheroid or ovoid 'head' or 'knob' at or near the end of the shaft. Heads are described as 'terminal' if they are located at the end of the shaft, 'subterminal' if they occur just before the end of the shaft and 'distinctly subterminal' if they occur a short distance before the end of the shaft. The 'neck' is the region just behind the head.

Spicule mounts were prepared in the following way. A small piece of tissue (choanosome) of an unidentified species was extracted from the bored substrate, placed in a pyrex test tube and boiled in concentrated nitric acid. After dissolution of all organic matter the remaining acid (containing suspended spicules) was diluted with distilled water and transferred to a centrifuge tube. The spicules were centrifuged out and the supernatant was aspirated using a suction pipette. More distilled water was added and the above procedure repeated to wash the spicules. After thorough washing the spicules were pipetted onto a microscope slide on a hot plate. When the excess water had evaporated the spicules were mounted in Canada balsam and

covered with a cover slip.

The range and mean values (in brackets) of spicule length and width, given for each species, are based on 25 measurements of both length and width for each specimen. Four specimens of each species (except Siphonodictyon specimens) were measured wherever possible. Spicule dimensions are expressed in microns and width is measured at the maximum diameter of the spicule.

The colour code (e.g. 8A8-8B8) used in describing the colour of the ectosome and choanosome of sponges is derived from charts drawn up by Kornerup and Wanscher (1967).

Order HADROMERIDA

Family CLIONIDAE

Cliona vermifera Hancock, 1867

Ectosome: The papillae of this species are conspicuous. They are bright orange-red (8A8-8B8) in colour and are roughly circular or oval. Circular papillae measure 0.5-1.5 mm (1.0 mm) in diameter. Oval papillae reach 2.0 x 1.5 mm.

Choanosome: The bright reddish-orange (7A8-7B8) to orange-red choanosome is elastic and only partly fills the chamber.

Excavations: Chambers are roughly spheroid to ovoid. They usually have an irregular, often polygonal outline (Plate A1A). Spheroid chambers measure from 1-4 mm (2 mm) in diameter. Ovoid chambers range from 1.5 x 1.0 mm to 5.0 x 3.0 mm (3.0 x 2.0 mm). Separating walls are thin and are perforated by small foramina.

Spicules: Spiculation (Plate A5A) is distinctive and consists of tylostyles and microscleres. There are two distinct size classes of tylostyles:

1) shorter tylostyles which are relatively stout and slightly curved; a few are straight. The shaft is of fairly uniform diameter and tapers to a sharp point in the last third of its length. Heads are spheroid and many are subterminal.
2) long slender tylostyles which are almost straight and taper to a sharp point in the lower half to one third of the shaft. Heads are spheroid to ovoid and typically subterminal.

Microscleres are distinctive smooth spiral rods which are of uniform diameter throughout their length and have rounded ends.

Spicule dimensions:

Type 1 tylostyles, length x width: 140-250 x 5.0-12.5 (228 x 10.4)
Type 2 tylostyles, length x width: 230-320 x 3.0-10.0 (293 x 7.5)
Spirasters, length: 37.5-55.0 (46.0)
Number of bends: 2-8 (5)

Substrates: This species is common in coral rubble. It is present in several massive coral species (A. agaricites, S. siderea, M. annularis, M. cavernosa and Diploria spp.) and in cor-algal substrate but was not found in any branching corals.

In some substrates (esp. M. annularis) chambers are usually arranged in rows producing a string-of-beads appearance.

Distribution: Cliona vermifera occurs throughout the depth range investigated but was most commonly found in very shallow or deep water. It occurs in coral rubble (often in association with C. lampa) in depths of 1 m or less in the swash zone and in platy colonies of M. annularis and P. astreoides in depths of 20-40 m on the sloping sides of the bank reef.

Remarks: This species is similarly distributed on the reefs of Discovery Bay, Jamaica (Pang, 1973). It occurs mainly between 1-2 m and 18-52 m and was not found at intermediate depths.

C. vermifera is widely distributed geographically (Pang, 1973). It occurs in the tropical Atlantic, Mediterranean, Adriatic and Indo-Pacific. It was first reported in the West Indies from Jamaica by Hechtel (1965).

Cliona ensifera Sollas, 1878

Ectosome: Yellow papillae protrude from the substrate surface. They are roughly circular, 0.5-1.5 mm (1.0 mm) in diameter, and occur in clusters of 4 or 5. No papillar fusion was observed.

Choanosome: Chambers are usually completely filled with brownish-yellow (5C8) choanosome (Plate A1B).

Excavations: Chambers are ovoid (long axis parallel to substrate surface) and range in size from 6 x 4 mm to 16 x 7 mm (10 x 6 mm). They are connected to the substrate surface by narrow cylindrical papillary canals, 1 to 5 mm long. The diameters of the circular papillary perforations and papillary canals correspond to those of the papillae. Four or 5 canals serve each chamber. Chambers may occur in groups of 2 or 3. Adjacent chambers usually are not connected.

Spicules: Tylostyles (Plate A5B) are relatively short and slightly curved. Some are distinctly bent in the upper third of the shaft. They are of fairly uniform length but show a wide range of widths. They flare (increase in diameter) gradually from the neck region and reach their maximum diameter in the lower half of the shaft. They taper to a sharp point in the last quarter of the shaft.

Heads (Plate A5C) are spheroid or ovoid and many have a distinctive droplet shape. Many (especially on the thinner tylostyles) are subterminal and a few are distinctly subterminal.

Malformed tylostyles are quite common. Sharply bent tylostyles, which appear to have broken then fused, occur. A few double shafted spicules with a common head are present. In some spicules secondary annular swellings occur behind the head. Some of these swellings form a short distance down the shaft from the neck region and produce a second knob. Several tylostyles are shorter than normal and terminate in a rounded end.

Microscleres (Plate A5C) are spiney spirasters of which there are two types:

1) relatively few short stout spirasters which are straight or slightly curved and bear prominent spines which are distributed irregularly along the shaft.
2) more numerous longer, delicate spirasters which have a thinner, more spiralled shaft from which short spines protrude.

Spicule dimensions:

Tylostyles, length x width: 180-260 x 2.5-13.5 (223 x 8.8)
Type 1 spirasters, length: 15.0-22.5 (18.0)
number of turns: 1-3 (1)
number of spines: 8-13 (11)
Type 2 spirasters, length: 17.5-40.0 (27.0)
number of turns: 1-5 (3)
number of spines: 9-23 (15)

Substrates: C. ensifera occurs in several massive coral species (M. annularis, S. siderea, P. astreoides, C. natans, A. lamarcki) and is most abundant in S. siderea. It is also common in P. porites and in cor-algal reef rock.

Distribution: C. ensifera occurs throughout the depth range 1-33 m but is most abundant in depths of 1-6 m on the fringing reef.

Remarks: This is the first record of this species in the western Atlantic region.

Cliona mucronata Sollas, 1878

Ectosome: The papillae are reddish-orange (7A8-7B8) and circular and measure 0.5-1.0 mm (0.8 mm) in diameter. They are level with the substrate surface, closely spaced and show little tendency to fuse (Plate A1C).

Choanosome: The choanosome is orange (5B8, 6B8) and completely fills the small chambers. The colour of the choanosome changes to light yellow (4A5) or lighter orange (5A7) in specimens from depths greater than 20 m on the bank sides.

Excavations: A honeycomb network of small chambers is produced by this sponge (Plate 6A-D). Chambers are spheroid to ovoid and measure 1.0-2.5 mm (1.5 mm) in diameter. Adjacent chambers communicate through small foramina. Chambers start approximately 1 mm beneath the substrate surface and extend up to 30 mm into the substrate.

Spicules: Two types of tylostyle (Plates A5D, A5E) are present:

1) short tylostyles which have a distinctive sword shape. The majority are slightly curved although a few are straight. The diameter gradually increases from the neck region to the end of the shaft which is mucronate. Heads are spheroid and many are subterminal. Some are distinctly subterminal and bear a swelling some distance from the top of the shaft. Some heads tend to be ovoid with their long axis normal to the shaft axis.
2) longer more slender tylostyles which are less numerous than the first type also occur. The majority are slightly curved although a few are straight. They taper to a point in the last third of the shaft. Heads are mostly ovoid and somewhat elongate (long axis parallel to shaft axis) and many are not well developed. Most are subterminal

and many are asymmetrical. Some subtylostyles and styles are present.

No microscleres are present.

Spicule dimensions:

Type 1 tylostyles, length x width: 80-155 x 5.0-12.5 (109 x 8.5)
Type 2 tylostyles, length x width: 130-200 x 3.0-6.0 (169 x 4.5)

Substrates: This sponge is a common inhabitant of all of the massive coral species. It is relatively rare in cor-algal substrate, very rare in branching corals (only recorded once in P. porites) and is absent from coral rubble.

Distribution: C. mucronata occurs throughout the depth range from 1-33 m.

Remarks: This species has not been previously recorded from the western Atlantic region.

Cliona schmidti (Ridley), 1881

Ectosome: Numerous conspicuous purple (15A8) ostial and oscular papillae are scattered over the substrate surface. They are roughly circular and measure 0.5-1.8 mm (1.0 mm) in diameter.

Choanosome: The chambers are partly filled with purple (15A8) choanosome. The tissue dries to a bright purple colour.

Excavations: Chambers are basically spheroid to ovoid and are rather irregular and ragged in outline since the separating walls are often partly removed (Plate A1D). Separating walls are thin and are perforated by foramina. Papillary canals are 1.0 to 3.5 mm in length and correspond in diameters to those of the papillae. Chamber formation extends as far as 10 mm into the substrate. Tissue strands, along which new chamber formation is evident, radiate out into the substrate from the chambers.

Spicules: Tylostyles (Plate A5F) are long and slender and are straight or slightly curved in the lower half of the shaft. Most are of uniform diameter in the upper half of the shaft and taper to a sharp point in the lower half. Some attain a maximum diameter, which is only marginally greater than the

diameter in the neck region, in the mid-region of the shaft. Heads are spheroid or ovoid (elongate) with the long axis parallel to the shaft axis. Some are subterminal and others possess annular swellings in the neck region just behind the head.

The microscleres (Plate A5F) are highly distinctive. There are two main types:

1) prominent short stout, curved or straight spirasters which are covered by thick thorn-like spines.
2) more numerous spirasters which are longer, thinner and more spiralled. Some are almost straight or slightly curved, others are partly straight and partly curved. They bear small spines which protrude from the outer edge of the spirals and appear themselves to be spirally arranged.

Spicule dimensions:

Tylostyles, length x width: 220-305 x 3-7 (270 x 5)
Type 1 spirasters, length x width: 25.0-42.5 x 5.0-10.0 (32.5 x 6.5)
number of bends: 0-2 (0)
number of spines: 13-26 (22.5)
Type 2 spirasters, length x width: 35.0-50.0 x 1.0-7.0 (43.5 x 2.5)
number of bends: 0-8 (5)
number of spines: 23-37 (30)

Substrates: This sponge occurred in several massive coral species (M. annularis, S. siderea, P. astreoides and A. agaricites) but was not found in coral rubble or in cor-algal reef rock.

Distribution: This sponge is one of the rarer clionid species. Seven specimens were found during the course of the study. Three were from the fringing reef, two from the bank top and two from the bank sides. The depth range of the species is 3-32 m.

Remarks: This species is conspicuous and easily recognized due to the distinctive colour of its endosome and ectosome and characteristic spiculation.

C. schmidti has been reported frequently from shallow waters in the Adriatic and Mediterranean seas (Pang, 1973). The first record of its

occurrence in the West Indies (Jamaica) was made by Pang (1971). In Jamaica it occurs in deeper waters (15-47 m) than in Barbados.

Cliona caribbaea Carter, 1882

Ectosome: The papillae (Plate A1E) are greyish-brown (5F3), roughly circular or oval and measure 0.5-3.0 mm (1.5 mm) in diameter. They are closely spaced and commonly fused.

Choanosome: The choanosome is yellow (4A6-4A7) and partly fills the irregular shaped cavities (Plate A1F). Tissue strands extend vertically and horizontally into the adjacent substrate and initiate new chamber development.

Excavations: Chambers are not well-defined. They are usually irregular in shape and ragged in outline. Chambers occupy an elongate (up to 60 mm long) subsurface layer which starts 1 to 3 mm beneath the substrate surface and reaches depths of as much as 16 mm. Papillary canals are cylindrical and flare towards the cavities. They open in papillary perforations which are the same size and shape as the papillae.

Spicules: Tylostyles (Plate A5G) are long. Most are slightly curved (bend in lower half of shaft) although some are straight. They attain their maximum diameter in the mid-region of the shaft and taper to a sharp point in the last third. Heads (Plate A5H) are spheroid or ovoid (long axis normal to the spicule axis) and are always terminal.

Spirasters (Plate A5H) are delicate with a slender spiralled shaft from which small (up to 2 microns long) spirally arranged spines protrude.

Spicule dimensions:

Tylostyles, length x width:	300-490 x 5.0-13.5 (391 x 9.0)
Spirasters, length x width:	12.5-37.5 x 0.5-1.5 (27.3 x 1.0)
number of bends:	2-9 (6)

Substrates: C. caribbaea occurs commonly in all of the substrate types except coral rubble from the swash zone. It is particularly common in A. cervicornis.

Chamber definition is good in dense corals such as S. siderea and is poor in porous corals such as P. porites.

Distribution: C. caribbaea is the most abundant clionid sponge on Barbados reefs. It occurs commonly throughout the 1-20 m depth range and is especially abundant on the fringing reef where extensive papillar fields are conspicuous on exposed reef surfaces encrusted by coralline algae. Its preference for exposed surfaces is demonstrated by the occurrence of papillae only on the upper surface of A. cervicornis branches. The abundance of C. caribbaea decreases in depths greater than 20 m. Its preference for well-lit areas is due to the presence in its tissues of zooxanthellae.

Remarks: In Curaçao more extensive infestation by C. caribbaea was observed. The surface of many massive coral colonies was partly or completely covered by a layer of sponge ectosome. The layer was not continuous since papillar fusion was never complete. This degree of infestation was not observed in Barbados.

The presence of C. caribbaea papillae near the periphery of the living coral surface usually leads to recession of the adjacent coral tissue. This suggests that the presence of the sponge causes the death of the coral tissue in its immediate vicinity.

C. caribbaea has been previously reported from several areas in the West Indies (see Pang, 1973: p. 24).

Cliona ?rovignensis Volz, 1939

Ectosome: The papillae are pale yellow, roughly circular and measure 0.5-1.5 mm (1.0 mm) in diameter.

Choanosome: The choanosome completely fills the cavities. It is greyish to olive yellow (3B6-3C6) in colour and is soft and mucous.

Excavations: This species forms single roughly ovoid cavities (Plate A1G) which measure 5 x 3 mm to 8 x 7 mm (7 x 4 mm). They are irregular in outline. Papillary perforations which correspond in diameters to those of the papillae connect with the cavities by cylindrical canals which are 1.5 to 3.0 mm long.

Spicules: Spiculation (Plate A6A) comprises:

1) few scattered tylostyles,
2) oxea (two types).

Tylostyles are long and curved. They reach their maximum diameter in the mid-region of the shaft and then taper gradually to a point. Heads are spheroid.

Type 1 oxea are abundant. Most are curved and a few are sharply bent in the mid-region of the shaft, some are almost straight. They are abruptly pointed and many are mucronate.

Type 2 oxea are shorter and less numerous. They are similar in curvature to the longer oxea but are less abruptly pointed.

Spicule dimensions:

Tylostyles, length: 175-350 x 3-10 (294 x 6)
Type 1 oxea, length: 75-105 x 2-5 (90 x 4)
Type 2 oxea, length: 35-45 x 2.5-4.0 (40 x 3.0)

Substrates: C. ?rovignensis occurs in most of the massive corals which were sampled on the bank reef and fringing reef. It was found very rarely in coralgal substrate and branching corals (only in A. cervicornis) and was absent from coral rubble from the swash zone.

Distribution: The sponge occurs on both the fringing reef and bank reef and is most common in corals below 20 m on the bank sides.

Remarks: The colour of the choanosome in specimens from the fringing reef and bank top is olive yellow. The colour changes to greyish-yellow in specimens from the bank sides.

C. rovignensis was first described by Volz (1939) from the Adriatic. This is the first record of its occurrence in the western Atlantic region.

Cliona lampa Laubenfels, 1950

Ectosome: The papillae (Plate A2A) are small and inconspicuous and do not protrude above the substrate surface. They are vivid red (9A8), circular and 0.2-0.8 mm (0.5 mm) in diameter. Papillar fusion was not observed.

Choanosome: The choanosome is reddish-orange to brownish-orange (7A8-7C8) and completely fills the chambers. Choanosome may also infiltrate natural pore space.

Excavations: 1) C. lampa commonly forms a honeycomb network consisting of small roughly spherical chambers 0.5-1.5 mm (1.0 mm) in diameter (Plate A1H). Individual chambers are closely spaced and communicate through numerous small foramina. Chamber formation starts almost directly beneath the substrate surface and extends to depths of up to 25 mm. The honeycomb network of chambers is usually spheroid in shape.

2) C. lampa also forms more discrete spheroid to ovoid chambers which are larger than those described above (Plate A2B). Spheroid chambers measure from 1.5 to 3 mm in diameter and ovoid chambers measure up to 4 x 2.5 mm. Chambers are connected to the substrate surface by 2-3 mm long, narrow papillary canals which flare slightly towards the chamber. Adjacent chambers are not connected and no honeycomb pattern is developed.

This type of boring pattern is less common than the one described above.

Spicules: Spiculation (Plate A6B) is very distinctive. There are three types:

1) tylostyles
2) spiney oxea
3) spiney microrhabds

Tylostyles are less abundant than the other two types of spicule.

The tylostyles are of moderate length, straight and thin and taper gradually to a sharp point. Heads are small, spheroid or ovoid (long axis parallel to shaft axis) and are always terminal.

Oxea are curved (bend in mid-shaft) or straight and are densely covered by small spines except in the central region of the shaft where more prominent spines occur.

Microrhabds are straight and bear prominent spines.

Spicule dimensions:

Tylostyle, length x width: 230-330 x 3-6 (287 x 5)
Oxea, length x width: 80-115 x 2.5-6.0 (95 x 4.0)
Microrhabds, length x width: 12.5-18.5 x 2.0-3.0 (15.5 x 2.2)

Substrates: This species was found in all of the massive corals except C. natans and in all of the branching corals sampled. It is most abundant in coral rubble from the swash zone and in cor-algal substrate.

Distribution: C. lampa is most common in shallow subtidal areas up to 1 m in depth. It is widespread in coral rubble in the swash zone. It was also recorded frequently in corals from 25-33 m on the sides of the bank reef but was rarely found in intermediate depths.

Papillae are usually located on basal and shaded marginal surfaces. They occur locally on exposed surfaces.

Remarks: Ruetzler (1974) has described three distinct morphological forms of C. lampa from Bermuda. These forms are C. lampa forma lampa, forma occulta and forma flavida. Of the two forms which occur in Barbados the more common one (type 1 borehole) is considered to be occulta since it closely resembles this form. The rarer form (type 2 borehole) does not correspond to any of Ruetzler's three forms and is considered to be a new form (form 4).

The encrusting form C. lampa forma lampa was not observed in Barbados but was noted in Carriacou and Curaçao. This form is conspicuous since the ectosome forms a continuous layer of fine tissue over the substrate surface.

Cliona delitrix Pang, 1971

Two distinct morphological forms of this sponge occur on Barbados reefs. The first and more conspicuous variety is the encrusting form which was first described, from Jamaica, by Pang (1971). The sponge ectosome overgrows the live surface of coral colonies and forms a continuous layer of bright reddish-orange tissue which, except in early stages of sponge growth (Crocker, 1977), is inhabited by numerous small white symbiotic zoanthids, Parazoanthus parasiticus (Duchassaing and Michelotti). Boring extends into the upper surface of coral colonies beneath the overgrowth. The second form is similar to the early stages of the encrusting form but shows no tendency to overgrow the substrate. It occurs mainly in shallower water and bores into the dead base of most massive coral species and some branching species. Discrete ostial and oscular papillae are established on the substrate surface.

Cliona delitrix form 1

Ectosome: The reddish-orange (7B8) ectosomal tissue partly or completely overgrows the living surface of massive coral colonies. The encrustations which begin as small circular or oval patches formed by fusion of individual

papillae (Plate A3A) can enlarge until the entire live surface is almost completely or completely covered (Plate A3B). Many large partly overgrown colonies and several smaller completely overgrown colonies were observed in the bank reef study area. Large prominent oscules with diameters of up to 8 mm and raised rims are scattered over the surface of these colonies (Plate A3C). Ostial papillae cover the entire surface between the oscules. Only in early stages can individual ostial papillae be discerned. Numerous small white zoanthids are dotted over the surface of the sponge.

Choanosome: The choanosome is brownish-orange (7C8) and completely fills the chambers.

Excavations: Removal of sponge tissue from the bored substrate using sodium hypochloride shows that the sponge boring has removed much of the original coral skeleton leaving a delicate 'lacy' network of remnant coral (Plate A3D). Chambers are long (3-23 mm) and cylindrical (2.5-5.0 mm in diameter) and are oriented parallel to the direction of the coral structure. They show a preference for the endothecal regions of corallites and apparently develop by removal of endothecal dissepiments and septa. The separating walls between adjacent chambers are perforated by circular foramina 0.5-1.0 mm in diameter. The lacy appearance results from the partial removal of many of the separating walls between adjacent chambers. Chamber formation begins directly beneath the surface of the corallum and extends downward as far as 50 mm into the coral skeleton. Large holes, 2.5-6.0 mm in diameter, which are present in the corallum surface represent the site of former oscules. These lead into tunnels (exhalent canals), 4-7 mm in diameter, which cut through the bored network.

Spicules: Tylostyles (Plate A6C) are long. Most are slightly curved (bend is one quarter way down shaft from head) and a few are straight. They show a wide range of diameters but the majority are fairly stout. The maximum diameter is reached at the bend in the shaft and is maintained until the beginning of the last quarter of the shaft where they start to taper to a sharp point. Heads are not well developed. Most are spheroid or ovoid and many are elongate. Some are rudimentary and a few styles are present. Most heads are subterminal and some are distinctly subterminal. Some are asymmetric, others malformed and some possess annular swellings in the neck

region. The tip of the shaft of some spicules is rounded. Spirasters are absent.

Spicule dimensions:

Tylostyle length x width: 280-425 x 3.0-16.5 (353 x 9.8)

Substrates and Distribution: This form was found on the bank reef between 12.7 and 40 m. Its percentage abundance in different coral substrates was determined in a 10 m wide transect across the top of the bank reef. The coral substrates in which it occurs and the percentage of occurrences in each substrate are as follows: S. siderea (51%), M. cavernosa (30%), M. annularis (8%), D. labyrinthiformis (5%), P. astreoides (3%), D. strigosa (1%), C. natans (1%) and Meandrina meandrites (1%).

Cliona delitrix form 2

Ectosome: The papillae are conspicuous and protrude above the substrate surface. They are a bright reddish-orange (7B8) colour and are mostly circular or locally oval in shape. They occur commonly in clusters of up to 4 or 5 and are closely spaced (2-5 mm apart). Diameters of circular papillae range from 1.5 to 5.0 mm (2.0 mm) and of oval papillae from 3 x 2 mm to 5 x 4 mm (4 x 3 mm). Ostial papillae are mound-shaped and oscular papillae cone-shaped. Papillar fusion was not commonly observed.

Choanosome: Breaking up the substrate exposes chambers which are completely filled with soft brownish-orange (7C8) choanosome (Plate A2C).

Excavations: Chambers are single and usually ovoid with the long axis parallel to the substrate surface. They measure from 6 x 4 mm to 25 x 22 mm (13 x 8 mm). Each is connected to the substrate surface by 3 to 5 papillary canals, 2 to 6 mm in length. The canals commonly flare towards the chamber and many are perpendicular to the substrate surface. They also contain choanosomal tissue.

Spicules: same as for form 1.

Substrates: On the fringing reef this form was observed in M. annularis, S. siderea and P. astreoides but not in A. agaricites. It was commonly found in

P. porites and M. mirabilis but was not found in A. cervicornis. It was common in cor-algal substrate blocks sampled from the fringing reef but was absent from coral rubble from the swash zone. It was not commonly observed in massive corals from the bank reef.

Distribution: This form is most common in depths of 2-8 m in the shallower fringing reef environment but also occurs on the bank reef. Papillae are found mainly on basal and shaded marginal surfaces but are also found on exposed upper surfaces.

Cliona amplicavata Ruetzler, 1974

Ectosome: The papillae are yellow, circular and measure 1.0-2.0 mm (1.5 mm) in diameter. They protrude slightly above the substrate surface and show no tendency to fuse.

Choanosome: The yellow (4A8-4B8) choanosome is soft and mucous and completely fills the chambers.

Excavations: The chambers are basically ovoid and measure 7 x 4 mm to 16 x 5 (10 x 4 mm). The long axis is always parallel to the substrate surface. Adjacent chambers are locally confluent. Papillary canals are 1-4 mm long and commonly flare towards the chamber.

Spicules: The spiculation (Plate A6D) of this species is distinctive and comprises three main categories:

1) stout tylostyles with subterminal heads
2) shorter styles - subtylostyles
3) rhaphides

The long stout tylostyles are curved (bend is usually one third way down shaft from head) and taper gradually to a point in the last half or third of the shaft. The maximum diameter is reached in the middle section of the shaft and is approximately double the diameter of the neck. Heads are spheroid and subterminal. Under low power transmitted light a black dot is visible in the centre of the heads. A secondary swelling produces a second knob a short distance down the shaft from the head in some spicules.

Some styles and subtylostyles which are slightly curved and shorter than the tylostyles also occur. The subtylostyles have a slightly developed head which is small and subterminal.

Rhaphides appear in transmitted light as fine slightly curved lines. These are easily overlooked at low magnifications.

Spicule dimensions:

Tylostyles, length: 260-335 x 3-13 (303 x 9)
Styles, subtylostyles, length: 175-225 x 3.5-5.0 (195 x 4.5)

Substrates and Distribution: C. amplicavata was not found in the bank reef environment. It is very rare in massive corals from the fringing reef (2 occurrences in S. siderea) but occurs frequently in P. porites. Specimens were also found in cor-algal substrate and in coral rubble from the swash zone.

Remarks: C. amplicavata has not been previously described from the West Indies. It was first described, from Bermuda, by Ruetzler (1974).

As pointed out by Ruetzler (1974) C. amplicavata and C. flavifodina can be confused in the field since they are of similar colour. The more regularly ovoid chambers and soft mucous consistency of tissue of C. amplicavata distinguish it from C. flavifodina. In P. porites where both species form cylindrical boreholes in the axial parts of branches distinction can be based on tissue consistency.

Cliona flavifodina Ruetzler, 1974

Ectosome: The papillae are yellow (4B8), roughly circular and measure 1.0-4.0 mm (2.5 mm) in diameter.

Choanosome: The irregular cavities are filled with dark yellow (4B8-4C8) choanosome (Plate A2D). The tissue is tough and tends to cling to the walls of the borehole.

Excavations: This sponge forms large irregular cavities beneath the substrate surface. Flaring papillary canals 2-6 mm long lead into the cavities. The length and height of cavities range from 6 x 4 mm to 26 x 16 mm

(14 x 8 mm). Cavity outlines are usually polygonal (Plate A2D). Tapering tunnels, filled with choanosome, radiate out into the adjacent substrate around the cavities.

Spicules: This species possesses tylostyles and microscleres (Plate A6E).

Some of the tylostyles are straight but most are bent a short distance down the shaft from the neck. They attain their maximum diameter in the central part of the shaft and taper gradually to a point in the lower half. Heads are large and terminal and exhibit a wide range of shape. Some are spheroid, others ovoid (often elongate) and several are droplet-shaped. Some are malformed and others have annular swellings in the neck region. The characteristic violin-shaped heads (produced by secondary swellings), noted by Ruetzler (1974), were observed in Barbados specimens.

The microscleres (Plate A6F) are numerous. Although some are straight the majority are spiral. Prominent sharp spines (up to 5 microns in length) are spirally arranged along the shaft and protrude from both ends. Up to 5 terminal spines, some of which bifurcate, are present.

Spicule dimensions:

Tylostyles,	length x width:	195-385 x 3.5-14.0 (325 x 9.0)
Spirasters,	length x width:	12.5-37.5 x 1.0-2.0 (26.5 x 1.5)
	number of bends:	1-5 (3)
	number of spines:	11-20 (17)

Substrates and Distribution: C. flavifodina is rare. It is most commonly found in cor-algal substrate on the fringing reef. It does not occur in the swash zone or in branching corals and was rarely found in massive corals on the fringing reef (recorded once in P. astreoides and once in A. agaricites). Only one specimen was recorded, in a M. cavernosa colony, on the bank top. A specimen was also found in P. porites rubble from a depth of 15 m in an A. cervicornis stand to the north-east of the study area. Cavities formed in P. porites branches are cylindrical and occupy the central axis of the branch.

Remarks: This is the first record of C. flavifodina from the West Indies. It was first described, from Bermuda, by Ruetzler (1974).

Cliona paucispina Ruetzler, 1974

Ectosome: Ectosomal tissue is olive brown (4F7-4F8) and forms irregular shaped encrusting patches in the substrate surface. Small oscules which are surrounded by lighter coloured tissue are scattered over the surface of the encrustation. The tissue turns greyish-brown in alcohol.

Choanosome: The light brown choanosome fills irregular spaces or crevices in the substrate surface.

Excavations: This species has limited excavating ability. Its boring activity is limited to the surface of the encrusted substrate. Pre-existing spaces and irregularities in this surface are enlarged but no new cavities are produced.

Spicules: Tylostyles (Plate A6G) are long and slender. The majority are bent in the upper part of the shaft shortly behind the head. Some are straight. Their maximum diameter is reached at or just below the mid-region and they taper to a point in the last third or fourth of the shaft. Heads are not well developed. Most are narrow and elongate and many are subterminal. Malformed and asymmetric heads are common. A few styles are present.

Delicate spirasters, with a thin, usually spiral (some are straight or irregularly bent) shaft which has spines distributed along its length and at each end, occur. The size of the spines varies. Some bear small (up to 1.5 microns) spines, others bear longer (up to 3 microns) more prominent spines.

Spicule dimensions:

Tylostyles, length x width: 170-410 x 5.0-12.5 (332 x 9.0)
Spirasters, length x width: 10-35 x 0.5-2.0 (23 x 1.3)
number of bends: 1-5 (3)
number of spines: 10-27 (18)

Distribution: This species was recorded on the underside of a flat piece of coral rubble in the shallow subtidal zone at Graves End on the south coast of Barbados, in P. porites rubble in shallow sea grass beds at Bath on the east coast and in cor-algal reef rock on a fringing reef north of the Bellairs reef. No specimens were observed in the study area. In all 3 areas the sponge appeared to be an encrusting form. It was only on close examination

that the boring habit became evident.

Remarks: C. paucispina was first described from Bermuda by Ruetzler (1974). The present report is the first record of its occurrence in the West Indies.

Cliona sp. 1

Ectosome: The papillae of this species are easily overlooked since they are small and do not protrude above the substrate surface. They are orange-red (8B8), roughly circular and usually measure between 0.5 and 1.0 mm in diameter. A few reach 1.5 mm diameter. No papillar fusion was observed.

Choanosome: The small chambers are completely filled with orange (6A8-6B8) to reddish-orange (7A8) choanosome. Fine strands of tissue extend upward from the chambers into the zone beneath the live surface of the corallum.

Excavations: This sponge forms a honeycomb network of small chambers (Plates 6E-H). The chambers are roughly spheroid to ovoid and measure 1.5-2.5 mm (2.0 mm) in diameter. The walls between adjacent chambers are perforated by numerous small foramina. Chamber formation usually starts 0.5 to 4.0 mm beneath the substrate surface and extends 10 to 20 mm into the substrate. The diameters of the cylindrical papillary canals correspond to those of the papillae.

Spicules: Two types of tylostyles occur (Plate A6H):

Type 1 tylostyles are numerous, relatively short and most are sharply bent (bend is usually one third way down shaft from neck). Some are straight. The shaft increases in diameter from the neck region, reaches a maximum diameter at around the beginning of the lower third of the shaft and then tapers to a sharp point. Heads are distinctive. They are ovoid (long axis normal to spicule axis) and subterminal.

Type 2 tylostyles are fewer in number and more slender than type 1 tylostyles but are of similar length. They are straight or slightly curved and taper to a sharp point from mid-shaft. Heads are spheroid or ovoid (elongate) and subterminal.

Microscleres are short spirasters which are either straight or curved.

They bear prominent thorny spines, some of which bifurcate.

Spicule dimensions:

Type 1 tylostyles, length x width: 175-230 x 6.0-11.5 (203 x 8.5)
Type 2 tylostyles, length x width: 170-250 x 2.5-5.5 (208 x 4.0)
Spirasters, length x width: 12.5-20.0 x 2.0-4.0 (17.5 x 2.5)
number of spines: 14-23 (17)

Substrates and Distribution: This sponge is common in massive corals from depths of 2-26 m on the fringing and bank reefs but does not occur in branching corals. It was present in cor-algal substrate but was not found in coral rubble from the swash zone.

Remarks: This species closely resembles C. mucronata in tissue colour and consistency; papillae size, shape and colour; and borehole morphology. The two species can be distinguished by examining their spicules.

Cliona sp. 2

Ectosome: The papillae are small and inconspicuous. They are pale yellow in colour, roughly circular and measure 0.2-1.0 mm (0.5 mm) in diameter.

Choanosome: The choanosome is brownish-orange (6C6) and completely fills the chambers.

Excavations: This species forms an extensive honeycomb network of small interconnecting chambers (Plates 7G, H). Individual chambers are spheroid to ovoid. Spheroid chambers measure 1-3 mm (2 mm) in diameter and ovoid chambers from 1.5 x 1.0 mm to 4.5 x 2.5 mm (2.5 x 1.5 mm). Adjacent chambers communicate through small circular foramina. Chamber networks start a few millimetres beneath the substrate and penetrate 30-80 mm into the substrate. Cylindrical papillary canals are 1-3 mm long and have diameters which correspond in size to those of the papillae.

Spicules: Tylostyles (Plate A7A) are moderately long and are quite sharply bent at a point one third way down the shaft from the neck. The shaft increases in diameter from the neck region, reaches a maximum diameter in the lower half, and tapers to a point in the last third. Points of some spicules

are sharp but the majority are obtuse. Heads are spheroid or elongate ovoid and subterminal. Some are reduced (poorly developed) and others possess secondary swellings in the neck region a short distance behind the head.

No microscleres are present.

Spicule dimensions:

Tylostyles, length x width: 170-275 x 3.5-13.5 (219 x 9.5)

Substrates and Distribution: *Cliona* sp. 2 occurs in *M. annularis*, *M. cavernosa* and *P. astreoides* from the bank reef and in *M. annularis*, *P. astreoides* and *A. agaricites* from the fringing reef but is relatively rare. It is more common in cor-algal substrate on the fringing reef. It does not occur in any branching corals or coral rubble from the swash zone.

Remarks: Of all of the clionids encountered during the study this species forms the most extensive chamber networks. On the bank reef it occurs mainly in *Montastrea* species and commonly infests the entire corallum of specimens. Chamber formation takes place preferentially in the denser exothecal-thecal areas of *Montastrea* skeletons (Plates 7G, H). Individual chambers are commonly aligned to form a string-of-beads appearance. Infestation is much less intense in fringing reef corals and cor-algal substrate. Chamber formation is commonly confined to the outer algal crust of cor-algal specimens.

Thoosa sp. 1

Ectosome: The papillae are small and inconspicuous. They are brownish-yellow in colour, measure 0.2-0.8 mm (0.4 mm) in diameter, and are densely scattered over the surface of the substrate. Although they are closely spaced they show no tendency to fuse.

Choanosome: The choanosome which is brownish-yellow (5C7-5C8) and of tough consistency completely fills the chambers.

Excavations: Chambers are roughly spheroid to ovoid or cylindrical (Plate A2E). Spheroid chambers measure 1.5-3.5 mm (2.0 mm) in diameter; ovoid chambers measure 1.5 x 1.0-4.0 x 2.5 mm. Adjacent chambers communicate through small foramina of which there are only a few per chamber. Chamber formation

begins directly beneath the substrate surface and extends 5-8 mm into the substrate.

Spicules: The spiculation (Plate A7B) of this species is very distinctive and comprises:

1) numerous short amphiasters
2) less numerous delicate amphiasters
3) tetractine spicules

Type 1 amphiasters (a) are short and squat and are more abundant than type 2 amphiasters (b). Each has a central axis bearing two whorls of 6 rays which project outward from the axis. The rays and the sections of the axis beyond the whorls are the same length and terminate in a mucronate knob which is covered with small spines.

Type 2 amphiasters are longer and more delicate than type 1 amphiasters. Each bears two whorls of 3 rays, one whorl on either side of the axis centre. The sections of the axis beyond the whorls, and the rays, are straight and taper gradually towards their extremities. They have a rough surface texture and terminate in a small bulb.

Tetractine spicules are larger than the amphiasters and are less abundant. Individual rays are slender and smooth, terminate in a sharp point and are curved, usually near their extremities.

Spicule dimensions:

Type 1 amphiasters, length x whorl width:	20.0-25.0 x 12.5-17.5 (22.5 x 15.0)
Type 2 amphiasters, length x whorl width:	32.5-47.5 x 12.5-20.0 (39.5 x 17.5)
Tetractinal, ray length:	37.5-47.5 (42.0)

Substrates and Distribution: This species was found only rarely in massive corals from the bank and fringing reefs and was absent altogether from branching corals. It was encountered in an encrusting colony of A. agaricites on the surface of one of the cor-algal substrate blocks from transect 2 and in a randomly collected M. annularis colony from the same area. In the M. annularis specimen boring was confined to the less dense corallite regions where cylindrical chambers, 2.5-4.0 mm long and around 2.5 mm in diameter (diameter

of corallites) were formed by removal of the septa and endothecal dissepiments.

It was abundant in cor-algal substrate and was commonly found within thick encrustations of coralline algae or in the dead coral underlying these encrustations. Fewer chambers are formed in this type of substrate and adjacent chambers are more widely spaced and usually do not communicate. Papillary perforations on the substrate surface connect with the chambers through cylindrical canals, 2-4 mm long, which flare towards the chamber. Only one specimen of Thoosa sp. 1 was recorded in coral rubble from the swash zone.

Remarks: This is the first record of Thoosa spp. in the western Atlantic.

Thoosa sp. 2

Thoosa sp. 2 closely resembles Thoosa sp. 1 in tissue colour and consistency and boring pattern. The two can only be distinguished by examining the spicules. Thoosa sp. 2 was found only in cor-algal substrate on the fringing reef. Its boring pattern is the same as that described for Thoosa sp. 1 in this type of substrate.

Spicules: This species possesses two types of amphiasters (Plate A7C).

Type 1 amphiasters are short and stout and are more abundant than type 2 amphiasters. Two whorls, each of 6 rays, project from either side of the axis centre. The rays and the sections of the axis beyond the whorls are of similar length and bear a terminal (locally mucronate) knob which is covered with small spines.

Type 2 amphiasters are longer and thinner. The central axis bears two whorls, each of 3 rays. The rays and the sections of the axis beyond the whorls taper towards their extremities. They bear a terminal knob and have a rough surface texture.

Spicule dimensions:

Type 1 amphiasters, length x whorl width:	18.0-27.5 x 15.0-20.0 (23.0 x 17.0)
Type 2 amphiasters, length x whorl width:	37.5-72.5 x 17.5-32.5 (49.5 x 21.5)

Remarks: The spicule complements of Thoosa spp. 1 and 2 are similar. The two can be easily distinguished since Thoosa sp. 2 possesses 'fatter' amphiasters and has no tetractine spicules.

Thoosa sp. 3

Thoosa sp. 3 was recorded only once in a S. siderea colony from a depth of 5 m on the southwest coast of Curaçao. The choanosome of this species is similar in colour and consistency to the other two Thoosa species. Chambers are completely filled by the choanosome. Chambers formed by Thoosa sp. 3 are larger than those formed by Thoosa spp. 1 and 2. They are usually spheroid (3-6 mm in diameter) and are located 2-3 mm beneath the substrate surface.

Spicules: The spiculation (Plate A7D) of this species is highly distinctive and comprises:

1) amphiasters
2) toxas
3) rhaphides

Short amphiasters are abundant and vary considerably in size. Two whorls of rays, usually 6 or 7 per whorl, project outward from either side of the centre of the axis. Both the rays and the extremities of the axis taper towards a knob which bears a sharp terminal spine. Small spines are present on the surface of the knob.

Slender toxas and rhaphides are also present.

Spicule dimensions:

Amphiasters, length x whorl width: 17.5-26.0 x 10.0-20.0 (21.5 x 15.5)
Toxas, length: 80-110 (99)
Rhaphides, length: 120-170 (140)

Remarks: Individual rays of the amphiasters of Thoosa sp. 3 are longer, more distinctly mucronate and bear less of a terminal swelling than those of Thoosa spp. 1 and 2.

Family SPIRASTRELLIDAE

Spheciospongia sp.

Ectosome: Ectosomal structures consist of either single roughly circular or oval papillae or thin membranes of tough tissue which are perforated by circular holes. These holes probably represent oscular openings. Both papillae and membranes are dark greyish-brown or almost black in colour. They lead directly into tunnels in the underlying substrate. Circular papillae measure 2 to 3 mm in diameter. The membranes are more extensive and can be either roughly circular or oval. Circular membranes measure 7 to 9 mm in diameter. Oval membranes measure from 6 x 4 mm to 28 x 11 mm. Individual oscular perforations are circular and around 2 mm in diameter. As many as 15 can be present on one membrane.

Choanosome: The tough yellow-brown (5F8) to olive-brown (4D8) choanosome lines the walls of the tunnels (Plate A2F).

Excavations: The apertures on the substrate surface lead directly into branching tunnel systems (Plate A2G) which penetrate as far as 10 to 12 cm into the substrate. Tunnels are circular or elliptical and ragged in outline. Their diameters are not uniform and they are commonly sinuous. Circular tunnels range in diameter from 5-12 mm (10 mm); elliptical tunnels range in diameter from 9 x 7 mm-16 x 10 mm (13 x 9 mm). New tunnels radiate out into the adjacent substrate from the main tunnels.

Spicules: Tylostyles (Plate A7E) show considerable size variation. Most are slightly curved (bend occurs one third way down shaft from the neck region) and a few are straight. The shaft is fairly uniform in thickness throughout most of its length (from bend until point where it begins to taper) and tapers to a point in the last fourth or fifth of its length. Heads are small and are mainly elongate ovoid. Some are spheroid.

Spirasters are very small and are rare. They bear small spines.

Spicule dimensions:

Tylostyle, length x width: 160-400 x 5-12 (306 x 9)
Spirasters, length x width: 7.0-15.0 x 1.0-2.0 (10.0 x 1.5)
number of bends: 0-5 (2)

Substrates: This species occurs commonly in massive and branching corals and in cor-algal substrate. It was not found in coral rubble from the swash zone.

Distribution: Spheciospongia sp. occurs on both the fringing and bank reefs.

Remarks: This species is similar in many features (borehole morphology, tissue colour, spicules) to Spheciospongia othella described by Ruetzler (1974) from Bermuda. Unlike S. othella this species does not tend to overgrow the surface of the infested substrate. The ectosomal structures correspond to the third type of openings described by Ruetzler (1974, p. 29).

Order POECILOSCLERIDA

Family ACARNIDAE

Acarnus sp.

This species forms a red encrustation on the substrate surface. Sponge tissue penetrates into and etches the underlying substrate but no distinct chambers are formed.

Spiculation is highly distinctive and comprises cladotylotes, toxas and small isochela (see Boury-Esnault, 1973).

The poecilosclerids, Acarnus and Acanthacarnus spp., have been described from the Brazilian coast by Boury-Esnault (1973). The Barbados specimens correspond most closely to the Acarnus sp. (in colour, spiculation and habit). Scanning electron microscopic examination of coral substrates, from Florida and the Bahamas, infested by acarnid sponges (Pomponi, 1976) showed evidence of boring. This is the first report of boring by poecilosclerids.

Order and Family Uncertain

Alectona jamaicensis Pang, 1971

Ectosome: The papillae are inconspicuous. They are small, circular (less

than 1 mm in diameter) and are light yellow.

Choanosome: The chambers are completely filled by brownish-orange (6C6) choanosome which is of tough consistency.

Excavations: Chambers are roughly spheroid or ovoid. Spheroid chambers measure from 3 to 5 mm in diameter, ovoid chambers from 4 x 3 mm to 7 x 5 mm. Adjacent chambers are connected by short cylindrical tunnels. Papillary perforations correspond in diameter to those of the papillae and are connected to the chambers by cylindrical papillary canals 1 to 4 mm in length.

Spicules: The genus Alectona has very distinctive spiculation (Plate A7G). There are three types of spicules:

1) stout diactinal spicules which are covered with tubercles
2) smaller and thinner diactinal spicules which are usually smooth
3) amphiasters which bear 2 whorls of tylote rays

The stout tuberculate diactinal spicules (Plates A7F, G) are mostly curved. Some are partly curved and partly straight and others are almost straight or sharply bent. The bend is either in mid-shaft or offset from the centre producing a V-shaped spicule with arms of unequal length. The arms themselves are often curved. In some spicules a swelling or protruberance is present, usually in the centre of the shaft, on the convex side of the spicule. The shaft tapers slightly from the central region to rounded tips at each end. The diameter in mid-shaft is roughly twice the diameter at the ends. Tubercles are distributed evenly over the surface of the spicule and are best developed on the stoutest spicules. The more prominent ones reach up to 5-7 microns in height.

Thinner diactinal spicules (Plate A7G) are more abundant and exhibit a wide range of forms. A distinctive central swelling which appears like a knot or twist (Pang, 1971) is present in the central region of these spicules. Most are curved or almost straight and a few are sharply bent. They taper from the central region to a pointed tip at either end. The arms themselves are often curved and some are sharply bent near their extremities. Incipient tubercle formation is evident on some of these spicules.

Amphiasters are abundant and very distinctive (Plate A7G). A whorl of rays (5-6) is developed on each side of the central region. The diameter is

greatest in the central part and the shaft tapers slightly from the whorls towards the extremities which are either blunt or pointed. The shaft in these sections is rather rough.

Spicule dimensions:

Stout diactinals, length x width: 300-380 x 15-25 (348 x 19)
Thinner diactinals, length x width: 270-390 x 5.0-12.5 (325 x 9.5)
Amphiasters, length x whorl width: 30.0-47.5 x 6-11 (42.0 x 8)

Substrates and Distribution: A. jamaicensis is rare. On the bank reef 3 specimens were found, 2 in M. cavernosa colonies on the bank top and 1 in an A. lamarcki colony at a depth of 30 m on the bank sides. Two species were found on the fringing reef, one in cor-algal substrate and one in a P. porites colony.

Remarks: A. jamaicensis can be mistaken for S. coralliphagum forma obruta in the field since their borehole morphology and choanosome colour are similar. The softer consistency and more mucous nature of the choanosome of S. coralliphagum can be used to distinguish the two without looking at the spicules.

A. jamaicensis was first described from Discovery Bay, Jamaica by Pang (1971).

Species X

Ectosome: The papillae are inconspicuous. They are small, circular, pale yellow and measure 0.2-0.8 mm (0.5 mm) in diameter.

Choanosome: The small chambers are completely filled by pale yellow (4A3: cream colour) choanosome.

Excavations: This species forms a network of small chambers (Plates 7D-F). Individual chambers measure from 0.5-2.0 mm (1.0 mm) in diameter and are roughly spheroid. The thin separating walls between adjacent chambers are perforated by very small foramina. Chamber development begins directly beneath the substrate surface and extends from 25 to 45 mm into the substrate.

Spicules: The spiculation (Plate A7H) of this species is highly distinctive

and consists of oxea and spirasters.

Oxea are abundant and show considerable size variation. Most are bent (some slightly, others sharply) and a few are almost straight. In most the bend is in mid-shaft, in others it is off-centre. In some oxea a second bend occurs between the mid-point and the tip. The tips of stouter oxea are rather abruptly pointed, those of more slender oxea taper gradually to a point in the last quarter of their length. Most tips are smooth, some are stepped and a few are mucronate.

Some styles and strongyles are present. Tylostyles also occur but are thought to be foreign.

Spirasters are abundant and have a distinctive cork-screw shape. They are smooth spiral rods which are of uniform diameter throughout their length. Their ends are rounded.

The microscleres of this sponge resemble those of C. vermifera but have a more uniform spiral shape. The very small size of chambers formed by this sponge makes tissue extraction difficult. The risk of contamination is high since extraneous material may inadvertantly be introduced during tissue collection.

Spicule dimensions:

Oxea, length x width: 360.0-630.0 x 4.0-32.5 (518.5 x 18.0)
Spirasters, length x width: 17.5-72.5 x 2.0-3.5 (42.0 x 3.0)
number of bends: 3-8 (5)

Substrates and Distribution: Species X occurs in M. annularis, M. cavernosa, S. siderea, A. agaricites and D. labyrinthiformis on the bank reef and is most frequently found in the Montastrea species. Only two specimens were found on the fringing reef; both were in cor-algal substrate.

The denser exothecal-thecal areas of Montastrea are preferentially bored. Individual chambers are arranged in rows which extend along the denser exothecal-thecal areas (Plates 7D-F).

Remarks: This species is easily overlooked. The small size of the chambers and the cream colour of the choanosome make it difficult to distinguish.

Order HAPLOSCLERIDA

Family ADOCIIDAE

Siphonodictyon spp.

The spicules of *Siphonodictyon* species are distinctive. All species possess oxea, the lengths of which are distinctive of the various species. Species differ in morphology and distinction between different species, and different forms of individual species, is based on differences in gross morphology and spicule dimensions (Ruetzler, 1971).

Descriptions of the different *Siphonodictyon* species and forms encountered during this study appear in the following section. Some of the species and forms correspond to those described by Ruetzler (1971), others are described here for the first time.

Siphonodictyon cachacrouense Ruetzler, 1971

Ectosome: Prominent conical mounds of ectosomal tissue which are greyish-brown (5F3) and bristly (Plate A4A) occur on the living surface of coral colonies and on dead encrusted parts of colonies. They measure 20-35 mm (30 mm) in diameter and are 10-20 mm (15 mm) high. Each bears a central osculum, 5-10 mm in diameter, with an elevated rim. Ostia are present in the walls of the ectosomal mound around the oscule. Ectosomal patches are locally confluent.

Choanosome: The soft, mucous choanosome is brownish-orange (5C6) and completely fills the large chambers (Plate A4B).

Excavations: This species forms large spheroid chambers which are located beneath the live surface of the corallum. Chambers encountered during this study reached 30 mm in diameter. Splitting up highly infested colonies (Plate A4A) would undoubtedly have revealed larger cavities of the type recorded by Ruetzler (1971). Chambers are connected to the live surface of the corallum by as many as 6 closely spaced, roughly cylindrical canals, 2-4 mm in diameter and 10-15 mm long. Ectosomal tissue lines these canals.

Adjacent chambers are connected by tunnels.

Spicules: The spicules of the Barbados specimens (Plate A8A) correspond in morphology and dimensions to those of the holotype form described by Ruetzler (1971) from Scotts Head Bay, Dominica.

Spicule dimensions:

Stouter oxea, length x width: 172.2-217.3 x 3.2-7.2 (190.9 x 5.2)
Slender oxea, length x width: 147.6-188.6 x 1.6-3.2 (175.0 x 2.3)

Substrates: This species was found in the live surface of M. annularis (Plate A4A) and S. siderea colonies.

Distribution: This form is rare. It occurs on the bank reef and was observed in only 3 places in the study area. Three additional occurrences were noted elsewhere on the bank reef.

Remarks: Specimens of this sponge collected on Barbados reefs correspond closely to the holotype described by Ruetzler (1971). This record increases the geographic range of the species.

Siphonodictyon coralliphagum Ruetzler, 1971

Siphonodictyon coralliphagum was first described by Ruetzler (1971). Four forms are distinguished (obruta, typica, tubulosa, incrustans), each of which has a different morphology and spicule dimensions. Ruetzler suggests these forms may either represent different growth stages or be different eco-phenotypes.

This species is widely distributed throughout the Caribbean. Forma obruta was described from Barbados and Puerto Rico and forma typica from Jamaica and Dominica (Ruetzler, 1971).

Another form (form 5) which is morphologically different from the four described forms but which has spicules similar to those of forma obruta, also occurs. This form has a very distinctive boring pattern and like obruta occurs only in the dead basal parts of coral colonies.

Siphonodictyon coralliphagum forma typica

Only one specimen of this species was encountered during the study. It was found at a depth of 28 m in a Stephanocoenia michelinii colony on the fore-reef slope at St. Michaels Bay in Curaçao. The sponge occurred in dead encrusted substrate below the coral tissue periphery.

Ectosome: Ectosomal structures of this sponge are deep yellow (4A8) and are composed of tough tissue. They are basically conical with a broad base and thick walls which taper towards a terminal osculum. Ostia are scattered over the entire surface of these structures. In the specimens examined the structures measured 3 to 5 mm in diameter and 5 to 8 mm in length.

Choanosome: The choanosome is brownish-yellow (5C7-5C8), soft and mucous and completely fills the chambers (Plate A4D). A yellowish stain is apparent on chamber walls after tissue removal and drying.

Excavations: Chambers are single, roughly ovoid and measure up to 25 x 20 mm. They are connected to the substrate surface by 2 or 3 cylindrical canals which are approximately 5 mm in length and 4 mm in diameter.

Spicules: Spicules of the specimen found during this study (Plate A8B) are similar in morphology and dimensions to those described by Ruetzler (1971).

Spicule dimensions:

Stouter oxea, length x width: 131.2-168.1 x 3.2-7.2 (154.3 x 5.7)
Slender oxea, length x width: 110.7-155.8 x 1.6-2.4 (137.9 x 2.0)

Distribution: Ruetzler (1971) found that S. coralliphagum forma typica occurred most frequently in sheltered locations, between 10 and 70 m, which were not affected by heavy wave action and sedimentation. The specimen found during this study occurred in a sheltered location on the fore-reef slope.

Remarks: This record extends the geographic range of forma typica. It has been previously described from Jamaica and Dominica (Ruetzler, 1971).

Specimens similar to the holotype of the species described from Jamaica (Ruetzler, 1971), in which ectosomal structures protrude like chimneys from the live surface of coral colonies, were observed by the writer on Jamaican reefs. The ectosomal structures of the specimen observed in Curaçao

protruded from dead substrate on the coral base.

Siphonodictyon coralliphagum forma obruta

Ectosome: Ectosomal structures are white or yellow and are conspicuous (Plate A4E). Oscular structures are open-ended cylindrical tubes which bear a single osculum. They are 1.0-4.0 mm (1.8 mm) in diameter and 2.0-6.0 mm (4.6 mm) long. Ostial structures are finger-shaped cylindrical tubes which are generally smaller than oscular structures. They measure 1.0-3.0 mm (1.7 mm) in diameter and are 1.2-6.0 mm (3.3 mm) long. Ostia are distributed over the entire surface of these tubes. Fusion of ostial tubes was observed in some specimens.

Choanosome: The greyish-orange (5B5-5B6) choanosome is soft and mucous and completely fills the chambers.

Excavations: Chambers are spheroid to ovoid (Plate A4C). Spheroid chambers measure 4-10 mm in diameter. Ovoid chambers measure 5 x 3 mm-18 x 14 mm (10 x 7 mm). They are located 2-16 mm (7 mm) beneath the substrate surface and are connected to the substrate surface by 2 or 3 cylindrical canals. The canals are lined with ectosomal tissue and their diameters are smaller than those of the ectosomal tubes. The canals always run obliquely from the chambers to the substrate surface. The long axis of ovoid chambers is always parallel to the substrate surface.

Spicules: Specimens found during this study with spicules corresponding to those described for S. coralliphagum forma obruta (Ruetzler, 1971) were morphologically different from the obruta specimens described by Ruetzler from Barbados and Jamaica. All of the specimens collected possessed ectosomal structures in the form of white or yellow tubes. This gave rise to uncertainties in identification since the specimens described by Ruetzler have no ectosomal structures. Further confusion arose from the fact that specimens with yellow papillae corresponded morphologically to S. brevitubulatum, the species described by Pang (1971) from Jamaica. Forms with white and yellow ectosomal structures examined during this study are believed to belong to the same species since their spicules and morphologies do not differ

significantly. Both these forms (and S. brevitubulatum) are regarded as belonging to forma obruta since they closely resemble this form in spiculation and morphology.

Spicules of these forms vary in size and shape. Two groups of spicules, each of which differs in gross morphology, were distinguished. Group 1 oxea taper gradually towards their tips. Those of group 2 are of fairly uniform diameter throughout their length until the end of the shaft where they terminate abruptly. Both group 1 and 2 can be divided into subgroups (1A, 1B, 2A, 2B, 2C) on the basis of size range and tip morphology.

1A: Two size categories of gently curved oxea are present (Plate A8C). Type 1 oxea are stouter and more numerous than type 2 oxea. The tips of the stouter oxea are typically mucronate, some are stepped (usually gradually). Slender type 2 oxea terminate in a long sharp spine. A few styles are present.

Type 1 oxea, length x width: 110.4-155.8 x 2.4-6.7 (128.5 x 5.2)
Type 2 oxea, length x width: 77.9-155.8 x 0.8-4.0 (117.5 x 2.4)

1B: Two size categories of gently curved oxea are present. The tips of most of the thicker oxea are either stepped or mucronate. Some are blunt and a few have a broken appearance. Some of the tips have a rough surface texture. The slender oxea taper to a sharp point at the end of the shaft. A few styles and strongyles are present.

Type 1 oxea, length x width: 92.8-128.0 x 2.4-6.4 (105.4 x 4.3)
Type 2 oxea, length x width: 77.9-104.0 x 1.2-2.8 (91.9 x 2.0)

2A: Two size categories of curved oxea are present (Plate A8D). Type 1 oxea are stouter and more numerous than type 2 oxea. The degree of curvature of type 1 oxea varies: most are gently curved, some are distinctly bent and others are almost straight. Type 1 oxea are abruptly terminated. Tips are mostly stepped and some are mucronate. Type 2 oxea are slender and taper more gradually to a point. In one specimen secondary bends were present in the shaft producing a wavy appearance. No styles or strongyles are present.

Type 1 oxea, length x width: 131.2-161.6 x 2.4-7.2 (147.8 x 4.7)
Type 2 oxea, length x width: 118.9-147.6 x 1.2-2.8 (137.6 x 2.1)

2B: Two types of oxea are present (Plate A8G). Type 1 oxea are abruptly pointed and have distinctive tips. Most are mucronate and one or more distinct steps are present near the end of the shaft. Type 2 oxea are slender and taper more gradually to a sharp point. Styles and strongyles are present.

Type 1 oxea, length x width: 114.8-151.7 x 2.4-8.0 (133.8 x 4.8)
Type 2 oxea, length x width: 90.2-139.4 x 1.2-2.4 (118.8 x 1.8)

2C: Two distinct size categories of curved oxea are present (Plate A8H). Tips of type 1 oxea are rough and most are obtuse. Some are stepped and others are distinctly mucronate or mammiform. Type 2 oxea are shorter, more slender and most are mucronate.

Type 1 oxea, length x width: 110.7-147.6 x 2.4-9.6 (128.1 x 6.1)
Type 2 oxea, length x width: 102.5-123.0 x 1.0-3.2 (113.9 x 2.1)

Comparison of spicules of the type specimen of forma obruta with those of groups 1 and 2 showed them to be most similar to spicules of subgroup 2B.

Substrates: S. coralliphagum forma obruta was found in all of the substrates sampled.

Distribution: This species occurs in depths of less than 1 m in the swash zone to 26 m on the bank sides. Specimens collected by Ruetzler (1971) were from depths of 20-25 m.

Remarks: Ovoid chambers are always much larger than spheroid chambers and probably represent a later stage of boring. The long axis of ovoid chambers is always parallel to the substrate surface.

Specimens which live in sheltered habitats (such as on the protected undersides of coral rubble blocks or in corals from the deeper waters of the bank sides) develop unusually long ectosomal tubes.

Siphonodictyon coralliphagum form 5

Ectosome: Ectosomal structures are similar in colour and shape to those of S. coralliphagum forma obruta but are smaller (Plate A4F). The white tubular oscular structures are 0.5-1.5 mm (0.8 mm) in diameter and 1.0-2.5 mm (1.2 mm) long. Ostial structures are small mounds, 0.5-1.5 mm (0.9 mm) in diameter

and 1.0-3.5 mm (1.8 mm) high.

Choanosome: The choanosome is greyish-orange (5B5) and completely fills the small chambers. Like the tissue of the other Siphonodictyon sponges the tissue of this form is soft and mucous.

Excavations: A honeycomb network of small interconnecting chambers is formed (Plates 7A-C). Chambers are spheroid to ovoid or cylindrical and measure 1.0-2.5 mm (2.0 mm) in diameter. The thin walls between adjacent chambers are perforated by numerous small foramina. Chamber development begins around 1 mm beneath the substrate surface and extends 10-45 mm (20 mm) into the substrate.

Spicules: Spicules of this form are similar to those of group 1A.

Type 1 oxea, length x width: 99.2-151.7 x 2.4-6.4 (121.6 x 4.6)
Type 2 oxea, length x width: 89.6-128.0 x 0.8-3.2 (107.3 x 2.1)

Substrates: This form was found in massive corals and cor-algal substrate but was not present in branching corals or coral rubble. It occurs commonly in M. annularis, M. cavernosa, P. astreoides and S. siderea and is most commonly found in M. annularis. Its boring strategy is affected by coral structure. In substrates like M. annularis in which the corallite and intercorallite areas are of different density cylindrical chambers are formed by removal of septa and endothecal dissepiments. These chambers are up to 3 mm long and may occupy the entire corallite or part of the corallite. Individual chambers are separated by remnant tabular dissepiments and form a string-of-beads pattern down the corallite axis.

Distribution: This form occurs in all fringing reef zones except the swash zone. It is common on the bank reef in depths less than 26 m.

Remarks: This sponge was originally assigned by the writer to the genus Aka since it possesses oxea (no tylostyles) and forms a clionid-type boring pattern. However close examination of the spicules of several specimens revealed that the spicule compliment of some specimens corresponded to that of S. coralliphagum and that of other specimens to Siphonodictyon sp. The soft, mucous choanosomal tissue was also similar in both colour and consistency to that of Siphonodictyon species. Since the boring pattern is unlike

any produced by the clionid species studied it is unlikely that these borings are old clionid networks which have been later occupied by Siphonodictyon. Although the excavations are certainly not typical of the Siphonodictyon species described by Ruetzler (1971) this form is grouped with the genus Siphonodictyon on the basis of the close resemblance of its choanosome and spicule compliment to those of Siphonodictyon species.

Several other different borehole types, formed by Siphonodictyon species, were noted during the study. In Carriacou cylindrical Siphonodictyon borings, several centimetres in length, occupied the central axes of corallites of M. annularis specimens (Plate 8C). Another borehole type which possibly represents a transitional stage between the chamber network described above and the typical spheroid-ovoid Siphonodictyon chamber was occasionally seen. This type of boring was apparently produced by removal of the separating walls between individual chambers in the central parts of chamber networks. Remnant separating walls around the periphery of the cavity gives the cavity an irregular outline.

Siphonodictyon sp.

Siphonodictyon sp. form 1

This sponge occurs in the dead basal parts of coral colonies and closely resembles S. coralliphagum forma obruta in all features except spiculation. It may be a new species since its spicules are so distinctly different from those of any of the species described by Ruetzler (1971).

The spiculation of this species is distinctive. Oxea taper gradually from mid-shaft towards the end of the shaft. Two size classes of oxea are present (Plates A8E and A8F). Type 1 oxea are stouter than type 2 oxea and range in size from less than 50 microns to over 250 microns. Most are curved and some are distinctly bent. Tips are very distinctive. All are sharply pointed and the majority are stepped. Slender type 2 oxea are generally shorter and less abundant and taper gradually to a very sharp point. Some styles are present.

Type 1 oxea, length x width: 49.2-258.3 x 2.4-12.8 (144.6 x 5.2)
Type 2 oxea, length x width: 61.5-196.8 x 1.2-3.2 (119.9 x 2.1)

Siphonodictyon sp. form 2

This form corresponds in all features except spiculation to form 5 of S. coralliphagum. The spicules are similar to those described for form 1 above.

Type 1 oxea, length x width: 45.1-266.5 x 2.4-13.6 (143.9 x 6.9)
Type 2 oxea, length x width: 65.6-176.3 x 1.2-4.8 (115.4 x 2.7)

PLATE A1

A. Polygonal chambers of Cliona vermifera in Montastrea annularis. (bar = 5 mm)

B. Choanosome-filled chambers of Cliona ensifera in Siderastrea siderea. (cm scale)

C. Cliona mucronata papillae in coralline algal encrustation on a coral base. (scale in mm)

D. Cliona schmidti borehole. (bar = 1 cm)

E. Papillae of Cliona caribbaea in coralline algal encrustation on base of a Siderastrea siderea colony. (bar = 1 cm)

F. Cliona caribbaea boring exposed by breaking open the substrate shown in E. (cm scale)

G. Cliona ?rovignensis chambers. (bar = 1 cm)

H. Network of small chambers produced by Cliona lampa forma occulta. (scale in mm)

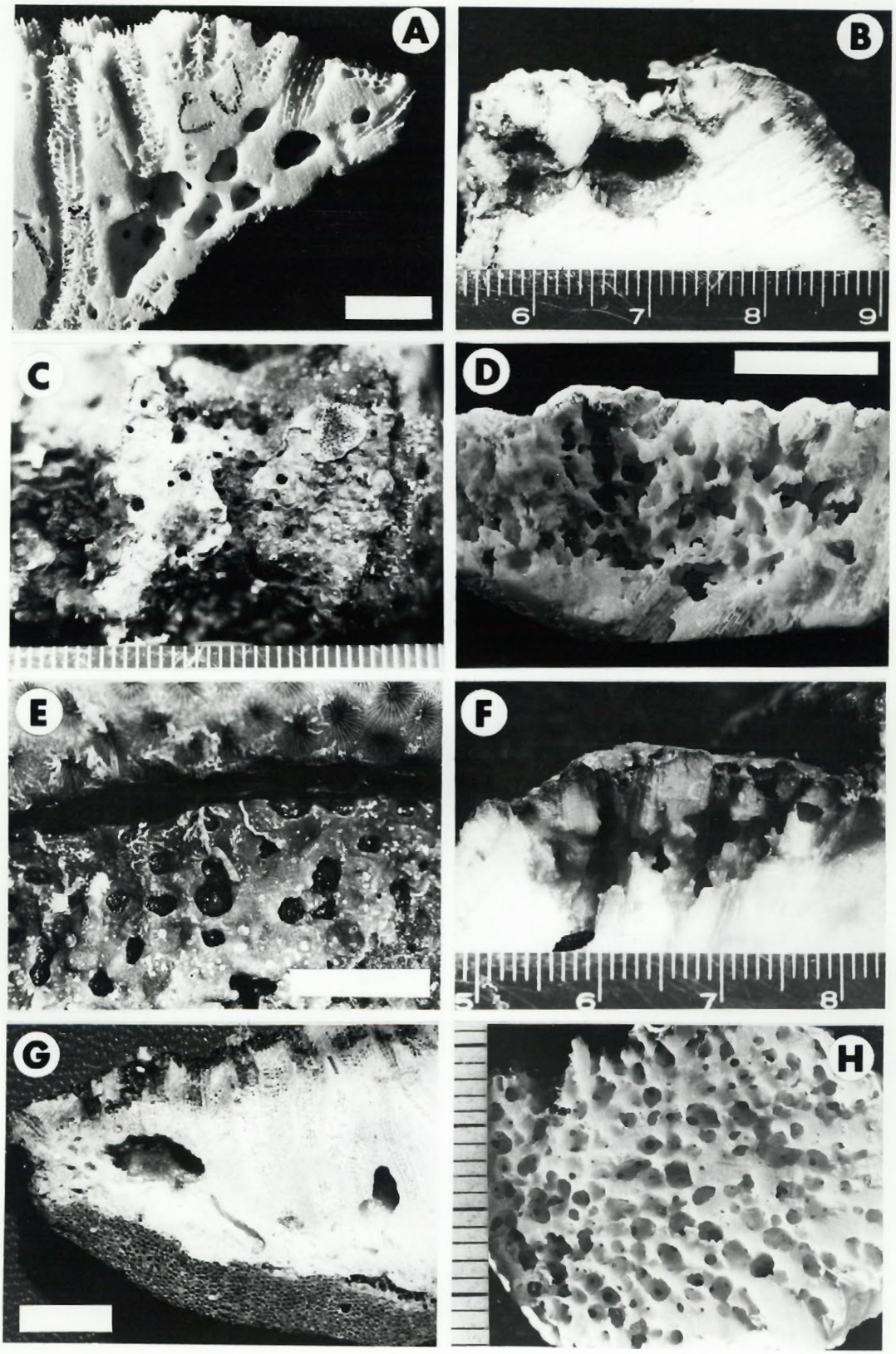
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PLATE A2

A. Cliona lampa papillae in coralline algal encrustation on base of coral colony. (mm scale)

B. Cliona lampa form 4 chamber. (scale in mm)

C. Choanosome-filled chamber of Cliona delitrix form 2 in the base of a Diploria colony. Note the prominent papillary canals which lead to papillae on the coral surface. (mm scale)

D. Choanosome-filled Cliona flavifodina chamber. (bar = 1 cm)

E. Chambers of Thoosa sp. 1. (mm scale)

F. Spheciospongia sp. boring in Siderastrea siderea. Walls of boring are lined with choanosome. (mm scale)

G. Spheciospongia tunnels in clionid-riddled Montastrea annularis colony. (mm scale)

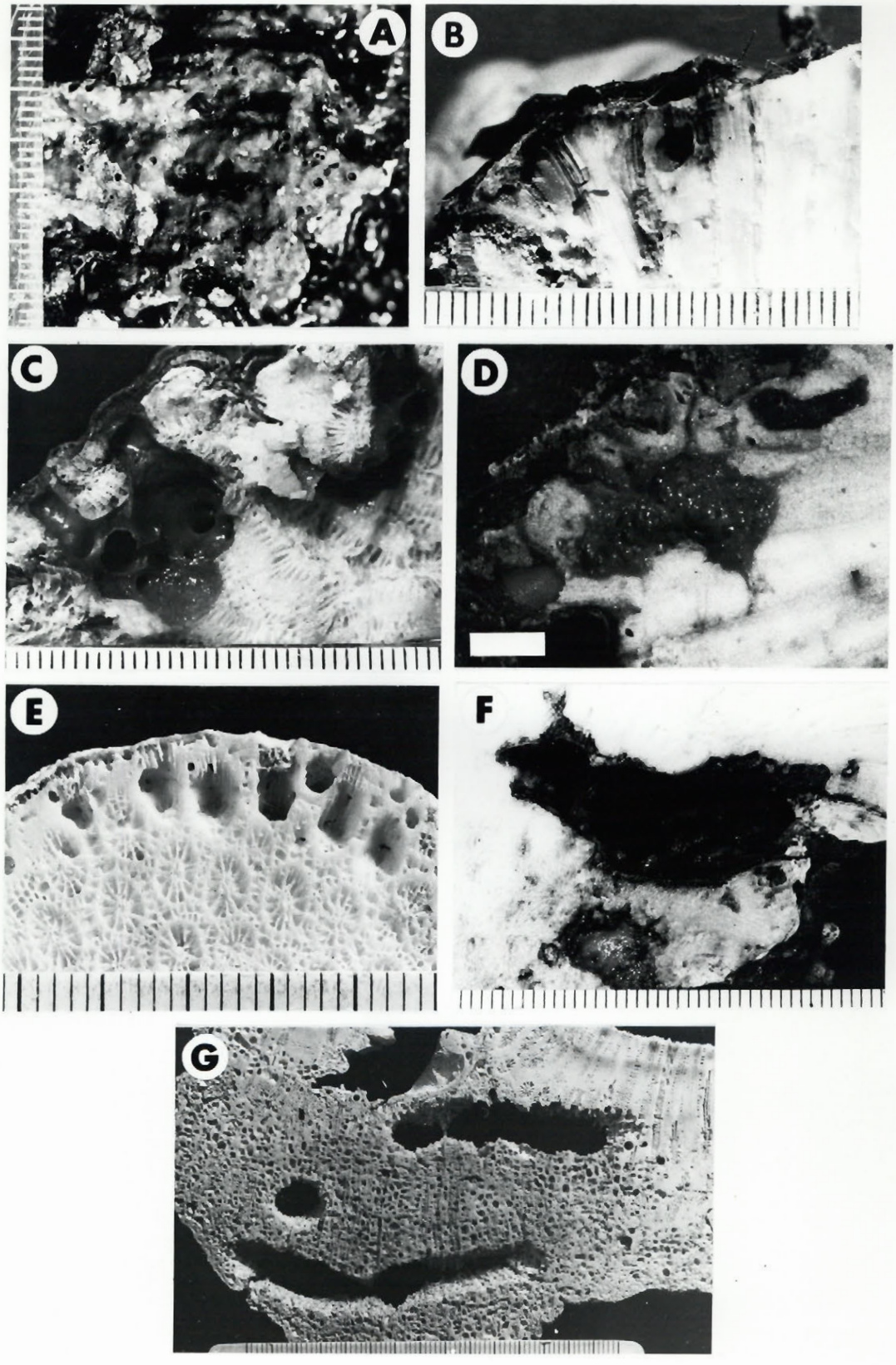

A
B
C
D
E
F
G

PLATE A3

A. Patch of Cliona delitrix form 1 which is encroaching on the live surface of a Siderastrea siderea colony. Coral tissue around the periphery of the sponge patch dies off forming a narrow band of dead coral which is colonized by filamentous algae. Spreading of the sponge infestation into this area of dead coral is accompanied by lateral migration of the band across the coral surface.

Four oscules (three are prominent) and numerous discrete ostial papillae can be discerned on the surface of this specimen. (approx. actual size)

B. Montastrea cavernosa colony which has been completely infested by Cliona delitrix form 1 (centre of plate).

C. Close-up of the surface of Cliona delitrix form 1. Note the large prominent oscules and numerous small white zoanthids dotted amongst the ostial papillae. (approx. actual size)

D. Cliona delitrix form 1 boring in the surface of a Siderastrea siderea colony. The sponge penetrates parallel to the direction of the corallites forming roughly cylindrical chambers. The chamber network has a lacy appearance due to partial breakdown of separating walls between individual chambers. (mm scale)

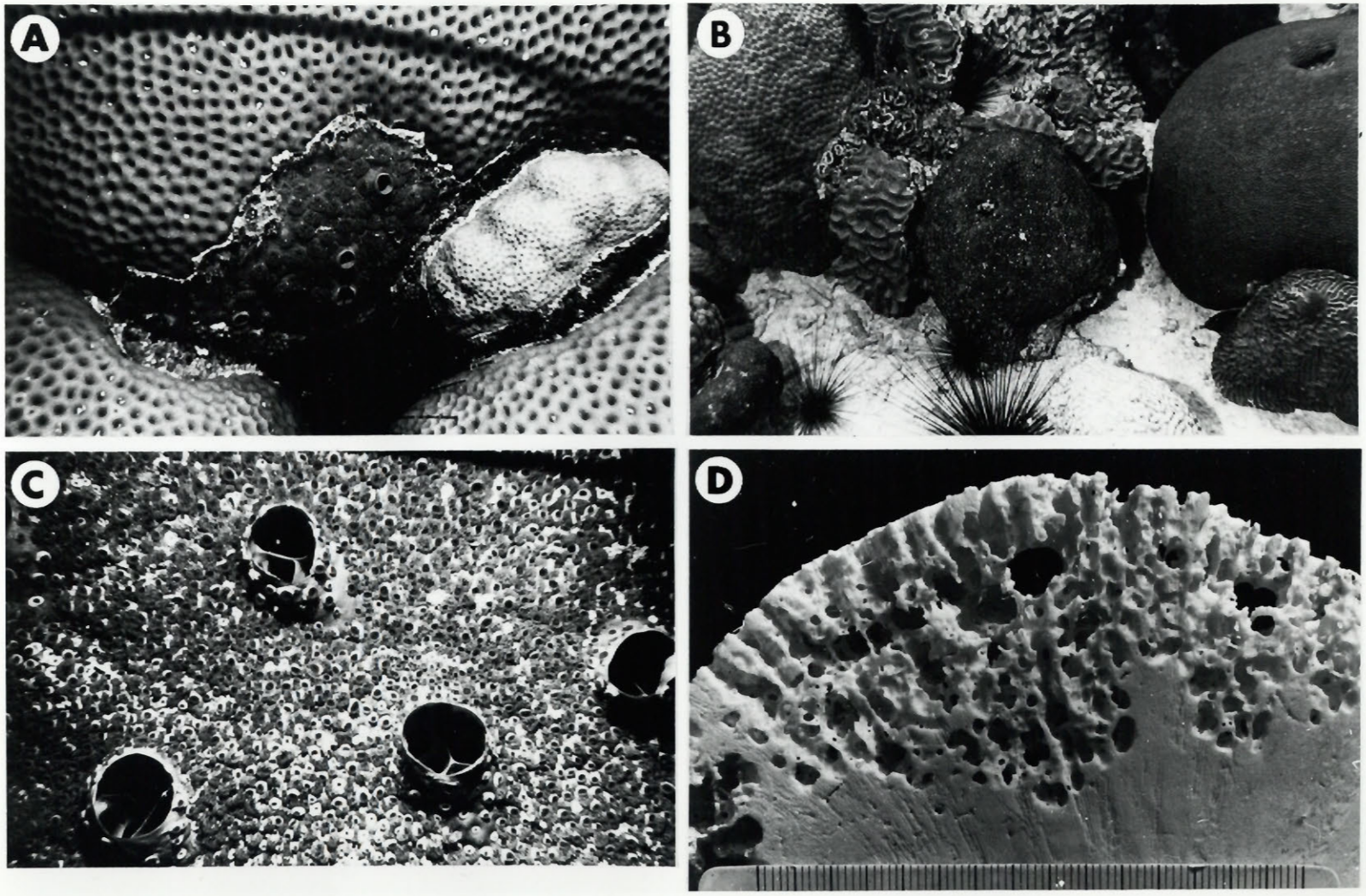

A
B
C
D

PLATE A4

A. Montastrea annularis colony infested by Siphonodictyon cachacrouense. Note large circular ectosomal structures on living surface of corallum. (scale = 0.5 m)

B. Choanosome-filled Siphonodictyon cachacrouense borehole beneath the live surface of a Montastrea annularis colony. Note the wide canal which connects the borehole with an ectosomal structure (similar to those shown in A) on the coral surface. (cm scale)

C. Choanosome-filled S. coralliphagum forma obruta boreholes in the dead base of a M. annularis colony. Each borehole is connected to tubular ectosomal structures (arrows) on the substrate surface by several canals. (mm scale)

D. Choanosome-filled borehole of S. coralliphagum forma typica. Note canal leading from borehole to a tubular ectosomal structure on substrate surface. (mm scale)

E. Oscule (a) and ostial structures (b) of S. coralliphagum forma obruta. (cm scale)

F. Oscule (open-ended) and ostial structures of S. coralliphagum form 5. (cm scale)

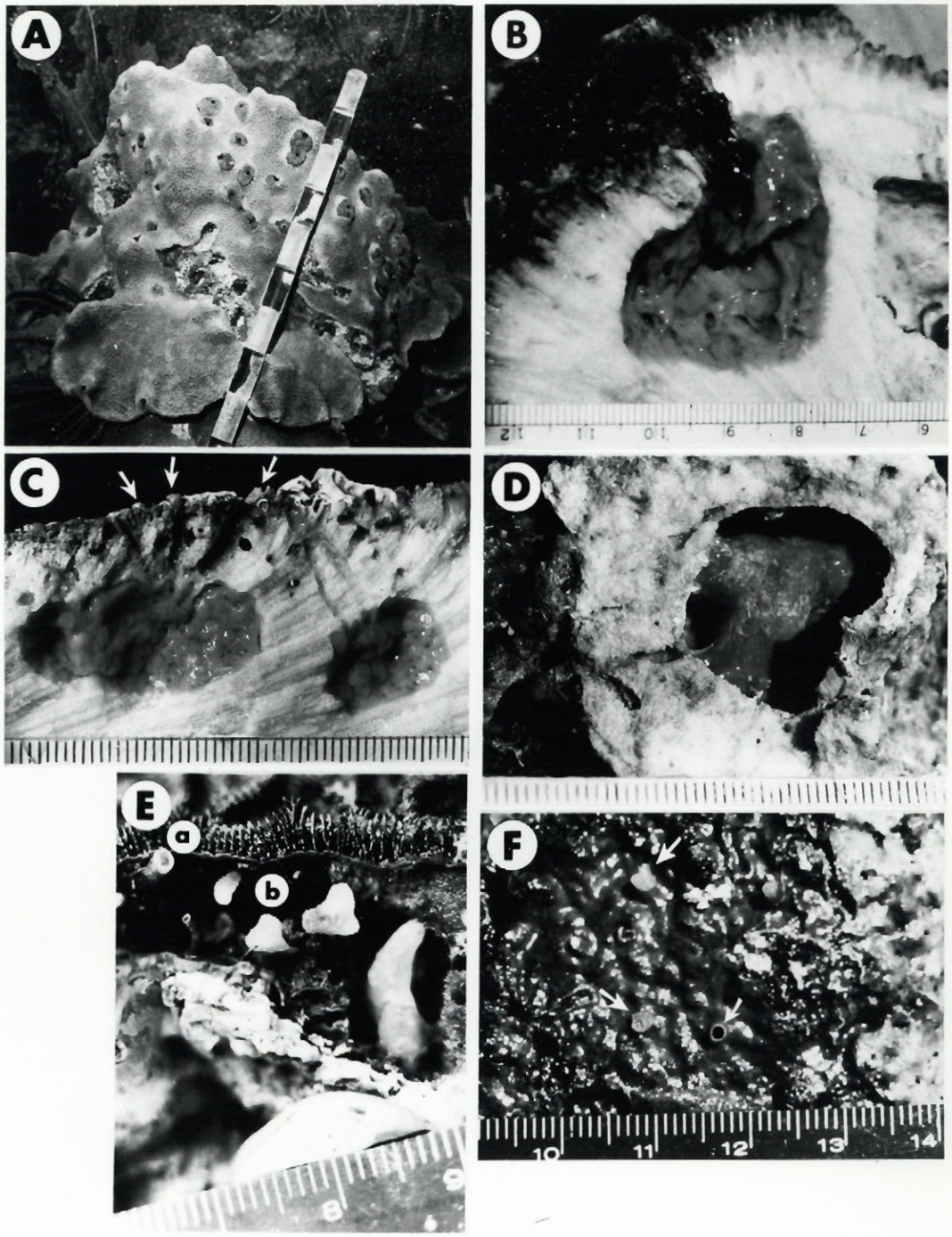

A
B
C
D
E
a
b
F

PLATE A5

A. Spicules of Cliona vermifera. Note the characteristic smooth spirasters. (x 175)

B. Cliona ensifera spicules. (x 110)

C. Tylostyle heads (x 270) and spiraster (insert, x 75) of Cliona ensifera.

D. Cliona mucronata tylostyles. (x 90)

E. Cliona mucronata tylostyles (x 225). Spiraster in lower left is foreign.

F. Tylostyle and spirasters (type 1:a; type 2:b) of Cliona schmidti. (x 250)

G. Tylostyles of Cliona caribbaea. (x 110)

H. Tylostyle heads (x 225) and spirasters (insert, x 300) of Cliona caribbaea.

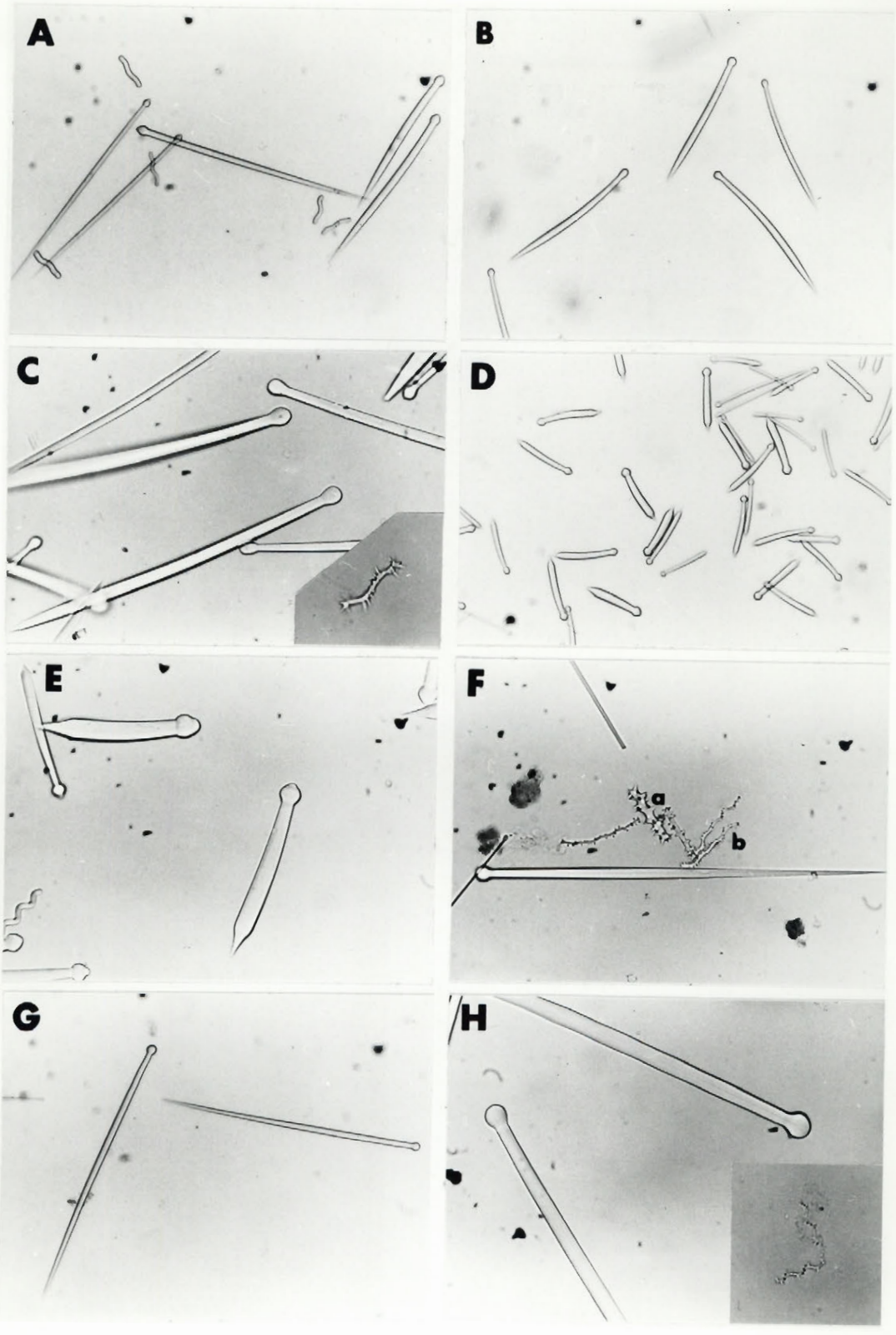

A
B
C
D
E
F
a
b
G
H

PLATE A6

A. Tylostyle and oxea of *Cliona* ?*rovignensis*. (x 100)

B. *Cliona lampa* tylostyle and oxea. (x 200)

C. Tylostyles of *Cliona delitrix*. (x 125)

D. *Cliona amplicavata* tylostyles. (x 125)

E. Tylostyles and spirasters of *Cliona flavifodina*. (x 100)

F. Spirasters of *Cliona flavifodina*. (x 35)

G. *Cliona paucispina* spicules. (x 75)

H. Spicules of *Cliona* sp. 1. (x 120)

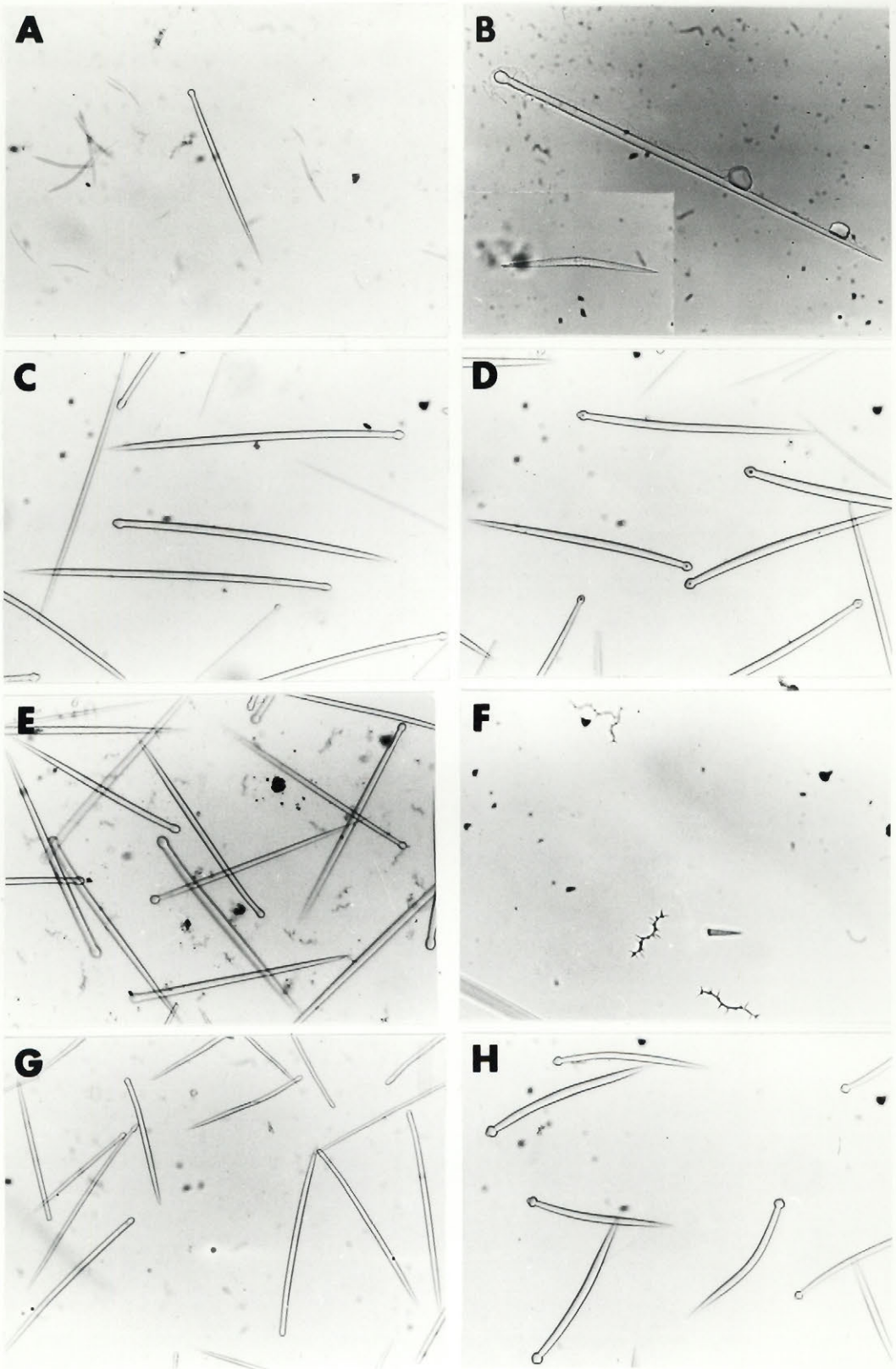

A
B
C
D
E
F
G
H

PLATE A7

A. Tylostyles of Cliona sp. 2. (x 110)

B. Type 1 amphiasters (a), type 2 amphiasters (b) and tetractine spicules (c) of Thoosa sp. 1. (x 225)

C. Type 1 amphiasters (a) and type 2 amphiasters (b) of Thoosa sp. 2. (x 225)

D. Amphiasters (a), toxas (b) and rhaphides (c) of Thoosa sp. 3. (x 225)

E. Spheciospongia sp. spicules. (x 80)

F. Stout tuberculate diactinal spicules of Alectona jamaicensis. (x 175)

G. Stout diactinal spicule (a), thin diactinal spicules (b) and amphiasters (c) of Alectona jamaicensis. (x 175)

H. Oxea and spirasters of species X. (x 100: insert of spiraster, x 475)

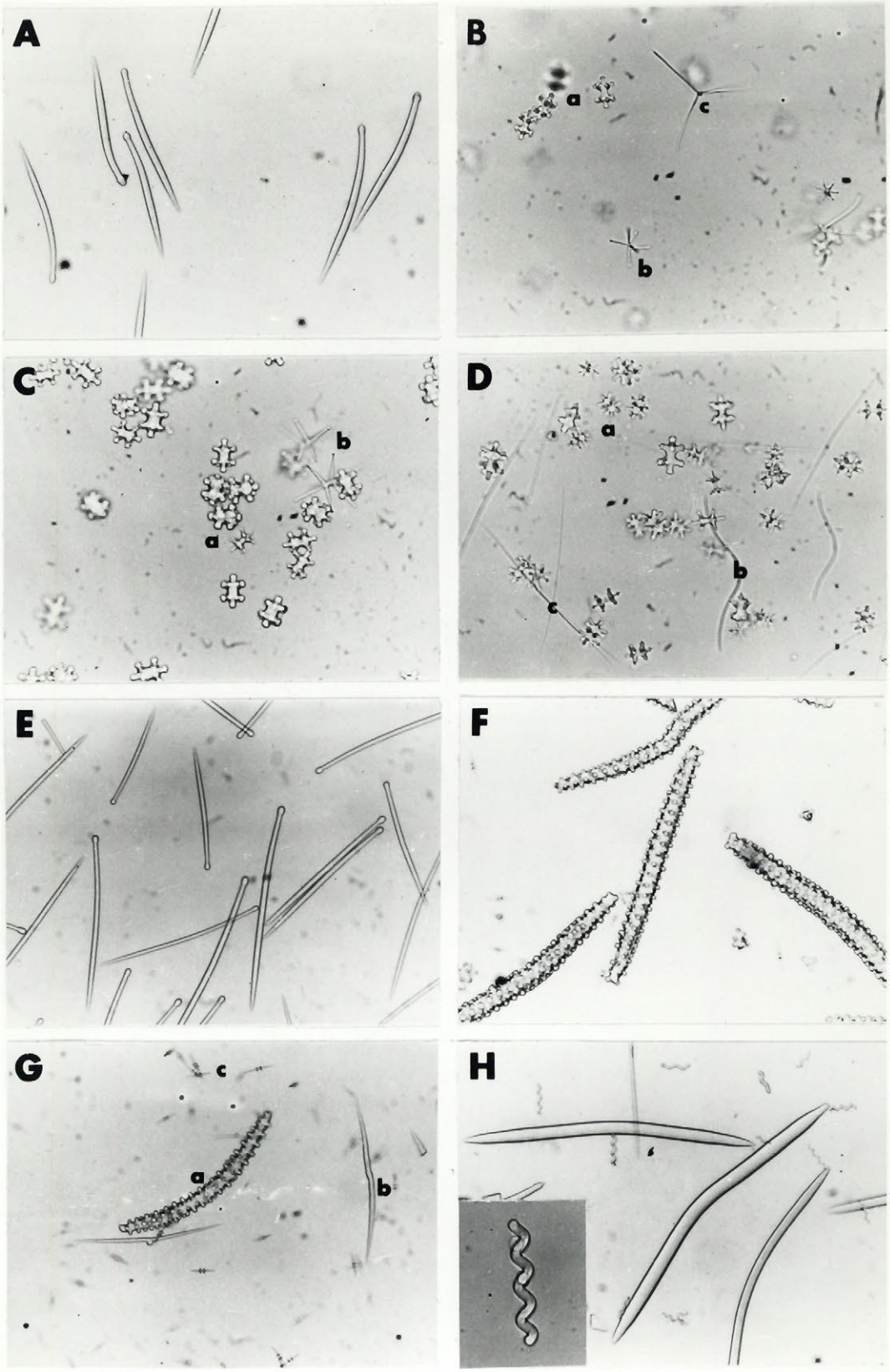

A
B
a
c
b
C
b
a
D
a
b
c
E
F
G
c
a
b
H

PLATE A8

A. Oxea of S. cachacrouense. (x 250)

B. Oxea of S. coralliphagum forma typica. (x 275)

C. Subgroup 1A oxea (S. coralliphagum forma obruta). (x 275)

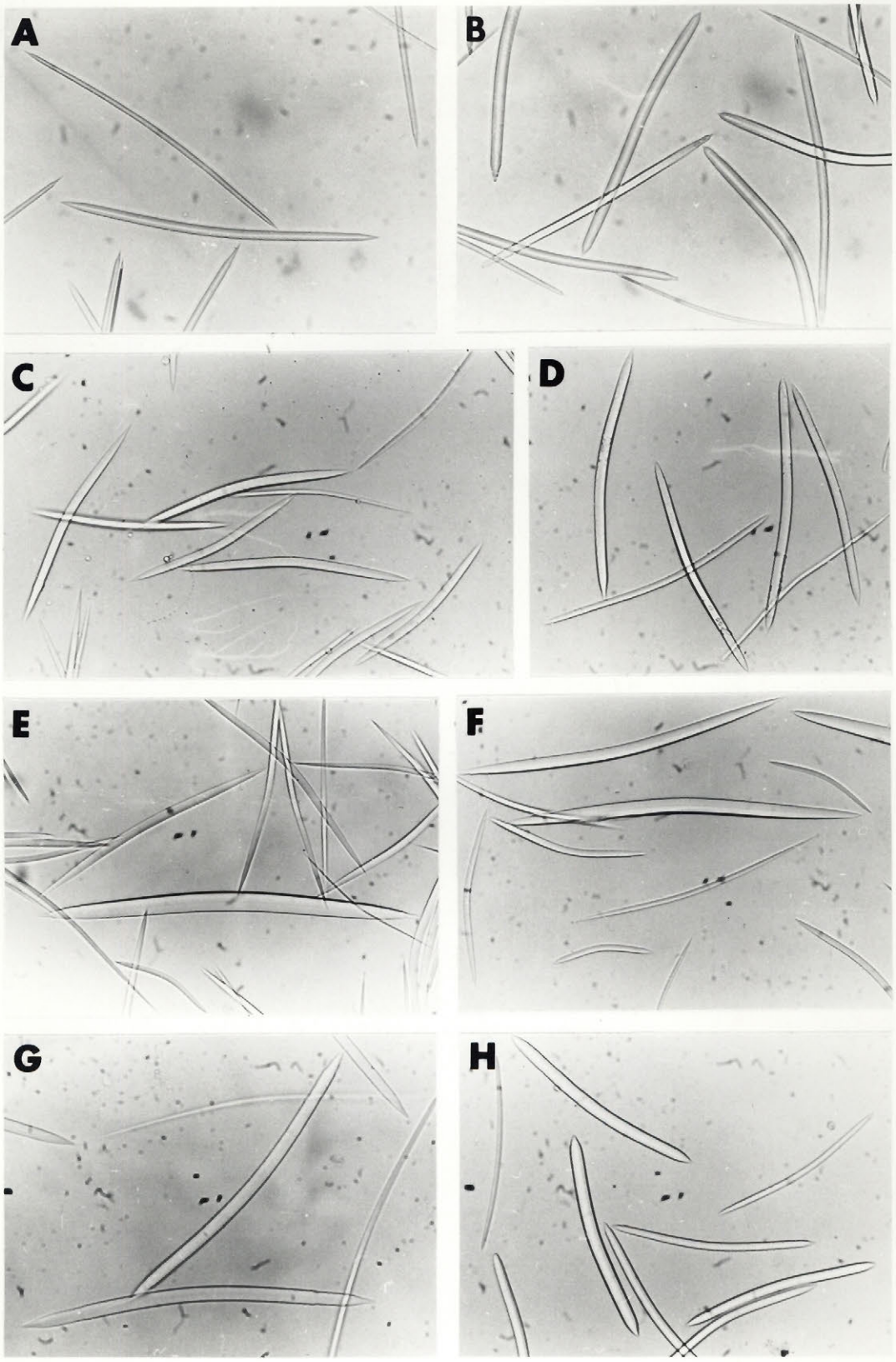
D. Subgroup 2A oxea (S. coralliphagum forma obruta). (x 275)

E. Siphonodictyon sp. oxea (x 275). Note the gradually stepped tips on the large oxea.

F. Siphonodictyon sp. oxea (x 275). Note the size variation in oxea.

G. Subgroup 2B oxea (S. coralliphagum forma obruta). (x 375)

H. Subgroup 2C oxea (S. coralliphagum forma obruta). (x 250)


A
B
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APPENDIX B

Foreword

Tables B1-5 list the sponge species which were present in specimens of each coral species which was sampled on the fringing reef. Tables B6-19 list the species which were present in coral specimens sampled on transects 4 and 5 on the bank reef. Specimen location (in metres offshore on the fringing reef and in metres across the reef on the bank reef) and depth (in metres) are indicated.

Tables B20-23 list the species which were present in P. porites, coralgal substrate and coral rubble on the fringing reef.

Tables B24-32 list age, volume bored (VB), area and weight removed by boring sponges in massive coral specimens of each coral species sampled on the fringing and bank reefs.

Abbreviations used for sponge species names in Tables B1-23 are listed below:

Cm - C. mucronata
Cc - C. caribbaea
Cd - C. delitrix form 2
Cv - C. vermifera
Cl - C. lampa
Ce - C. ensifera
Ca - C. amplicavata
Cs - C. schmidti
Cr - C. ?rovignensis
Cf - C. flavifodina
Cl - Cliona sp. 1
C2 - Cliona sp. 2
X - species X
T - Thoosa spp. 1 and 2
AJ - Alectona jamaicensis
S1 - S. coralliphagum forma obruta
S2 - Siphonodictyon sp. form 1
S3 - network-forming Siphonodictyon species (S. coralliphagum form 5 and Siphonodictyon sp. form 2)
Sp - Spheciospongia sp.

Other abbreviations:

Z - depth
Ss - *S. siderea*
Pa - *P. astreoides*
\+ - present

TABLE B1: Montastrea annularis sample -- Fringing reef transect 3

Specimen Location (m offshore)	Z	Sponge Species																		
		Cm	C1	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
120	1.3		+								+									
130	2.0		+											+					+	
140	2.7		+									+							+	
150	3.7	+											+							
160	3.3	+		+																
170	4.0		+		+															
180	4.0		+		+							+								
190	5.3							+				+								
200	6.0				+					+			+						+	
210	6.7	+		+									+							
220	7.0			+			+													
230	7.3											+								
240	8.0				+							+			+					
250	8.0	+		+			+													
260	8.7	+										+								

TABLE B2: Siderastrea siderea sample -- Fringing reef transect 3

Specimen Location (m offshore)	Z	Sponge Species																		
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	Sl	Cr	S2	X	AJ	T	Sp	Cf
130	2.0												+							
140	2.7																			
160	3.3	+																		
170	4.0									+			+						+	
180	4.0																		+	
190	5.3												+							
200	6.0																			
210	6.7																			
220	7.0	+					+													
230	7.3				+		+					+								
240	8.0																			
250	8.0			+																

TABLE B3: Porites astreoides sample -- Fringing reef transect 3

Specimen Location (m offshore)	Z	Sponge Species																		
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	Sl	Cr	S2	X	AJ	T	Sp	Cf
120	1.3												+							
130	2.0		+	+															+	
140	2.7																		+	
150	3.7	+										+	+							
160	3.3		+	+									+	+						
170	4.0				+														+	
180	4.0			+	+						+		+							
190	5.3			+			+													
200	6.0	+																		
210	6.7				+							+								
220	7.0												+						+	
230	7.3			+	+															
240	8.0											+								
250	8.0						+													

TABLE B4: Agaricia agaricites -- Fringing reef transect 3

Specimen Location (m offshore)	Z	Sponge Species																	
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
120	1.3																			
130	2.0			+																
140	2.7			+											+					
150	3.7						+											+		+
160	3.3	+									+									
170	4.0												+							
180	4.0												+							
190	5.3	+																		
200	6.0	+		+																
210	6.7					+							+							
220	7.0																			
230	7.3	+																		
240	8.0			+		+														
250	8.0																			

TABLE B5: Siderastrea siderea and Porites astreoides spot samples -- North lobe of fringing reef

Coral Specimen	Z	Sponge Species																		
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
Ss 1	3			+			+							+						
2	4								+										+	
3	3							+				+							+	
4	3			+				+												
5	4			+					+											
6	4					+		+												
Pa 1	1			+				+										+		
2	3			+				+										+		
3	2	+	+	+																+
4	4	+																		
5	4			+								+								
6	3			+																
7	3			+									+							

TABLE B6: Montastrea annularis sample -- Bank reef transect 4

Specimen Location (m across reef)	Z	Sponge Species																	
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
20	26.3									+	+									
22	25.0		+																	
22	25.0		+													+			+	
25	23.1	+	+								+									
30	20.7											+				+			+	
50	13.7			+			+												+	
60	13.0		+									+			+					
70	13.3		+									+	+							
80	13.7	+										+								
90	13.7	+		+		+										+				
100	14.0		+									+								
125	13.3		+																	
150	14.0		+													+			+	
180	20.0					+						+		+		+				
188	25.0											+			+			+		
190	26.0												+	+		+				
190	26.0													+		+				
210	32.0					+														
210	33.0	+		+				+						+						

TABLE B7: Montastrea annularis sample -- Bank reef transect 5

Specimen Location (m across reef)	Z	Sponge Species																	
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
0	33.3	+												+						
5	30.0	+												+		+				
10	26.7		+	+										+						
12	25.0		+										+							
12	25.0		+									+	+			+				
20	20.0	+		+								+			+					
20	20.0		+		+										+					
40	14.3	+																	+	
50	13.0			+									+	+						
60	12.7	+																		
65	12.7		+		+														+	
70	12.7	+						+							+					
80	12.7	+													+					
90	13.3		+												+	+				
100	13.7			+							+	+		+						
110	13.7		+			+									+					
120	13.3		+													+				

TABLE B8: Montastrea cavernosa sample -- Bank reef transect 4

Specimen Location (m across reef)	Z	Sponge Species																		
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	Sl	Cr	S2	X	AJ	T	Sp	Cf
0	33.3												+							
20	26.3		+	+										+		+				
22	25.0	+		+									+							
25	23.1	+																		
30	20.7	+										+				+				
50	13.7		+																+	
60	13.0		+										+			+			+	
70	13.3	+	+										+	+	+	+				+
80	13.7	+		+																
90	13.7	+												+						
100	14.0	+											+							
125	13.3	+												+					+	
150	14.0		+									+					+			
210	32.0						+						+	+						
210	32.0	+																		

TABLE B9: Montastrea cavernosa sample - Bank reef transect 5

Specimen Location (m across reef)	Z	Sponge Species																	
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	Sl	Cr	S2	X	AJ	T	Sp	Cf
10	26.7	+											+		+					
15	23.0										+		+							
20	20.0	+											+		+					
40	14.3	+											+							
50	13.0	+				+							+	+						
60	12.7										+									
65	12.7		+												+					
80	12.7											+			+				+	
90	13.3	+		+												+	+			
100	13.7	+																		
110	13.7	+	+												+					
120	13.3	+												+						

TABLE B10: Siderastrea siderea sample - Bank reef transect 4

Specimen Location (m across reef)	Z	Sponge species																		
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
20	26.3		+				+						+			+				
22	25.0			+								+		+						
25	23.1						+					+	+						+	
30	20.7		+									+							+	
50	13.7			+									+							
60	13.0												+							
70	13.3		+	+	+							+		+						
80	13.7			+		+						+	+						+	
90	13.7					+							+							
100	14.0		+													+				
125	13.3							+					+							
150	14.0		+	+								+								
210	32.0				+									+						

TABLE B11: Siderastrea siderea sample - Bank reef transect 5

Specimen Location (m across reef)	Z	Sponge species																	
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
10	26.7							+					+							
20	20.0			+				+				+								
40	14.3	+										+	+							
50	13.0	+	+	+																
60	12.7	+	+									+							+	
65	12.7		+	+									+	+					+	
65	12.7				+			+					+							
70	12.7			+																
80	12.7											+								
90	13.3			+				+					+		+					
100	13.7		+																+	
110	13.7	+		+								+	+	+						
120	13.3												+							

TABLE B12: Porites astreoides sample - Bank reef transect 4

Specimen Location (m across reef)	Z	Sponge species																	
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
0	33.3			+										+					+	
20	26.3											+	+							
22	25.0																			
25	23.1	+		+																
30	20.7			+	+							+								
50	13.7			+											+					
60	13.0			+										+						
70	13.3			+									+	+						
80	13.7	+		+																
90	13.7	+		+															+	
90	13.7											+	+						+	
100	14.0		+	+									+							
125	13.3			+								+		+	+					
150	14.0		+	+								+			+					
180	20.0						+						+						+	
188	25.0													+						
188	25.0												+							
188	25.0			+								+	+	+						
190	26.0						+							+						
190	26.0												+	+						
210	32.0			+	+															
210	32.0			+						+			+							
210	33.0				+								+	+						

TABLE B13: Porites astreoides sample - Bank reef transect 5

Specimen Location (m across reef)	Z	Sponge species																		
		Cm	C1	Cc	Cd	Cv	C1	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
10	26.7			+								+	+	+				+		
15	23.0		+					+				+		+					+	
20	20.0						+					+			+					
40	14.3																			
50	13.0			+								+	+						+	
60	12.7										+								+	
70	12.7																			
80	12.7											+		+						
90	13.3			+																
100	13.7	+		+																
110	13.7																			
120	13.3			+																

TABLE B14: Agaricia agaricites sample - Bank reef transect 4

Specimen Location (m across reef)	Z	Sponge species																		
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	Sl	Cr	S2	X	AJ	T	Sp	Cf
50	13.7	+	+				+						+							
60	13.0		+			+							+			+				
70	13.3		+							+				+						
80	13.7		+																	
90	13.7	+												+					+	
100	14.0		+										+							
125	13.3																			
150	14.0			+																

TABLE B15: Agaricia agaricites sample - Bank reef transect 5

Specimen Location (m across reef)	Z	Sponge species																	
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
50	13.0						+								+					
60	12.7				+															
70	12.7		+												+					
80	12.7												+	+					+	
90	13.3												+							
100	13.7	+																		
110	13.7					+														
120	13.3	+				+				+					+					

TABLE B16: Stephanocoenia michelinii sample - Bank reef transect 5

Specimen Location (m across reef)	Z	Sponge species																	
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
10	26.7						+							+						
20	20.0			+									+							
40	14.3						+						+					+		
50	13.0		+																	
70	12.7														+					
80	12.7	+																		
90	13.3	+		+									+							
100	13.7		+																+	
110	13.7	+	+																	
120	13.3	+																		

TABLE B17: Diploria sample - Bank reef transects 4 and 5

Specimen Location (m across reef)	Z	Sponge species																		
		Cm	C1	Cc	Cd	Cv	C1	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
T5-40	14.3			+			+							+		+				
50	13.0	+	+									+								
60	12.7		+										+							
80	12.7					+						+			+					
90	13.3						+						+							
100	13.7	+																		
110	13.7	+													+					
120	13.3	+	+			+													+	
T4-50	13.7					+	+						+		+					
60	13.0						+						+							

TABLE B18: Colpophyllia natans sample - Bank reef transect 5

Specimen Location (m across reef)	Z	Sponge species																		
		Cm	C1	Cc	Cd	Cv	C1	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
40	14.3	+																		
50	13.0	+	+	+	+								+		+					
60	12.7		+										+		+					
120	13.3	+						+					+							

TABLE B19: Agaricia lamarcki sample - Bank reef transects

Specimen Location (m across reef)	Z	Sponge species																		
		Cm	C1	Cc	Cd	Cv	C1	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
T4-20	26.3	+	+					+				+	+							
T5-5	30.0	+		+	+												+			
5	30.0	+																		

TABLE B20: Porites porites samples - Fringing reef transects 1-3

Specimen Location (m offshore)	Z	Sponge species																		
		Cm	C1	Cc	Cd	Cv	C1	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
T1-10	1.0				+			+	+											
20	3.0			+	+			+	+											
30	2.0			+															+	
40	2.3			+	+			+	+				+							
45	3.0			+	+			+					+							
50	3.3			+	+			+												
60	2.7			+	+			+												
70	6.0							+					+							
80	8.0				+			+												
T2-120	1.3			+																
130	2.3								+				+							
140	2.7			+					+				+						+	
160	3.3			+				+					+						+	
190	4.7			+					+				+							
210	3.0			+			+						+				+		+	
220	5.0				+															
T3-120	1.3				+															
130	2.0				+															
140 (1)	2.7			+																
140 (2)	2.7	+																	+	
160 (1)	3.3				+								+							
160 (2)	3.3				+			+					+							

TABLE B21: Cor-algal sample - Fringing reef transect 1

Specimen Location (m offshore)	Z	Sponge Species																		
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	S1	Cr	S2	X	AJ	T	Sp	Cf
0	1.0	+				+	+											+		
10	1.0						+						+						+	
20 (1)	3.0						+	+	+		+							+	+	+
20 (2)	3.0						+	+			+							+	+	
30	2.0			+				+										+	+	
40	2.3		+	+				+			+							+		+
50	3.3			+	+		+					+	+					+		
60	2.7			+	+							+								
70 (1)	6.0	+		+	+															
70 (2)	6.0			+	+						+							+		
80	8.0	+		+	+								+		+					+

TABLE B22: Cor-algal sample - Fringing reef transect 2

Specimen Location (m offshore)	Z	Sponge Species																		
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	Sl	Cr	S2	X	AJ	T	Sp	Cf
110	1.3			+	+		+				+								+	
120	1.3		+	+			+	+			+							+	+	
130	2.3			+												+		+	+	
140	2.7			+			+											+		
150 (1)	3.7						+	+											+	
150 (2)	3.7			+		+	+				+		+			+		+	+	
160	3.3		+	+							+		+				+			
170	3.7		+	+		+						+						+		
190	4.7			+	+			+	+			+	+						+	+
200	3.3	+		+							+	+	+		+					
210	3.0			+			+						+					+	+	
220	5.0	+		+	+				+			+	+							
230	4.3		+								+		+	+						+

TABLE B23: Coral rubble sample - Fringing reef transects 1-3

Specimen Location (m offshore)	Z	Sponge Species																		
		Cm	Cl	Cc	Cd	Cv	Cl	Ce	Ca	Cs	C2	S3	Sl	Cr	S2	X	AJ	T	Sp	Cf
T1-10	1.0						+													
10	1.0					+	+													
10	1.0																			
T2-2	0.3						+													
2	0.3																			
5	0.3					+														
6	0.4					+														
10	0.5					+														
10	0.5					+														
20	0.7					+							+							
20	0.7																			
30	1.0					+							+							
30	1.0						+		+				+					+		
T3-2	0.3					+							+							
2	0.3																			
10	0.5																			
10	0.5						+		+											
30	1.0					+		+												
30	1.0												+							

TABLE B24: Rates of boring in Montastrea annularis on fringing reef

Specimen Location	Age a	VB %	Area $m^2 \cdot 10^{-4}$	Weight removed $g/m^2/a$
T3-120	16	5.6	133	300
130	7	8.5	44	803
140	9	8.2	95	1007
150	11	3.7	113	394
160	9	4.2	78	482
170	9	2.4	165	282
180	15	5.6	154	727
190	10	2.3	177	259
200	13	5.2	380	674
210	13	2.2	95	289
220	13	0.8	154	110
230	11	8.9	113	895
240	8	1.5	78	242
250	12	2.5	133	261

Average weight removed = 480 $g/m^2/a$ (SD = 285)

VB - volume bored

TABLE B25: Rates of boring in Siderastrea siderea on fringing reef

Specimen Location	Age a	VB %	Area $m^2 \cdot 10^{-4}$	Weight removed $g/m^2/a$
T3-130	13	2.0	108	115
140	9	0.5	122	23
160	12	5.3	113	419
170	11	3.9	104	379
180	13	0.1	133	5
190	12	0.1	128	8
200	12	0	171	0
210	11	0.1	165	7
220	15	0.3	207	14
230	7	1.7	47	154
240	13	0	159	0
250	14	1.4	171	99

Average weight removed = 102 $g/m^2/a$ (SD = 148)

VB - volume bored

TABLE B26: Rates of boring in Porites astreoides on fringing reef

Specimen Location	Age a	VB %	Area $m^2 \cdot 10^{-4}$	Weight removed $g/m^2/a$
T3-120	11	1.0	100	49
130	10	11.0	82	744
140	10	3.1	122	186
150	11	1.5	122	84
170	14	4.5	143	291
180	13	4.5	86	316
190	12	2.8	128	217
200	11	0	108	0
210	12	12.0	91	621
220	10	0.2	86	15
230	10	0.7	133	36
240	8	0.5	75	28
250	10	0.7	86	43

Average weight removed = 202 $g/m^2/a$ (SD = 239)

VB - volume bored

TABLE B27: Rates of boring in Agaricia agaricites on fringing reef

Specimen Location	Age a	VB %	Area $m^2.10^{-4}$	Weight removed $g/m^2/a$
T3-120	8	0	24	0
130	12	0.7	50	38
140	12	10.3	28	569
150	12	11.8	38	447
160	8	14.5	24	598
170	11	0.7	64	47
180	8	5.5	16	204
190	12	15.1	38	631
210	9	3.0	28	159
230	12	17.8	57	1045
240	12	1.3	57	87
250	7	0.4	20	20

Average weight removed = 320 $g/m^2/a$ (SD = 332)

VB - volume bored

TABLE B28: Rates of boring in Montastrea annularis on bank reef

Specimen Location	Age a	VB %	Area $m^2 \cdot 10^{-4}$	Weight removed $g/m^2/a$
T4-20*	38	14.5	133	621
22*	16	8.9	143	452
22*	15	9.5	78	585
25*	20	11.0	133	573
30*	20	7.9	64	644
50	16	14.5	201	974
60	20	8.7	177	747
70	22	9.2	64	648
80	11	2.5	154	237
90	14	8.1	143	863
100	14	2.8	113	280
125	26	10.4	50	873
150	28	4.6	133	274
20 m**	15	12.0	113	766
25 m**	10	4.6	177	354
26 m**	11	15.8	85	1046
32 m**	15	22.6	201	783
33 m**	12	3.2	154	146
33 m**	13	4.9	177	220

TABLE B28: Continued

Specimen Location	Age a	VB %	Area $m^2 \cdot 10^{-4}$	Weight removed $g/m^2/a$
T5-0*	20	6.1	235	114
5*	32	20.3	227	674
10*	19	17.7	95	509
20*	25	15.1	78	929
50	40	15.9	154	589
60	11	9.3	38	546
70	12	4.0	78	281
80	25	18.4	64	1059
90	30	10.3	211	379
100	32	9.4	143	418
110	21	9.6	87	433
120	21	12.8	104	831

Average weight removed - bank top = 590 $g/m^2/a$ (SD = 274)
- outside edge = 567 $g/m^2/a$ (SD = 216)
- inside edge = 552 $g/m^2/a$ (SD = 363)

* outside edge

** inside edge

VB - volume bored

TABLE B29: Rates of boring in Montastrea cavernosa on bank reef

Specimen Location	Age a	VB %	Area $m^2 \cdot 10^{-4}$	Weight removed $g/m^2/a$
T4-20*	20	24.0	123	841
22*	16	1.7	95	73
25*	27	12.9	123	490
30*	35	24.6	95	884
50	40	11.9	154	456
60	26	20.9	154	789
70	23	9.1	113	312
80	18	4.5	143	264
90	24	19.0	87	560
100	12	16.4	113	470
125	24	29.3	227	1203
150	24	7.4	123	307
T5-10*	43	12.4	299	430
15*	21	11.6	154	745
20*	32	18.3	143	794
40	37	22.2	201	750
50	35	12.0	330	446
60	26	14.5	154	402
80	16	19.3	189	863
90	37	23.8	314	867
100	30	9.1	133	775
110	34	19.2	57	522
120	22	7.2	71	366

Average weight removed - bank top = 585 $g/m^2/a$ (SD = 263)
- outside edge = 608 $g/m^2/a$ (SD = 293)

* outside edge

VB - volume bored

TABLE B30: Rates of boring in Siderastrea siderea on bank reef

Specimen Location	Age a	VB %	Area $m^2 \cdot 10^{-4}$	Weight removed $g/m^2/a$
T4-20*	24	11.7	165	556
22*	22	18.9	86	703
25*	19	8.7	133	547
30*	18	10.0	188	471
50	15	1.7	177	132
60	12	2.4	113	181
70	21	6.3	254	433
80	26	13.1	201	709
90	14	1.1	154	76
100	20	9.4	113	516
125	19	9.1	122	415
150	16	2.3	133	106
T5-10*	27	9.8	133	513
20*	23	6.3	183	285
40	10	9.1	53	522
50	20	4.3	154	201
60	35	16.5	108	1417
70	15	6.6	100	323
80	16	2.9	177	233
90	30	14.9	227	852
100	13	5.2	113	396
110	18	8.3	201	636
120	15	1.5	104	113

Average weight removed - bank top = 427 $g/m^2/a$ (SD = 342)
- outside edge = 512 $g/m^2/a$ (SD = 136)

* outside edge

VB - volume bored

TABLE B31: Rates of boring in Porites astreoides on bank reef

Specimen Location	Age a	VB %	Area $m^2 \cdot 10^{-4}$	Weight removed $g/m^2/a$
T4-0*	20	14.0	177	471
20*	20	1.6	133	95
22*	25	20.4	133	656
25*	25	3.8	214	197
30*	19	3.5	133	157
50	13	1.2	78	84
60	13	6.7	78	549
70	14	8.1	78	392
80	15	2.9	71	172
90	21	9.8	113	479
90	18	6.4	201	454
100	17	6.9	122	415
125	18	2.9	154	165
150	18	6.1	154	292
20 m**	9	7.7	133	197
25 m**	15	1.0	201	30
25 m**	13	0.5	227	10
25 m**	20	1.1	177	46
32 m**	32	1.5	78	88
32 m**	16	2.6	78	100
33 m**	13	11.0	64	503
33 m**	11	5.1	113	207

TABLE B31: Continued

Specimen Location	Age a	VB %	Area $m^2 \cdot 10^{-4}$	Weight removed $g/m^2/a$
T5-10*	21	1.3	363	36
15*	28	7.3	247	267
20*	30	7.4	133	401
40	20	1.2	133	53
50	12	15.7	143	677
60	21	3.9	113	223
80	19	1.5	104	80
90	12	0.8	57	45
100	17	5.4	108	283
110	18	0.1	133	10
120	20	0.0	91	0

Average weight removed - bank top = 257 $g/m^2/a$ (SD = 207)
- outside edge = 285 $g/m^2/a$ (SD = 210)
- inside edge = 148 $g/m^2/a$ (SD = 161)

* outside edge

** inside edge

VB - volume bored

TABLE B32: Rates of boring in Agaricia agaricites on bank reef

Specimen Location	Age a	VB %	Area $m^2 \cdot 10^{-4}$	Weight removed $g/m^2/a$
T4-50	24	18.2	99	1029
60	23	12.3	78	722
70	22	12.4	95	584
80	16	4.3	64	214
90	23	20.8	104	1280
100	19	13.3	64	628
150	24	24.2	113	1455
T5-50	10	6.3	47	481
60	11	6.3	38	383
70	17	10.4	108	599
80	13	15.7	38	1324
90	11	2.3	38	151
100	26	20.7	95	1061
110	15	11.7	24	546
120	22	24.8	87	885

Average weight removed - bank top = 756 $g/m^2/a$ (SD = 402)

VB - volume bored