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by CHRIS M. BOERBOOM for
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Undergraduate course number GEOLOGY 4K06 at McMaster
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BIOEROSION AND MICRITIZATION IN THE DEEP SEA
A Look a the Coral *Desmophyllum cristagalli*

BIOEROSION AND MICRITIZATION IN THE DEEP SEA

A Look at the Coral *Desmophyllum cristagalli*

by

Chris M. Boerboom

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AUTHOR: Chris M. Boerboom

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Abstract

An assemblage of coral skeletons of the species *Desmophyllum cristagalli* were obtained from the top of Orphan Knoll, 550 km northeast of Newfoundland, from depths of approximately 1600 and 1800 m. The corals were observed for their macro- and micro-boring assemblages, and the boring morphologies documented, using binocular and scanning electron microscopy. Samples of coral were embedded with resin and etched for examination of the micro-boring assemblages.

The largest volumetric amount of skeletal material removed was by sponges forming *Entobia*. This further corroborates the assumption that various species of boring sponges are distributed ubiquitously throughout a wide bathymetric range.

Four distinct fungal forms were found, two tubular forms interpreted to be hyphal filaments and two bulbous forms interpreted to be sporangia. These forms were described on the basis of their shape, size, mode of branching, association with other structures and texture. They were then compared to other micro-boring assemblages found in previous studies from various bathymetric ranges. Some forms described in this study were found to be similar to forms described in other studies. Other forms in this study were not found to be documented. It is suggested, therefore, that certain forms, as well as low ichnodiversity, may indicate deeper water environments.

Destructive micritization structures were also found in resin casts as well as in thin section. The extent of micritization may indicate the intensity of the

parameters at the substrate that affect carbonate dissolution, such as CaCO_3 and CO_2 concentrations, pH, temperature, and salinity. It would therefore indicate the ambient water conditions at the substrate. If a sufficiently large database could be obtained, as well as distinct separation of the parameters responsible for carbonate dissolution, micritization may be used in a mapping of the carbonate compensation depth through time and depth ranges.

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1 INTRODUCTION

1.1 Background and Previous Work

1.1a Bioerosion

Bioerosion is a term that was suggested by Neumann (1966; *fide* Warne, 1975) to be "erosion of substrate by means of biological procedures". Any organism that contributes to the mechanical or chemical destruction of a hard substrate, whether by scraping and rasping on the substrate surface or by boring and tunnelling networks within the substrate, can be regarded as a bioeroder. What is left behind (post mortem of the bioeroder) are distinctive traces that may indicate the morphology and behavioral characteristics of the organism responsible.

Study of these traces has led to some confusion in the literature. Some researchers apply the taxonomic name of the trace maker to the trace itself (Thomas, 1911; *fide* Bromley, 1970a), while others use binomial ichnotaxonomy to distinguish between morphologically different borings (Bromley, 1970a). Ichnotaxonomy has been successfully developed in some areas, such as the application of the ichnogenus *Entobia* to traces made by the family Clionidae of the phylum Porifera. In other areas, such as the microboring world of fungi, algae and bacteria, no such system has been developed. In this study, therefore, the morphological characteristics of the microborings observed were simply described and compared with previous studies.

It has been suggested that assemblages of microborings within a substrate

may be a valuable tool in the reconstruction of paleoecology and especially paleobathymetry (Golubic *et al*, 1975, 1984; Zeff & Perkins, 1979; Budd & Perkins, 1980). Their distribution is ubiquitous both within the world's oceans and through geological history, from Cambrian to Holocene times (Budd & Perkins, 1980). This makes them a useful tool when cross referenced with other paleoecological indicators.

1.1b Micritization

The production of micrite (microcrystalline calcite) and micrite envelopes and their relation to microboring organisms, especially in warm, tropical waters supersaturated in CaCO_3 , is well documented (Alexandersson, 1972; Kobluk & Risk, 1977). Bathurst (1966) first described the process of micritization, and Kobluk and Risk (1977) documented the process of micrite envelope formation by precipitation of calcite on exposed algal filaments. Boring infilling by precipitation of calcite is also well documented. These processes, however, are only likely to occur in warmer surface waters supersaturated with CaCO_3 .

In colder waters undersaturated in CaCO_3 direct precipitation is less prominent. In this type of environment, dissolution of calcareous substrates is much more likely to occur (Alexandersson, 1972, 1978, 1979; Kobluk & Risk, 1977). This dissolution process, known as destructive micritization or selective leaching (Alexandersson, 1972), involves the removal of crystals of calcite or aragonite. What is left behind is a micritic structure of the remaining lamellae of

the crystal matrix (coral, shell, etc.).

The level in the oceans where the accumulation of calcareous substrate (through precipitation and/or sedimentation) is equal to its dissolution (destructive micritization) is referred to as the Carbonate Compensation Depth (CCD) (Edmond, 1973). Therefore, no net accumulation of carbonate substrate will occur below the CCD. Factors affecting the dissolution of calcareous substrates, and therefore the CCD, are the concentration of carbon dioxide, pH, alkalinity, salinity, temperature, and pressure (Berger, 1968). Another notable zonation in the oceans is the lysocline, the level above which no carbonate dissolution occurs. This feature, as well as the CCD, is likely to have fluctuated both geographically and through geological time. It is proposed, therefore, that the degree of dissolution, i.e. the extent of micritization, may indicate something of the paleoenvironmental conditions on ancient substrates. This may then be used in mapping variations in both the CCD and the lysocline in the world's oceans.

It should be noted as well that the topography of micrite formed during destructive diagenesis is controlled to some degree by spatial variations in mineralogy and composition of the matrix (Alexandersson, 1976). In today's oceans, high magnesian calcites are the most soluble of calcareous sediments and substrates, followed by low magnesian calcite and aragonite, with pure calcite having the lowest solubility.

1.2 Study Area

The corals used in this study were dredged from the top of Orphan Knoll, a topographically high submarine feature. Orphan Knoll is situated approximately 550 km northeast of Newfoundland, north of Flemish Cap, the exact position being 55° 25.57'N, 46° 22.05'W (Figure 1). Water depths at the top of the knoll range from 1800 m in the south to 2400 m in the north. It is bounded on all sides by relatively deep water, with depths of 2800 m to 3400 m to the west and south and up to 4000 m to the north.

The top of the knoll is covered by a blanket of sediments, with older, topographically high features protruding through. It is on these harder substrates that the corals grew, presumably dropping to the sediment after death. The sedimentation rate on the knoll has been fairly constant throughout the Plio-Pleistocene, with an average rate of 5 cm / 1000 yrs (Smith, 1993).

1.3 *Desmophyllum cristagalli*

The coral *Desmophyllum cristagalli* is solitary, azooxanthellate, and ahermatypic, and is ubiquitously distributed throughout the world's major oceans. It is also found in wide bathymetric ranges, from 35 - 2460 m. It attaches itself by a bulky pedicle generally to hard substrates that are vertical, or to the undersides of ledges. This leads to a number of corals piling up at the base of these hard, vertical substrates after dying, being knocked off or broken. It is presumed that it is from one

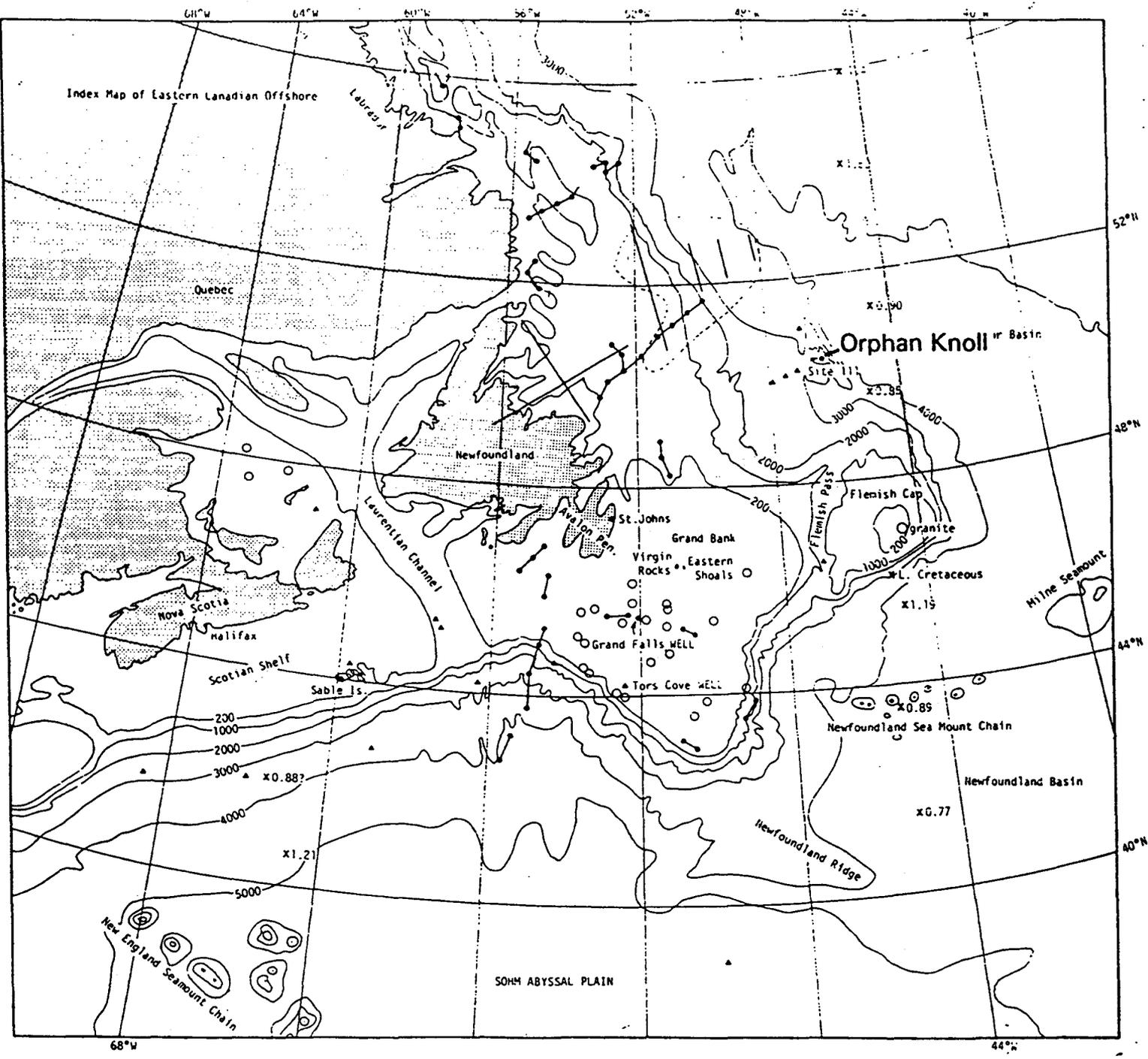


Figure 1: Map of Orphan Knoll and the surrounding area. Bathymetries can be seen to reach 4000 m around the Knoll (from Smith, 1993).

of these piles that the corals were dredged.

The corals were obtained from two dredges, 1628 and 1792 m depth, in 1978. Radiocarbon and U/Th dating on the corals revealed two general age groups, one 11 000 - 14 000 y BP, the other 50 000 - 60 000 y BP.

1.4 Methods

The initial intentions of the study were to observe and document the extent of bioerosion suffered by the corals, as well as the description and tabulation of the bioerosion traces. The initial steps were therefore general observation of the corals and macroborings through regular binocular microscope.

The next step was to document the extent and type of microborings within the coral. This was done by a resin casting technique, which was developed specifically for studying boring traces by Golubic *et al* (1970). This particular technique has revolutionised the study of borings in calcareous substrates, allowing for a three dimensional view of the networks and chambers created by the boring organisms.

The technique used in this study is a simplified version of that described by Golubic. Samples of the coral were taken from the theca and the septum and cut into approximately 1 cm cubes. They were then embedded with a resin (Spurr's medium), filling all voids within the sample including boring traces. One sample (sample 1) was then cut perpendicular to the theca (i.e. - perpendicular to the surface bored by the microorganisms). The other two samples (samples 2 & 3)

were ground down, just exposing the surface (theca) of the coral. All three samples were then washed in an ultrasonic bath for approximately 15 minutes and air dried for several days. Another sample (sample 4), without resin embedding and from the top of a coral including several septa, was given the same bath and dried.

The embedded coral samples were then etched in a 5% HCl solution for 35 - 40 seconds, and then dipped in a carbonate solution. This resulted in the dissolution and removal of several hundred microns of the coral matrix, exposing the fine structures of the borings left behind as resin casts.

All four samples were then taken to the scanning electron microscope (SEM) lab, mounted and sputter coated to give a gold film approximately 8 Angstroms thick. Samples were then analyzed and photographed using the SEM.

One other sample that was used in this study was a thin section, embedded in resin, a cross section of a pedicle of a coral.

2 RESULTS

2.1 Extent of Borings

Approximately 50 to 60 samples were studied, all approximately the same size, 10 to 12 cm long. Upon initial inspection of the corals through binocular microscope it was revealed that they had been thoroughly eroded by boring organisms. In general there seemed to be no areas of the corals that were preferentially bored or abraded. Small holes were found throughout the corals, with no patterns of concentrations of these holes. Mechanical erosion, abrasion and breakage, seemed minimal. Usually only pieces of theca and septa broke off, due to thinning of eroded chambers within the coral. Plate I is a composite SEM photo of the coral surface of sample 4, showing the variety of scrapes, holes and tunnels left by various organisms.

2.2 Sponge Borings: Ichnogenus *Entobia*

Although there were a small variety of scrapes and drill holes on the outer surface of the coral, the most prominently observed borings were that of sponges, leaving the ichnogenus *Entobia*. A very distinctive scalloping texture was easily recognizable under the binocular magnification. The scalloping texture is the result of a combination of chemical and mechanical removal of small chips, which can be from 10 to 125 μm in diameter (Futterer, 1974), and is the mechanism of substrate removal employed by sponges.

A rough estimation of the amount (volume) of material removed by sponges

is from 10 - 70%, which varies from sample to sample. Sponges were by far the greatest volumetric eroder in the corals studied.

An interesting feature observed within the sponge borings are what appeared to be linear "tracks" (Plate II). Several were found and were taken for SEM analysis (sample 4). The tracks are parallel both to each other and to the vertical axis of the septa, at least several millimeters apart, and are restricted to the inside of the sponge borings. Upon close examination with the SEM the inner surface of the "tracks" appeared to have a dissolution texture (Plate II, C). The scalloping texture is beautifully preserved and shown in this sample.

Sponge boring traces were also well preserved in the resin cast samples (Plate III, A-D). Plate III A shows a (relatively) large chamber, likely a sponge domicile. A tunnel (papilla) can be seen connecting the chamber with the outer surface of the coral (Plate III, B). Many other papillae were observed penetrating the coral surface (Plate III, C-D).

2.3 Microborings

Boring microorganisms generally consist of various species of algae, several fungi, and bacteria. In this study, the substrates observed were from a depth well below the photic zone, and as such no algal traces were found. In the samples that were taken, there were no traces that were known to be attributed to bacteria. Therefore, all boring traces were interpreted as fungal forms.

Upon analysis of samples 1 - 3 under SEM, expansive networks of

microboring traces were found (Plate IV, A-B). Microboring penetration occurred within approximately 100 μm of the coral surface. Vast networks were observed, consisting of two tubular forms of borings with the finer form intertwining considerably with the larger form. These widespread tubular networks are likely fungal hyphal filaments. A large number of bulbous sacs were also observed, interpreted to be the reproductive chambers (sporangia) of fungi (Plate IV, C-D). Two forms of sporangia were found, differing in size and shape.

2.3a Fungal Form I

Fungal form I is the larger of the two tubular forms, with diameters ranging from 6 - 8 μm (Plate V, A-C). Tubules are generally straight to slightly sinuous, with branching occurring frequently at angles between 45° and 90° . Their size and shape typically remains constant, with no enlargement at branching sites as is commonly observed in algal borings. The textures of the inner surface of the borings are very well preserved on the resin casts. Form I exhibits a regular coarse texture, interpreted to be the trabecular imprint of the coral matrix. Tubules generally either terminate abruptly with no enlargement, branch dichotomously, or exit to the surface of the coral. They form networks of connecting filaments, and were not observed to be directly related to any reproductive chambers.

2.3b Fungal Form II

Fungal form II is much finer than form I with diameters between 1 and 3 μm

(Plate V). Form II borings form expansive networks, intertwined with form I, and are closely associated with the two forms of reproductive chambers. Tubules are generally more sinuous than form I with no abrupt change in direction, and in many cases wrap around the surface of form I tubules (Plate V, B). Branching occurs less frequently in this form, with most tubules having an abrupt termination, exiting to the surface of the coral, or connecting with reproductive chambers. The surface textures are much smoother than form I, with some tubules appearing to be segmented (Plate V, B).

This form is also closely associated with, and in some cases penetrates, sponge boring chambers (Plate VI, A-B). This relationship, as well as with form I, may be symbiotic, parasitic, or most likely saprophytic. It could not be determined whether the relationship occurred during the life of the sponge or during post mortem decay.

2.3c Fungal Form III

Form III is a flask shaped chamber, most likely a reproductive sporangia chamber (Plate IV, D; Plate VI, C-D). They occur primarily near the surface of the coral, with the thinner end of the chamber exiting to the coral surface. They vary in size from 15 to 40 μm long, presumably in different stages of growth. The surface texture of the inner walls of the chambers is again well preserved, showing the same coarse texture as on form I, a trabecular imprint (Plate VII, A). This form seems to be more closely associated with the form II tubular borings, with hyphal

filaments radiating out at various points usually on the thicker end of the chamber (Plate VII, B).

2.3d Fungal Form IV

Form IV occurs less frequently than form III and seems to be associated primarily with form II tubules (Plate VII, C-D). Form IV borings are generally spherical in shape with diameters of 10 to 20 μm . They occur both exiting to the surface of the coral as well as connecting with hyphal filaments of form II (Plate IV, C). The surface texture is notably different from form III. The origin of this texture is not known, although close examination of Plate VII D may suggest a type of bacterium. No hyphal filaments were seen to radiate out from the chambers as in form III.

2.4 Micrite

Possible destructive micritization was found coincidentally in the resin cast samples (Plate VIII, A-B). These structures seem to be associated with a boring structure probably of sponge origin. What is shown is the remains of crystal lamellae, dissolved in undersaturated ambient water, as resin casts.

This find prompted thin sectioning of a resin cast cross section of a coral pedicle for observation under a polarizing microscope. The thin section (Plate IX, A) shows dark micritic rims around the surface of sponge borings (Plate IX, B, Plate X, A-B). The concave shape of the scalloping texture due to sponge boring

can be seen in thin section. These dark rims are the result of voids in the crystal matrix of the coral (i.e. voids created by the dissolution of crystal lamellae). Beyond the micritic fabric in both the rims and resin casts the remaining coral matrix is unaltered and unaffected by dissolution.

3 DISCUSSION

3.1 Sponge Borings

Sponges and their boring habit have been extensively studied in the shallow marine environment (e.g. Bromley 1970a,b, 1984; Ward & Risk, 1977). Volumetric amounts of skeletal coral material removed has been estimated to range from 3 to 12% (Risk & MacGeachy, 1977) in various species of corals. The large volume of material eroded in these deep water samples suggests two principles: sponges are ubiquitous from warm, shallow, tropical waters to cold, deep sea environments, and sponges rank very high in terms of volumetric amount of skeletal material removed in the deep sea.

Sponge borings were by far the most prevalent macroborer in these samples, and it is suggested that the diversity of macroborers in the deep sea is less than in shallower waters. Using a regular binocular microscope was not sufficient to determine ichnospecies of *Entobia*, therefore it is not known whether the species type and diversity of sponges are similar to shallow water environments.

The "tracks" observed within the sponge borings are a feature that was not found to be cited in any recent literature. Their parallel nature, dissolution-like texture and restriction to within sponge borings made them a curious feature, and several hypothesis as to their origin have been suggested.

One suggestion is that they may be the centers of calcification of the coral that have been exposed by the boring of the sponge. This would explain their

restriction to the boring cavities and their parallel nature. They do not, however, appear similar to other centers of calcification that were found. Also, they are too widely spaced. Another suggestion is that they are tracks of a parasitic or saprophytic organism feeding on the organic material of either living or dead sponge tissue. The dissolution-like texture may be the organism's mode of penetration into the coral matrix. The parallel nature of "tracks" may be explained by a path of least resistance taken by the organism along the septa and growth lines of crystals, although this has not been determined. This theory would also explain the restriction to within the sponge borings.

3.2 Microborings

3.2a Previous Work

It has been proposed by many researchers of microscopic boring endoliths (Golubic *et al*, 1975, 1984; Zeff & Perkins, 1979; Budd & Perkins, 1980; Perkins & Halsey, 1971, Young & Nelson, 1988) that assemblages within carbonate substrates and sediments may be used for a variety of paleoecologic applications. Golubic *et al* (1984) suggested that microbial assemblages, when cross referenced with other paleoecological indicators such as depth-dependent benthic foraminifera, would make for useful and more refined paleobathymetric studies.

Budd & Perkins (1980) studied the boring endolithic assemblages in Puerto Rican shelf and slope sediments in an attempt to characterize and establish bounding limits for upper photic, lower photic and aphotic zones. Their upper

photic zone included a variety of species of green and blue-green algae, several species of fungi, sponges, as well as some undetermined boring morphologies (Figure 2). Their lower photic zone contains several different species of algae, fungi and sponges. Their aphotic zone, which they defined as 75 m down to 550 m depth, comprised four fungal forms, two sponge forms (also found within the lower photic zone), and three other forms of uncertain affinity. It is clear from this study alone that microboring assemblages may prove useful in reconstructing paleobathymetry.

Perkins & Halsey (1971) in their look at Carolina shelf sediments suggested that the microboring assemblages found occur in linear trends, reflecting fossil photic zones. They also suggested that fluctuations in these trends may reflect changes in Pliocene sea level.

These studies have shown microbial assemblages in sediments at depths from the intertidal zone to 550 m and 780 m, respectively. Many other studies have concentrated on sediments and substrates strictly within shallow, intertidal zones. Very little work has been done on endolithic assemblages below 1000m. Golubic *et al* (1984) attempted one of very few studies done on abyssal sediments, from 200m to 4000m. A new, morphologically distinct, endolithic taxon was found between 2000 and 4000 m. The deepest record of boring endolithic activity is 5000 m (Riout & Dangeard, 1967; *fide* Golubic *et al*, 1984). Golubic's study also concluded that the endolithic boring habit is exclusively a benthic phenomenon.

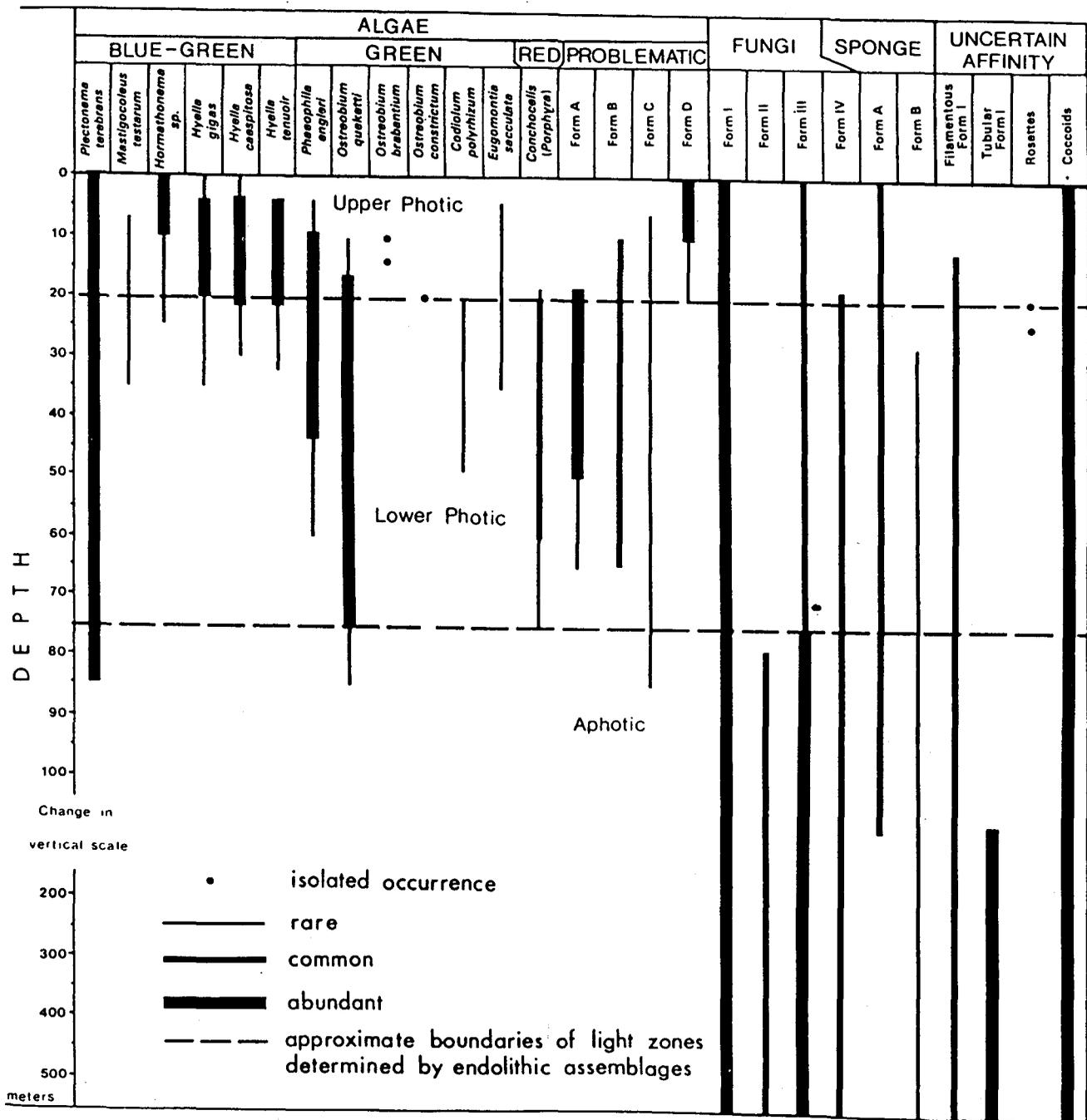


Figure 2: Table of the various boring species assemblages and boundaries of the upper photic, lower photic and aphotic zones in Puerto Rican shelf and slope sediments (from Budd & Perkins, 1980). Four fungal forms, two sponge forms and three uncertain forms are found in their aphotic zone. (Note change in vertical scale).

3.2b Orphan Knoll Microboring Assemblages

The microboring forms found within the Orphan Knoll corals also suggest that these types of microbial assemblages may be used to indicate certain bathymetric zonations. Budd & Perkins (1980) found one tubular form and three bulbous forms of fungal borings that extended into their aphotic zone. None of these forms, however, correlated well with those found in this study. Two of their uncertain affinity forms, tubular form I and their coccoidal form, appear similar to forms I and IV, respectively, in this study, but no conclusions can be drawn.

There are some striking similarities between forms II and IV in this study and some recent and fossil forms found in brachiopod shells in the study by Golubic *et al* (1984, figure 3). His recent forms, however, were from a known depth of 200 m. Other studies (Zeff & Perkins, 1979; Young & Nelson, 1988) have also described similar boring morphologies in carbonates from depth ranges of 100 m to 1400 m. The only attempt to attribute a fungal species to a particular boring was by Golubic, stating that the flask shaped bulbous form was likely created by the cladochytrid (lower fungi) *Dodgella priscus*.

It seems, from this and the few studies that have been carried out on deeper water carbonates, that some fungal forms are distributed ubiquitously throughout a wide bathymetric range. It also seems that other forms may be restricted to more abyssal depths. One may also speculate that the deeper oceans may contain less diversity among fungal morphological boring forms, or a least fungal species. Variations in boring microbial assemblages may indicate the depth zone

of the bored substrate. Other parameters, such as sedimentation rate, water chemistry and latitudinal variations, may also play a part in the distribution of endoliths, and should be considered.

In any case, it is clear that in order to make use of boring endoliths as paleoecological indicators much work needs to be done. This means constructing a sufficiently large database of globally and bathymetrically distributed morphological forms, as well as determining uniform terminology such as the binomial ichnotaxonomy of *Entobia*.

3.3 Destructive Micritization

As with microboring endoliths, micritization and the formation of micrite envelopes has received much more attention in shallow water environments than in the deep sea (e.g. Alexandersson 1972, 1976; Kobluk & Risk, 1977; Bathurst, 1966, 1971). Destructive micritization, described as selective leaching by Alexandersson, has been studied in colder water environments such as the North Sea (Alexandersson, 1978, 1979) and off the coast of Vancouver Island (Young & Nelson, 1988). Although carbonate dissolution in deeper waters and the level of the CCD have been explored (Edmond, 1973; Berger, 1968; Bathurst, 1971), deep sea micritization has not.

Alexandersson (1979) proposed constructive (calcite precipitation), inert (no precipitation or dissolution) and destructive (calcite dissolution) regimes within shallow water environments. It is suggested, then, that dissolution would continue

in deeper and colder water environments undersaturated in CaCO_3 . It is therefore not surprising to find destructive micritization occurring in the deep sea environment of Orphan Knoll. The question proposed is can the extent of micritization indicate the ambient water conditions at the substrate, and can this tell us anything about the depth of the CCD or the lysocline?

The micritic structures observed in this study are not dissimilar to those in shallower, cold water environments. As mentioned, factors affecting the dissolution of carbonate substrates are many, including carbon dioxide concentrations, pH, alkalinity, salinity, temperature and pressure, which can vary greatly throughout the world's oceans. Because of the number of parameters involved, it may prove difficult to separate these factors in terms of extent of responsibility for carbonate dissolution. It may also be difficult, therefore, to determine if an ancient substrate exhibiting destructive micritization was from a high latitude, shallow, cold water environment or a deep abyssal environment. It likely can be ruled out that it did not exist in a tropical, shallow, warm water environment. In any case, destructive micritization in a deep water environment has been documented, but in order to possibly become an environmental indicator much more data from a wide range of latitudes and bathymetries must be obtained.

4 CONCLUSIONS

This study was undertaken to observe and document the micro- and macro-boring assemblages contained within deep sea specimens of the coral *Desmophyllum cristagalli*, using primarily resin casting and scanning electron microscopy. What were found were vast chambers and tunnels within the coral skeleton, leaving *Entobia* traces of boring sponges (family Clionidae). This corroborates the fact that sponges are found ubiquitously in the oceans, from shallow tropical seas to abyssal depths.

On the microscopic level expansive networks of fungal tubes, associated with fungal chambers, were found penetrating the coral surface down to several hundred microns. Four fungal forms were observed, two tubular forms interpreted to be hyphal filaments and two bulbous forms interpreted to be fungal sporangia. No algal or known bacteria forms were found. Three characteristics of this assemblage are noted: i) some forms appear similar to fungal forms in other studies from many depth ranges, ii) other forms do not correlate well to any other known fungal morphologies, and iii) species diversity seems to be less than shallower water environments. It is suggested, therefore, that specific morphologic forms, which may occur with some ubiquitous forms, as well as low ichnodiversity may indicate a deep water environment. Much work and data collection needs to be done however.

Destructive micritization, or selective leaching, was also documented using

both scanning electron and petrographic microscopy. This was not a surprising discovery, and it is questionable whether the extent of micritization could be used as an indicator of ambient water conditions. Although shallow water micritization is well documented, little is known of gradients within the oceans of the parameters, such as CaCO_3 saturation, CO_2 concentrations, salinity and pH, that control calcite dissolution. More data would need to be collected from wide bathymetric and latitudinal ranges to make any possible conclusive statements.

APPENDIX

Plate I: SEM composite of outer surface of coral, sample 1. Scalloping texture can be seen in several sponge borings. A variety of other scrapes and holes can be seen (scale approximately 38 x).

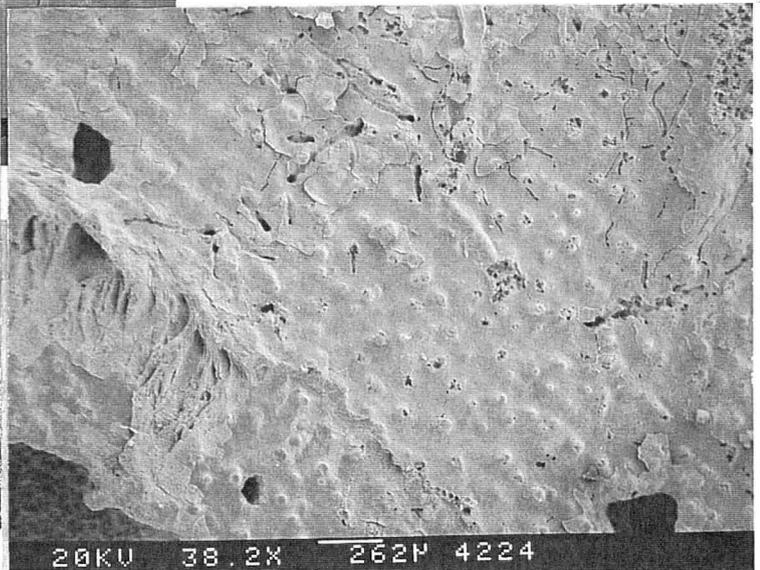
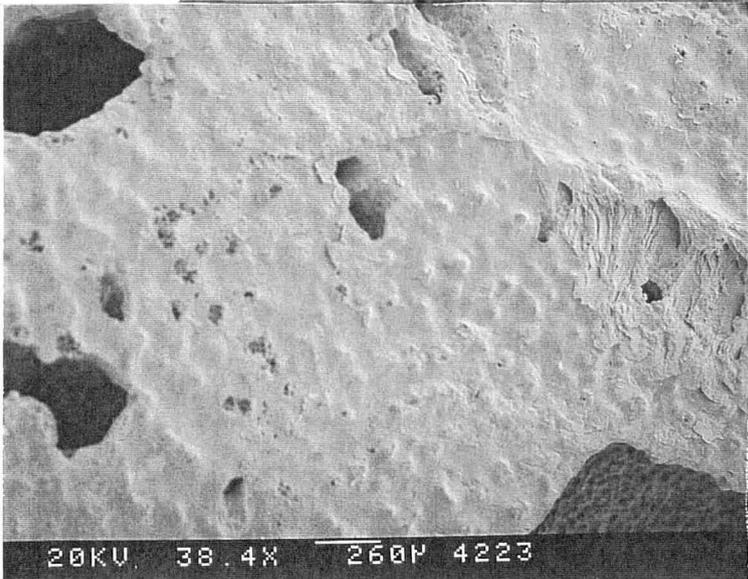
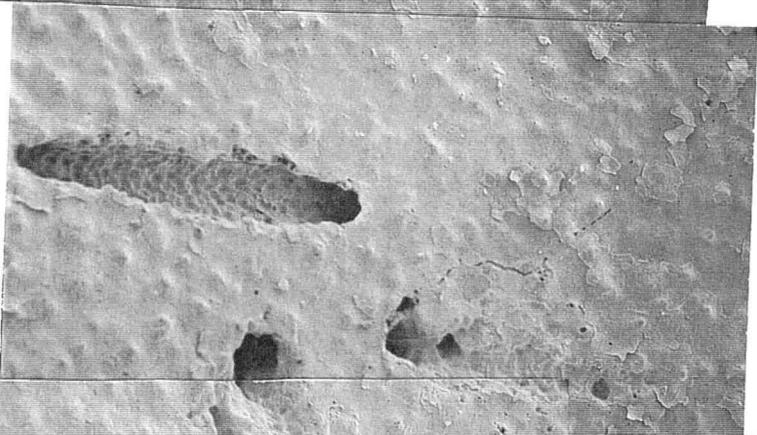
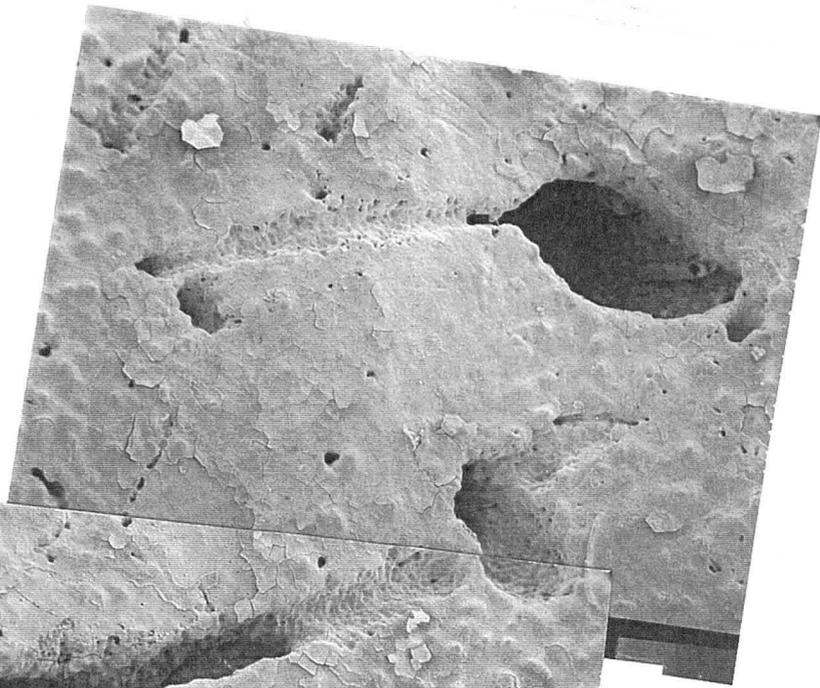


Plate II: Sample 1, "tracks" within sponge boring, SEM photographs.

A Two parallel traces preserved within the sponge boring, approximately 1.5 cm apart (42.2x).

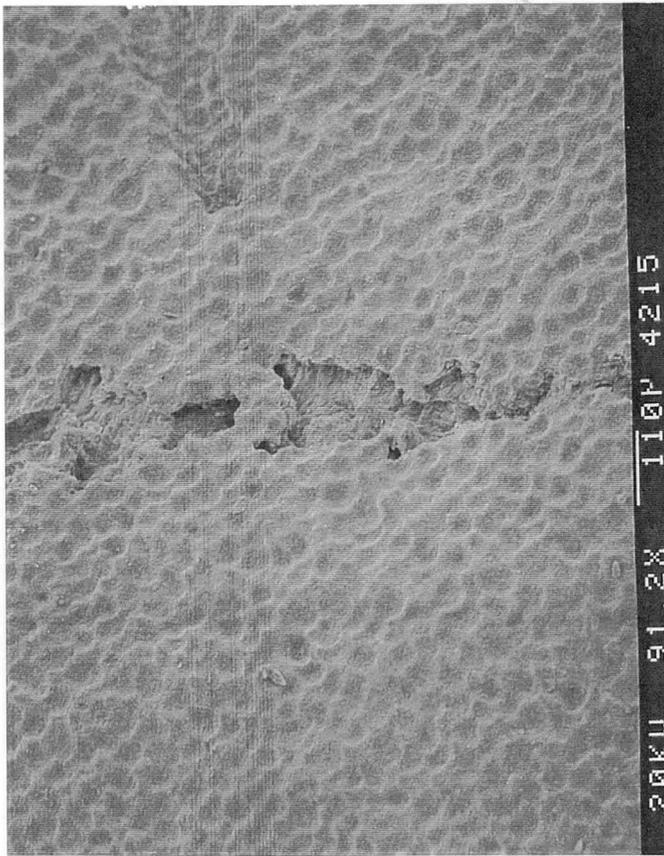
B Close up of trace on left side of A (91.2x)

C Close up of center of B. Scalloping texture can be seen, as well as the dissolution texture within the linear trace (346x).

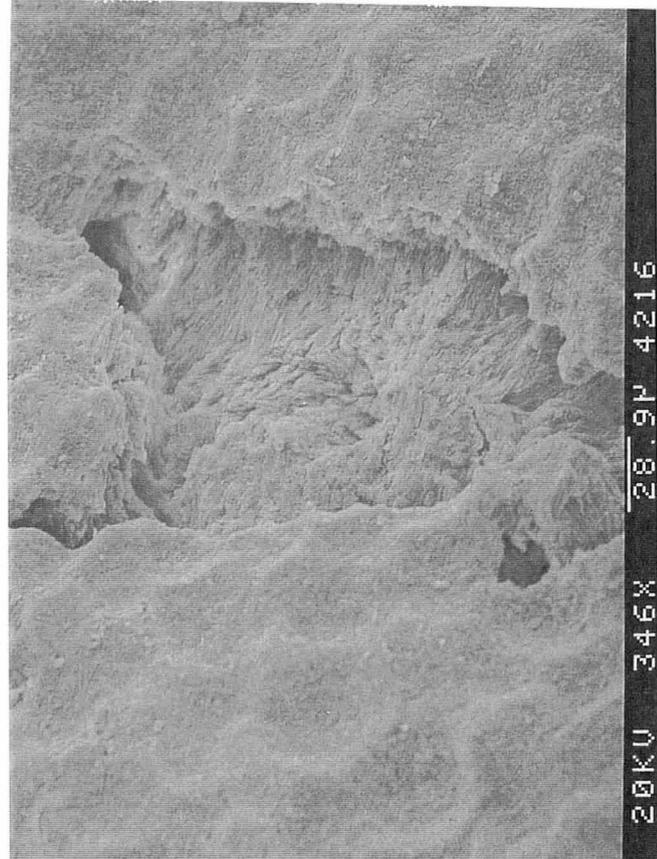
D Close up of trace on right side of A (163x).



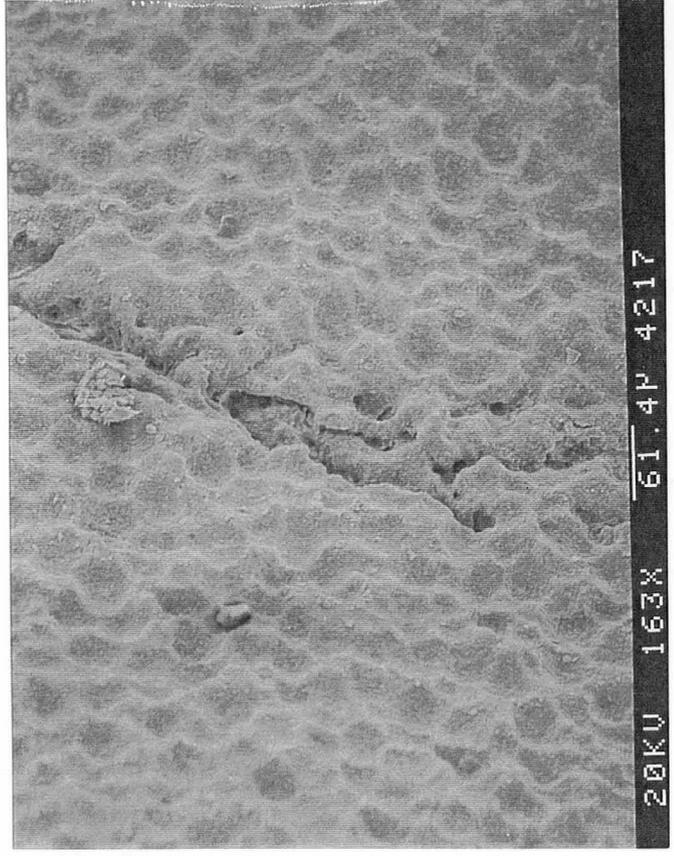
A



B



C



D

Plate III: Sponge borings observed in resin casts, SEM photographs.

A Sample 1; sponge boring within coral septa. Cross section of coral sample, linear feature from top left corner to bottom middle of photo is coral surface (microborings can be seen penetrating the surface). Large elliptical object in center is sponge boring (domicile). A papilla can be seen on the left side of the domicile connecting it to the surface of the coral (close up in B). Two circular features are bubbles in resin cast (35.5x).

B Close up of papilla in A, connecting the sponge domicile with the coral surface. Several microboring traces can be seen just below the coral surface (177x).

C Sample 1; coral surface extends from bottom right corner to top middle of photo, many microborings can be seen penetrating the coral surface. Several sponge papillae can also be seen penetrating deeper into the coral (82.2x).

D Close up of papillae in bottom middle of C. Scalloping texture can be seen (555x).

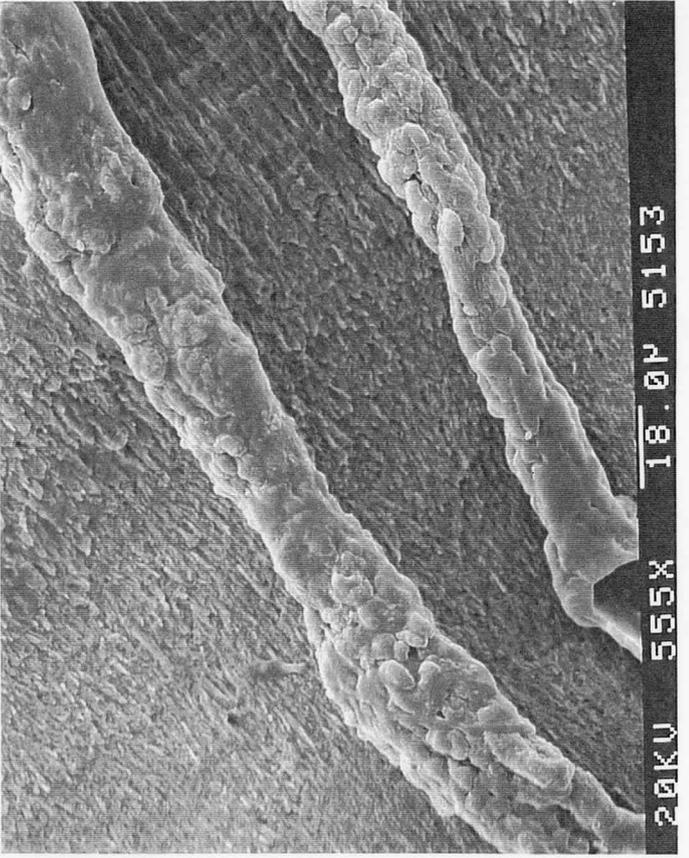
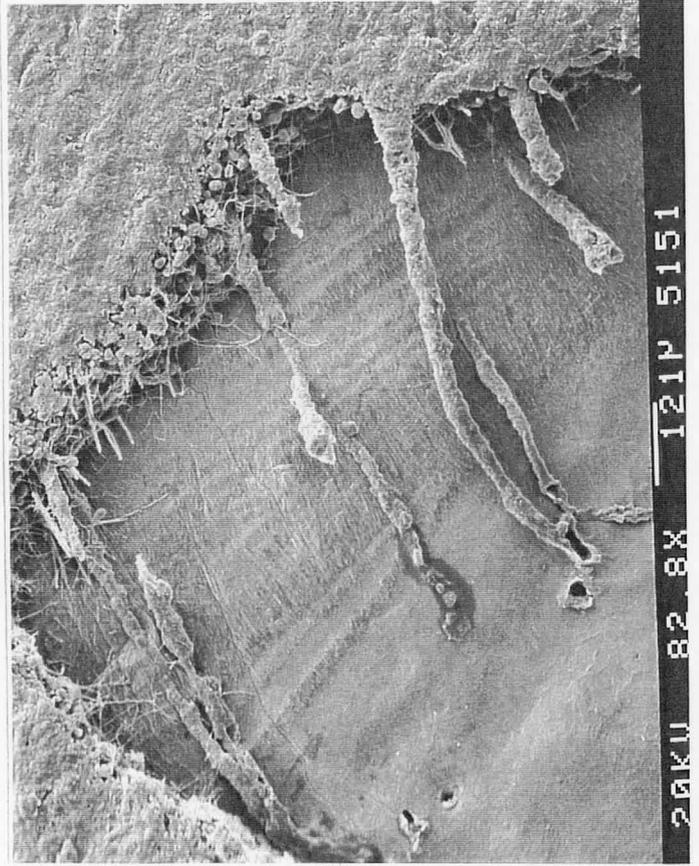
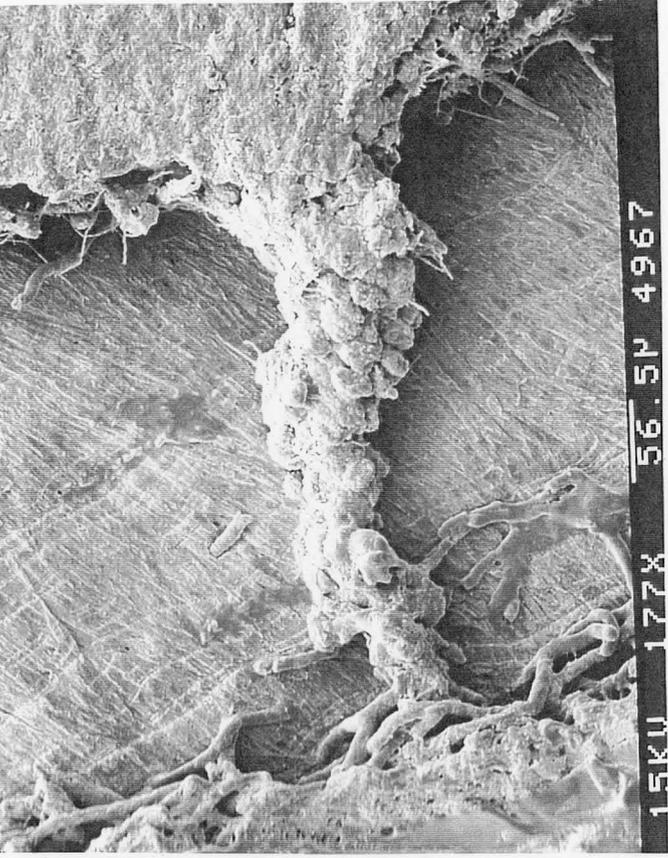
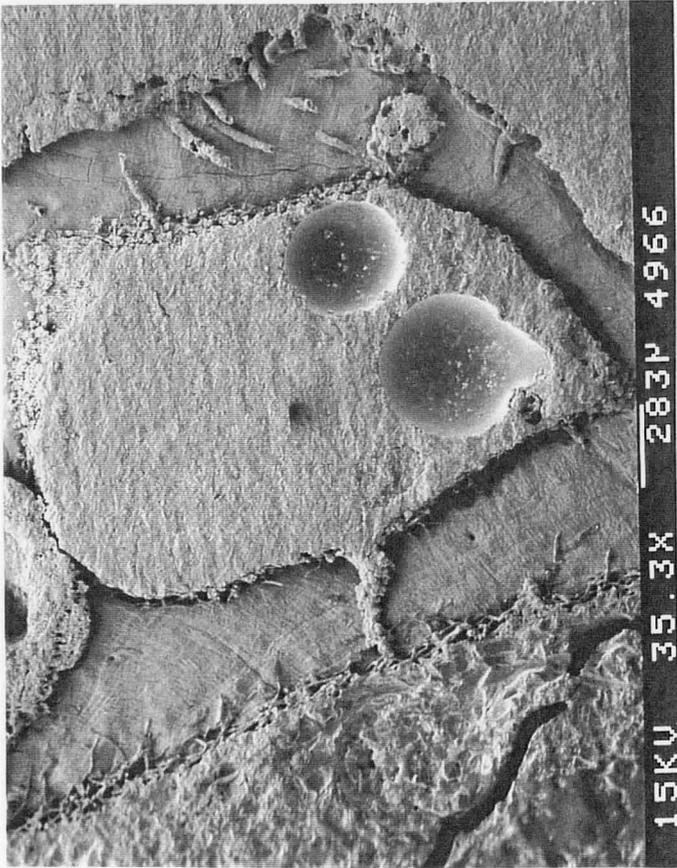
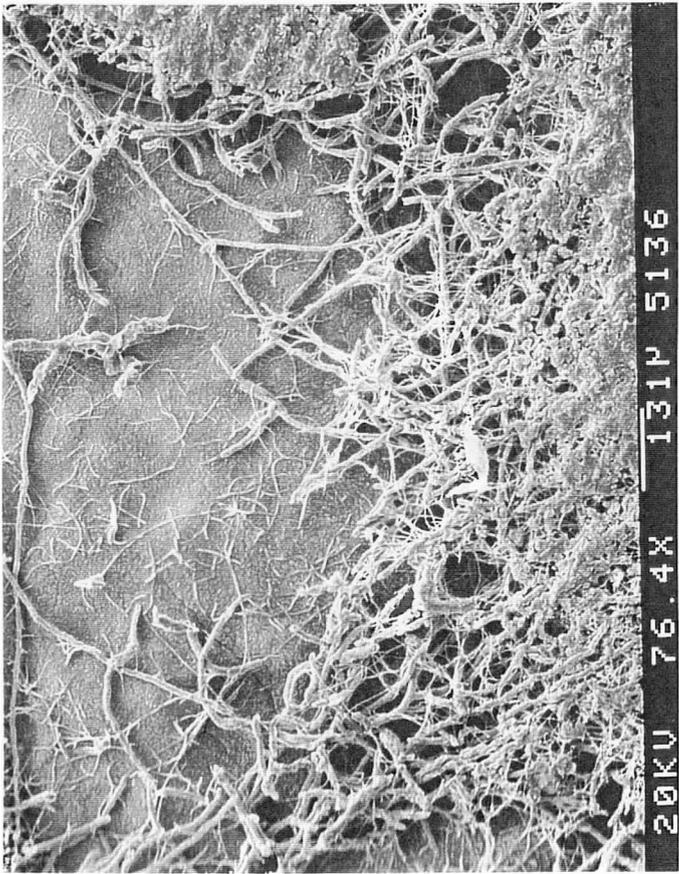


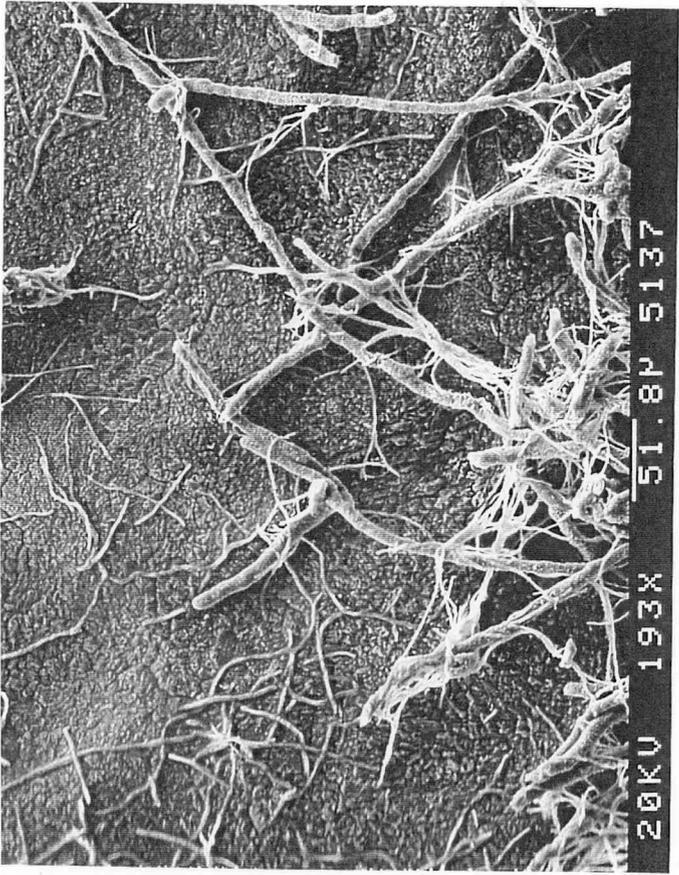
Plate IV: Microboring assemblages in samples 2 & 3 (A,B) and sample 1 (C,D).

A,B Expansive networks of fungal forms I and II (A-76.4x, B-51.8x).

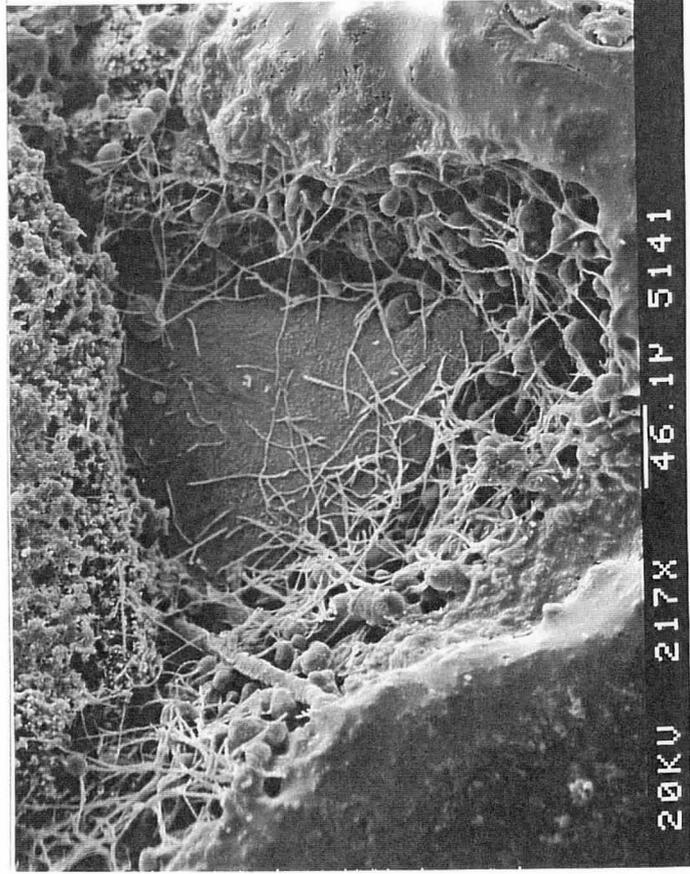
C,D Microborings penetrating the coral surface, showing primarily fungal forms II (C,D), III (D) and IV (C) (C-217x, D-554x).



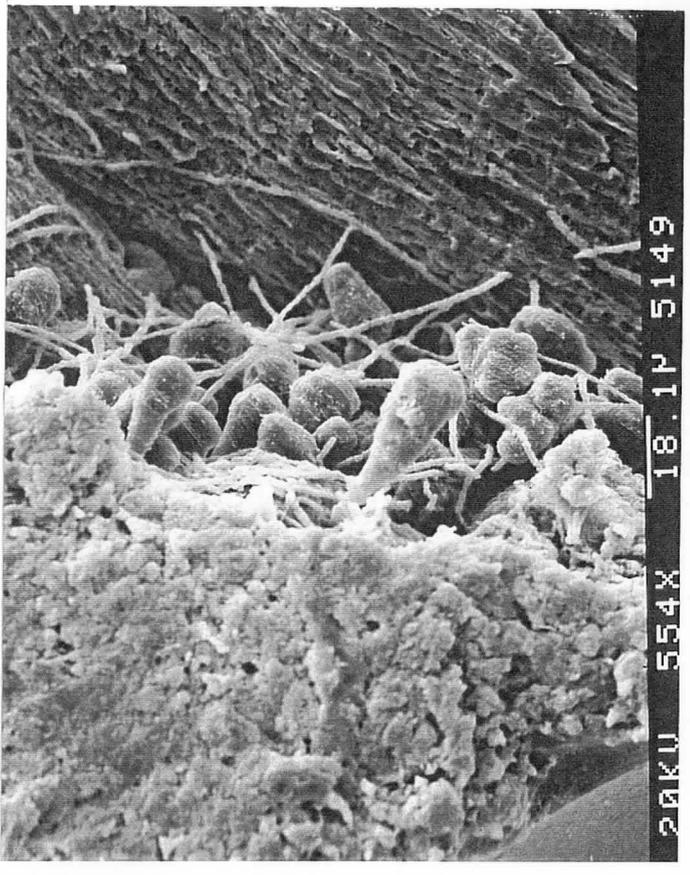
A



B



C



D

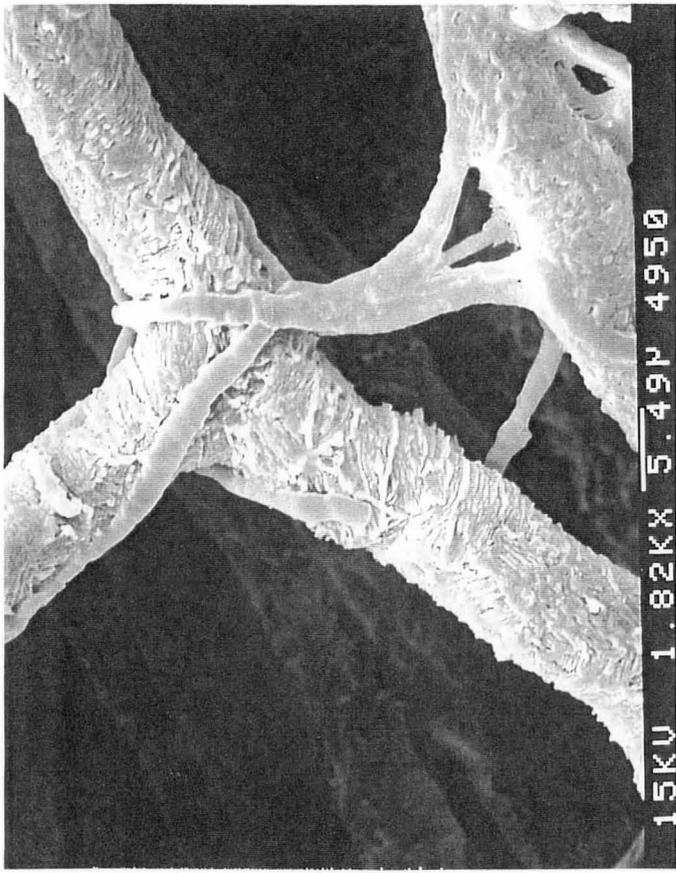
Plate V: Fungal forms I and II from samples 1 and 2.

A Larger tubules are fungal form I, with several form II tubes intertwined with form I (486x).

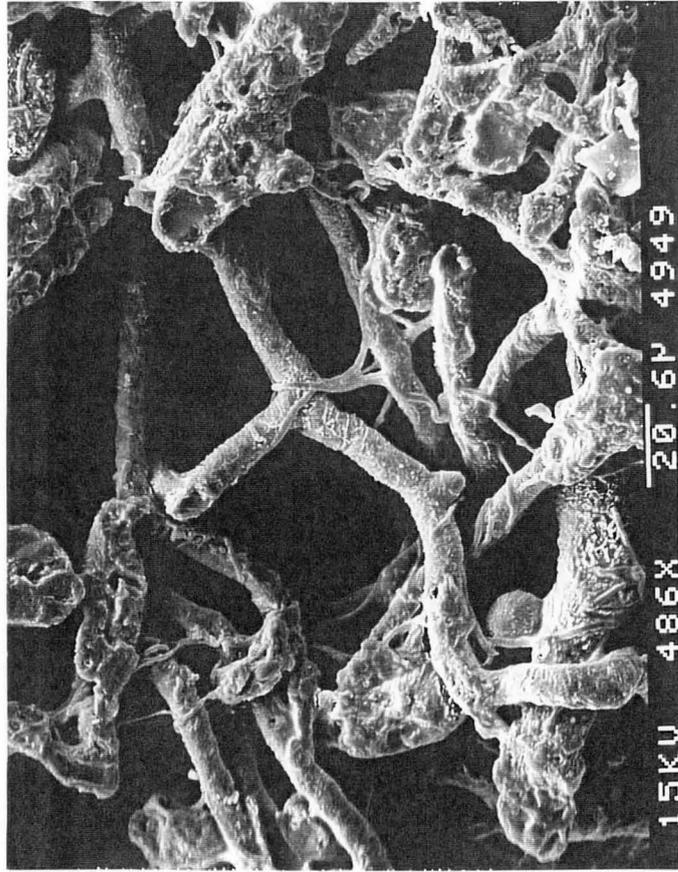
B Good example of the relationship between fungal forms I and II. The larger tube is form I with a course surface texture, probably the imprint of the trabecular matrix of the coral. Form II is finer and has a smoother texture (possibly segmented) (1.82kx).

C An abrupt termination of form I can be seen in the top right of photo. Large circular image in center of photo is likely the larger end of a form III sporangia. Form II tubules can be seen on the surface of the form III structure (1.78kx).

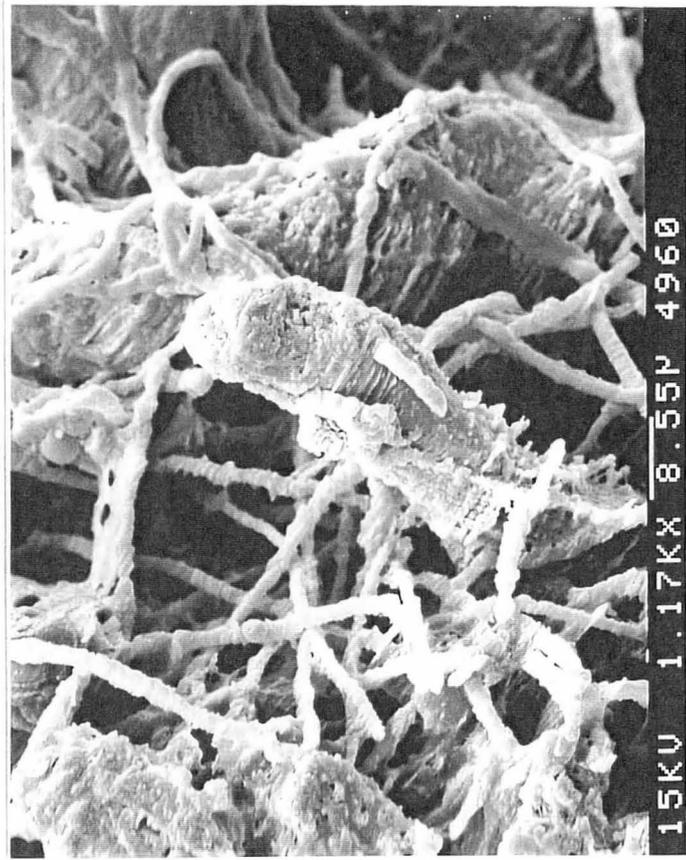
D Abrupt termination of a form I tubule in center of photo. A number of form II tubules are also shown(1.17kx).



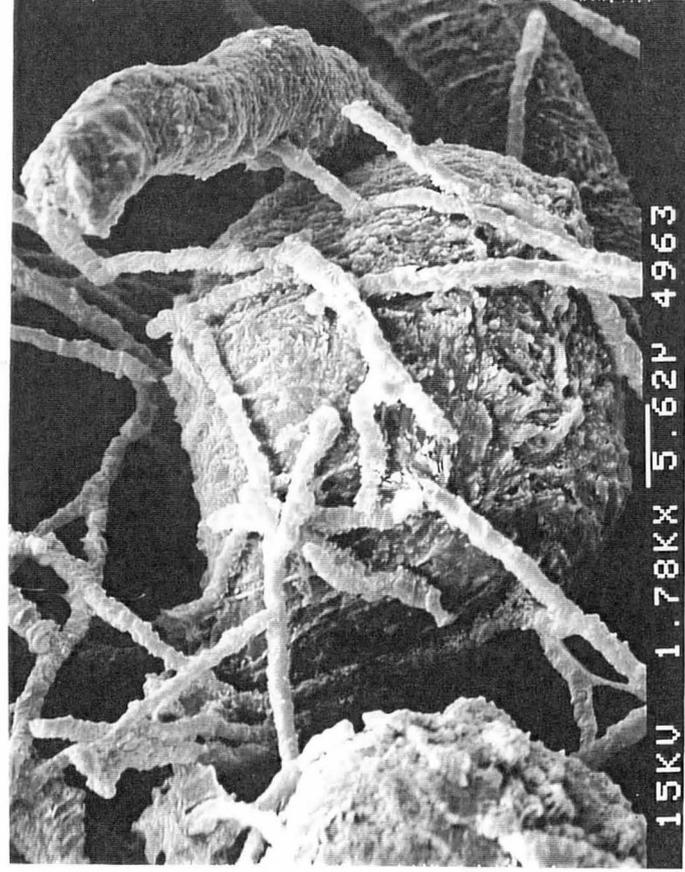
B



A



D



C

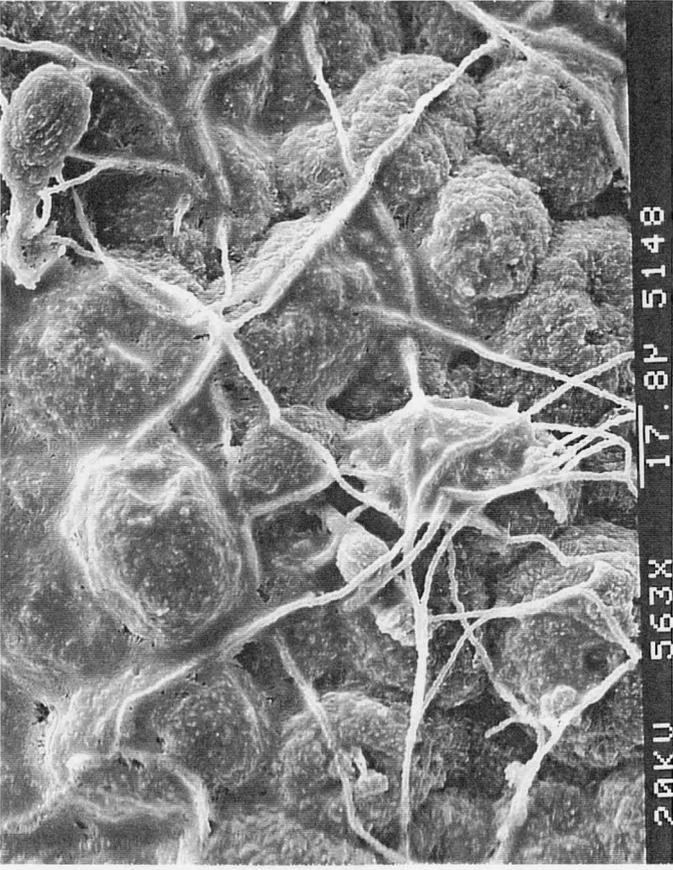
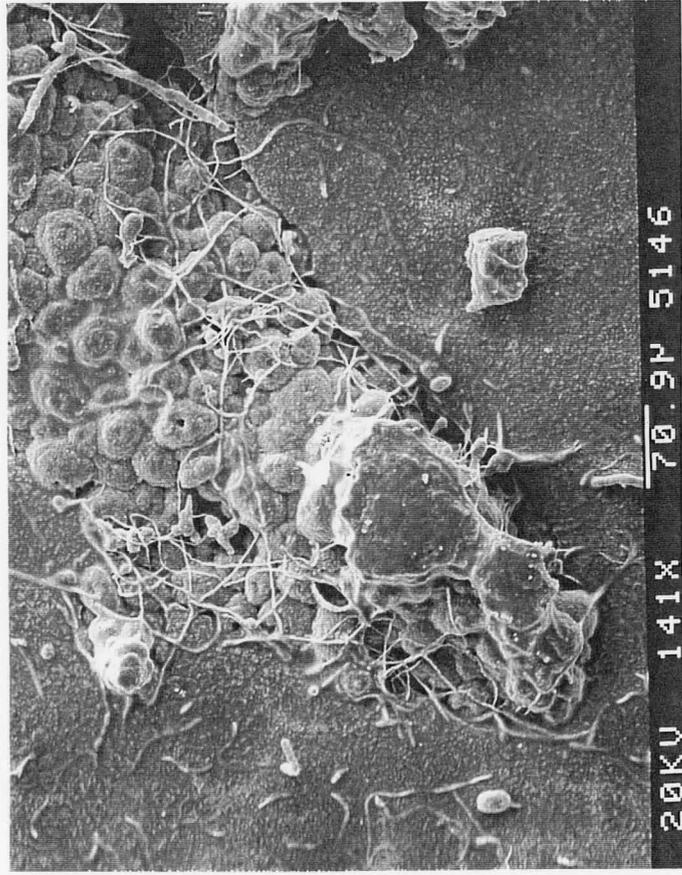
Plate VI: Sponge borings (A,B) and microborings (C,D).

A Photo showing the relationship between sponge borings (large structure with scalloping texture) and fungal form II.

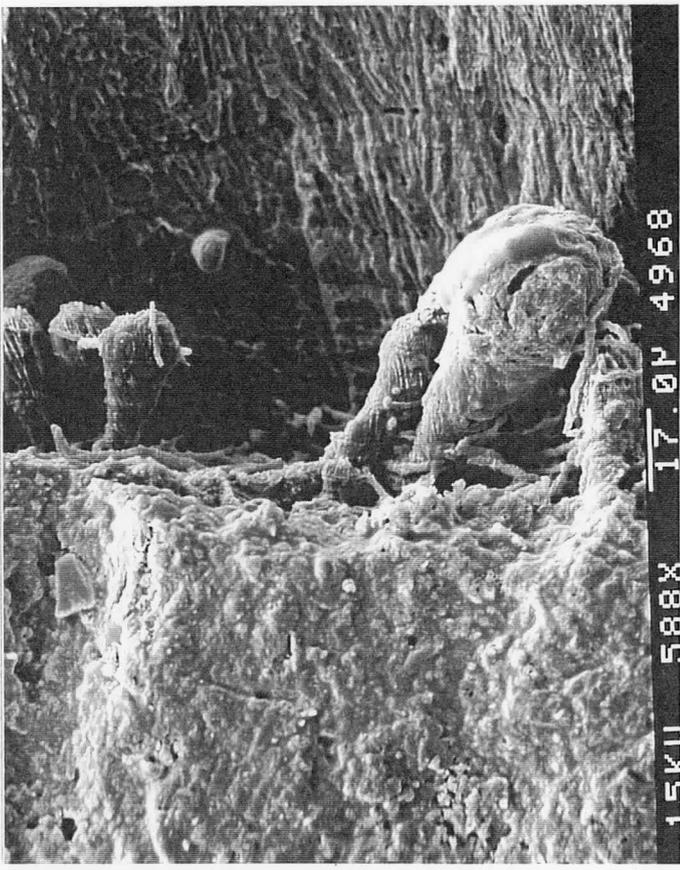
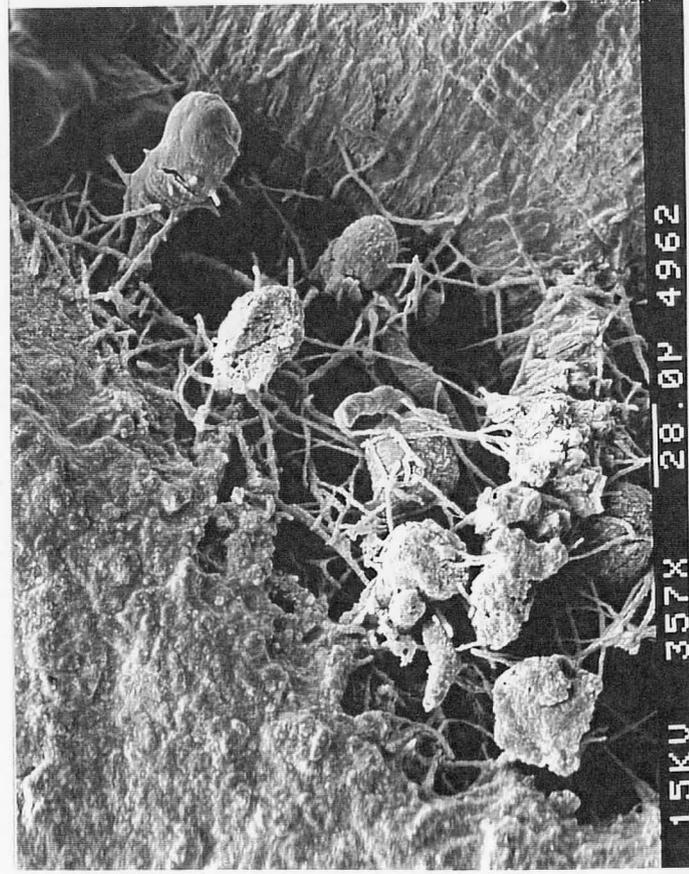
B Close up of center of A. Fungal sporangia (form III) can be seen top right of photo (563x).

C Sample 1; coral surface is from top right to bottom left of photo. Several fungal sporangia can be seen (357x).

D Sample 1; coral surface is from middle top to bottom. Several form III sporangia are shown penetrating coral surface (588x).



A B



C D

Plate VII: Fungal forms III (A,B) and IV (C,D).

A Sample 1; fungal form III, the thinner end exiting to the coral surface. Trabecular imprint can also be seen (4.17kx).

B Photo showing the relationship between fungal forms II and III. Form II can be seen radiating out from form III, as well as penetrating the coral surface (1.18kx).

C Fungal form IV, close up of top right of Plate IV C (2.89kx).

D Close up of C, showing the unusual coarse texture of this form (7.16kx).

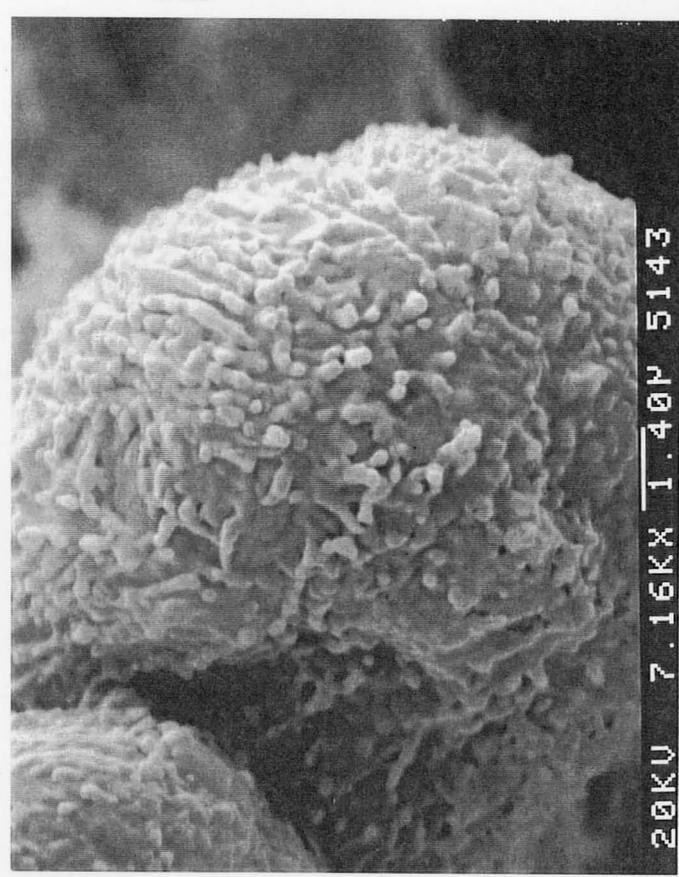
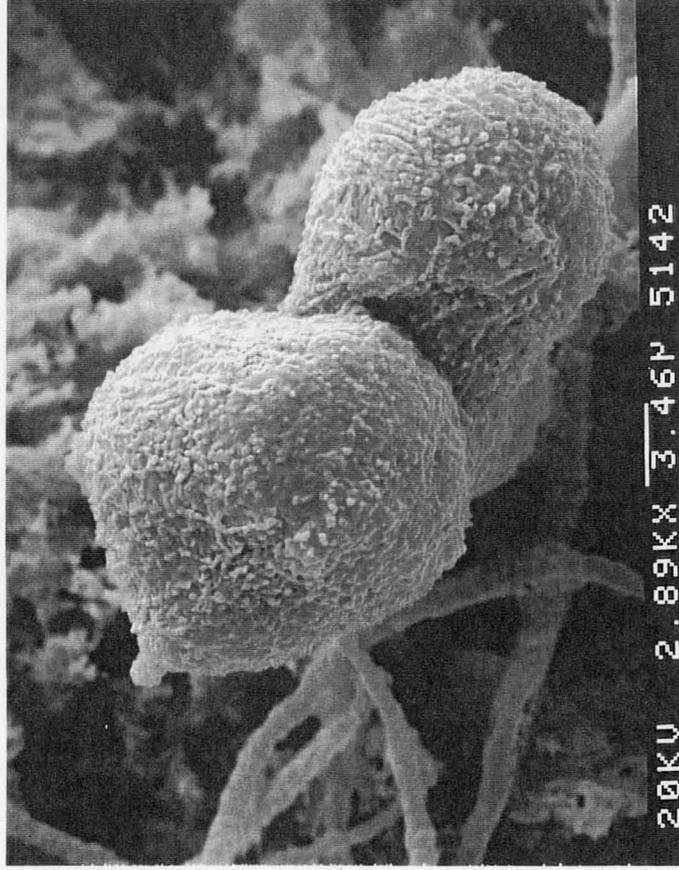
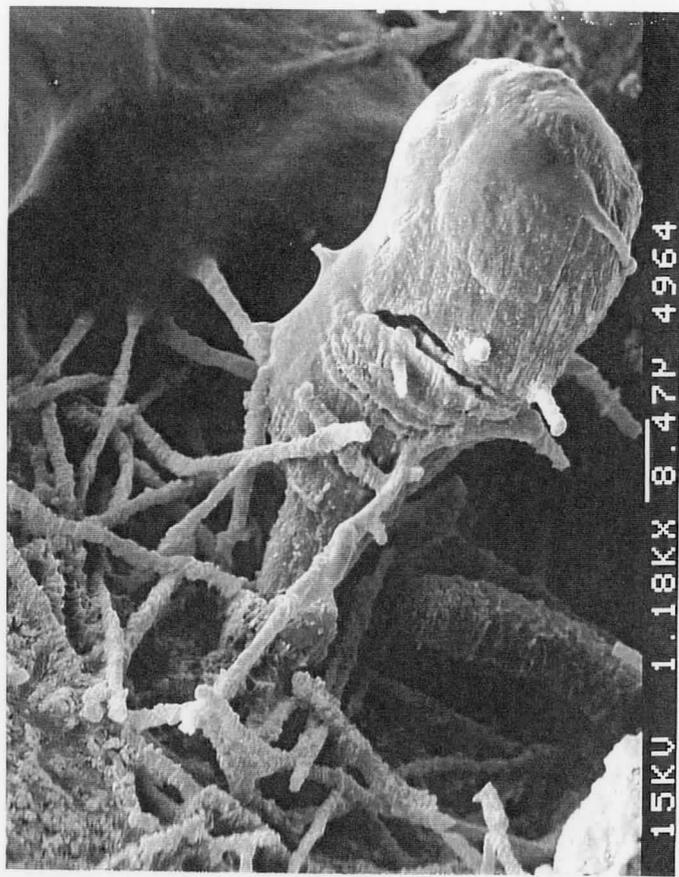
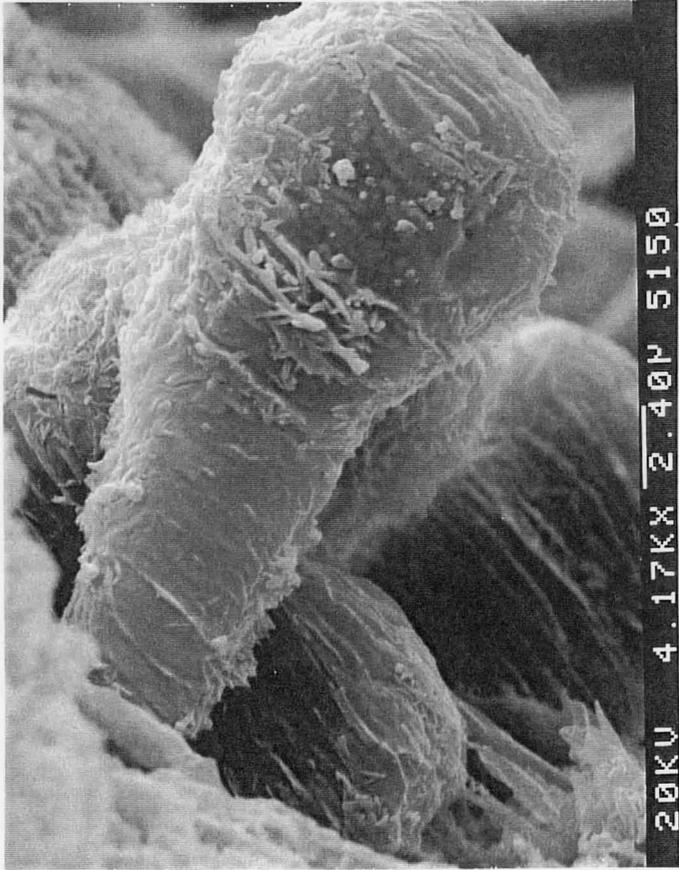


Plate VIII:

A Sample 2; micritic structures found near the surface of the coral. The structure seems to be associated with boring traces, probably of sponge origin (120x).

B Close up of lower middle of A. What is shown is the detail of the resin cast which is the surface texture, after some dissolution, of remaining lamellae (1.81kx).

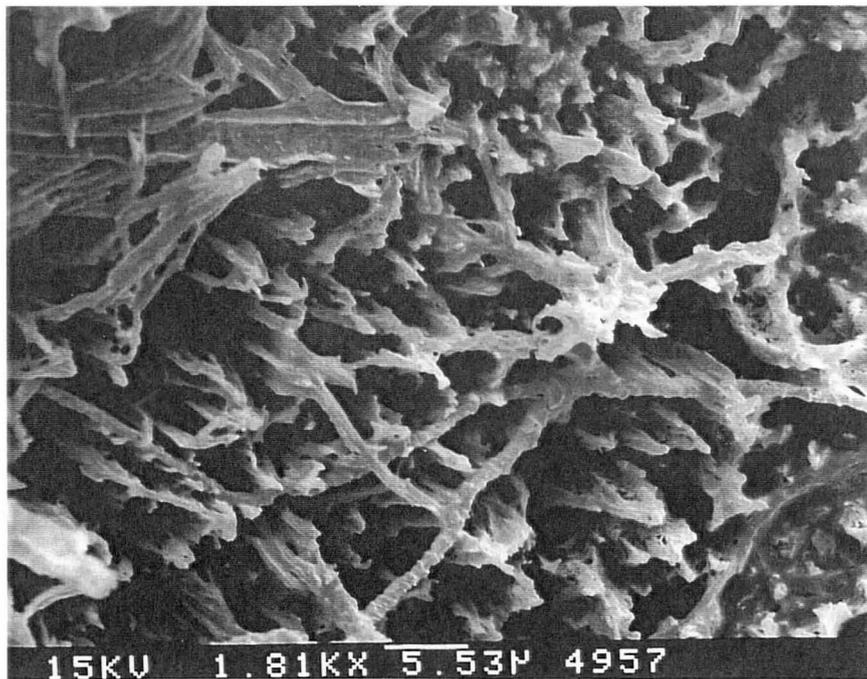
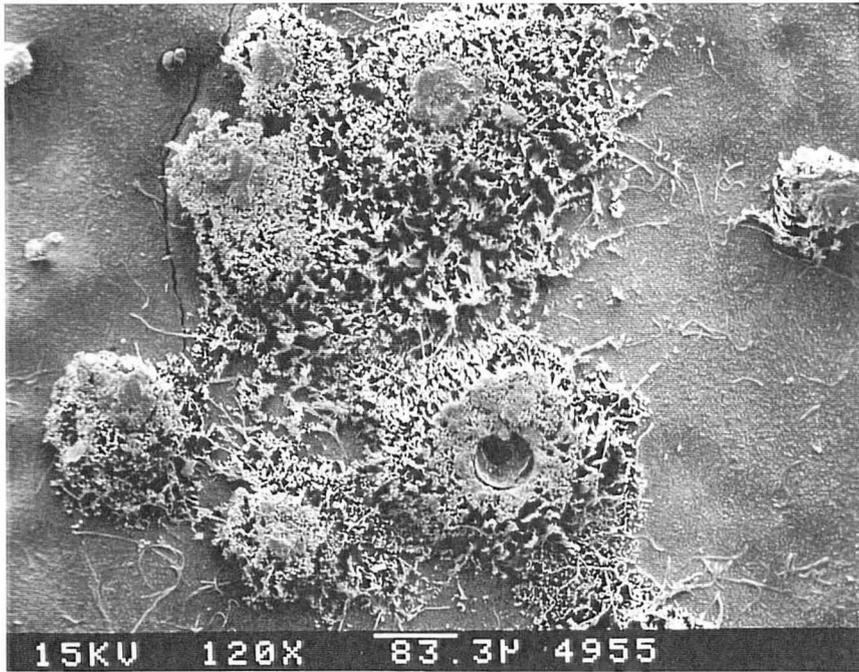
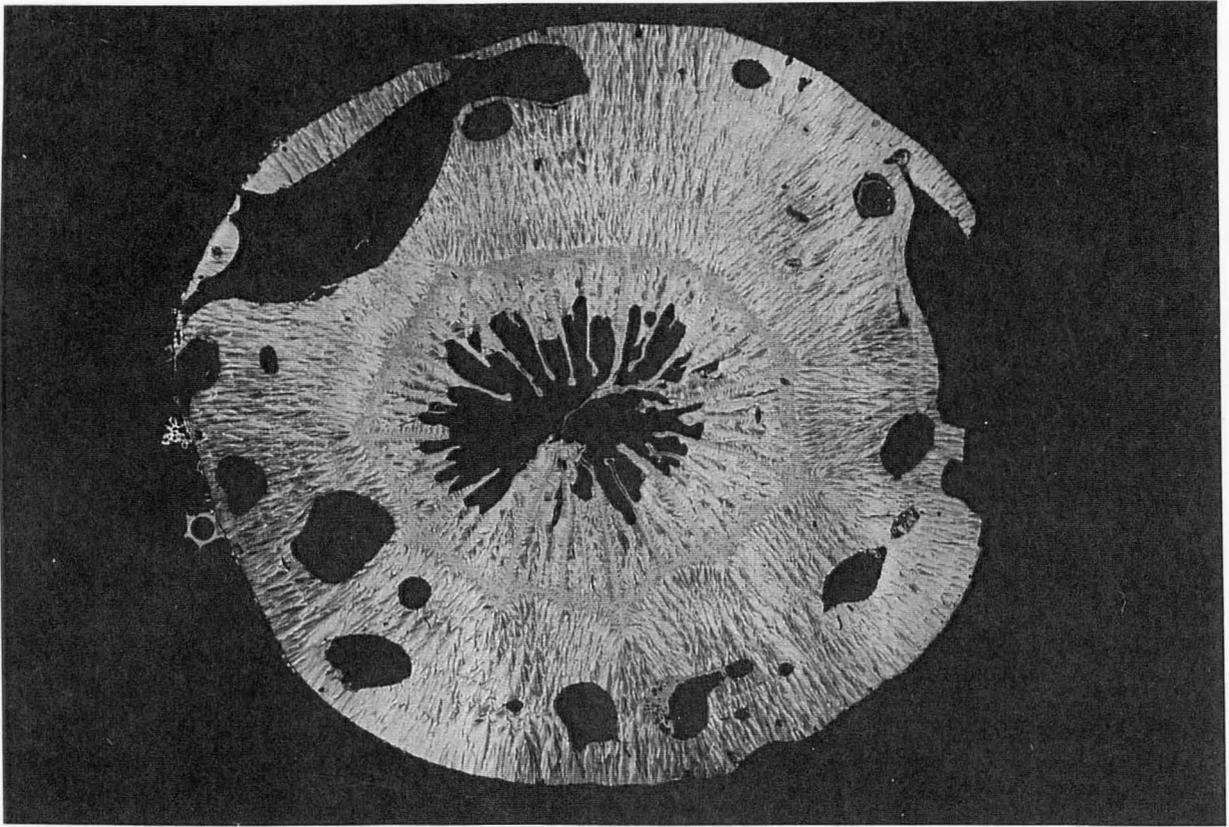


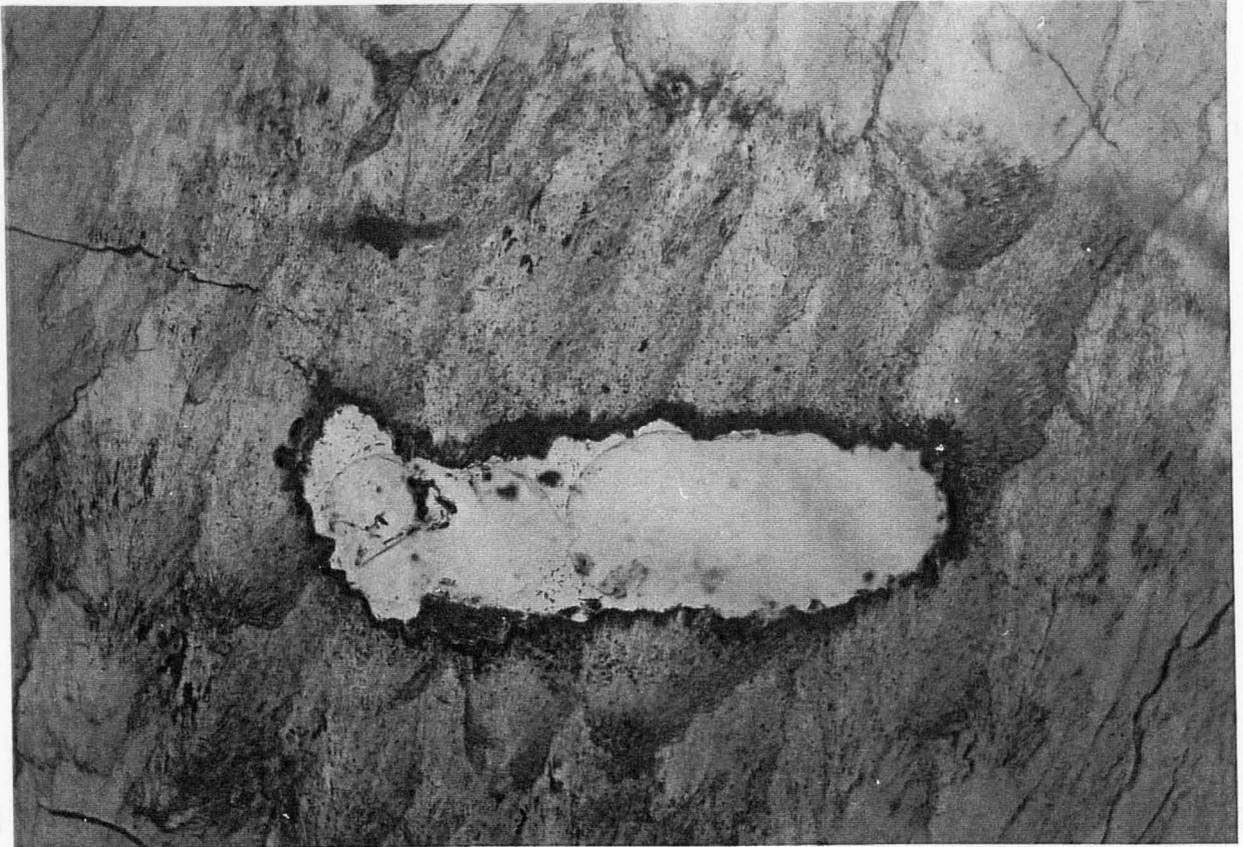
Plate IX:

A Thin section sample in reflected light. Dark circular patches are sponge boring traces in coral skeleton.

B Close up of sponge boring in A in plane polarized light. Scalloping texture can be seen as concave features on the inner walls of the boring. Dark rim around boring is micritic texture, black in plane polarized light due to small voids created from dissolution.



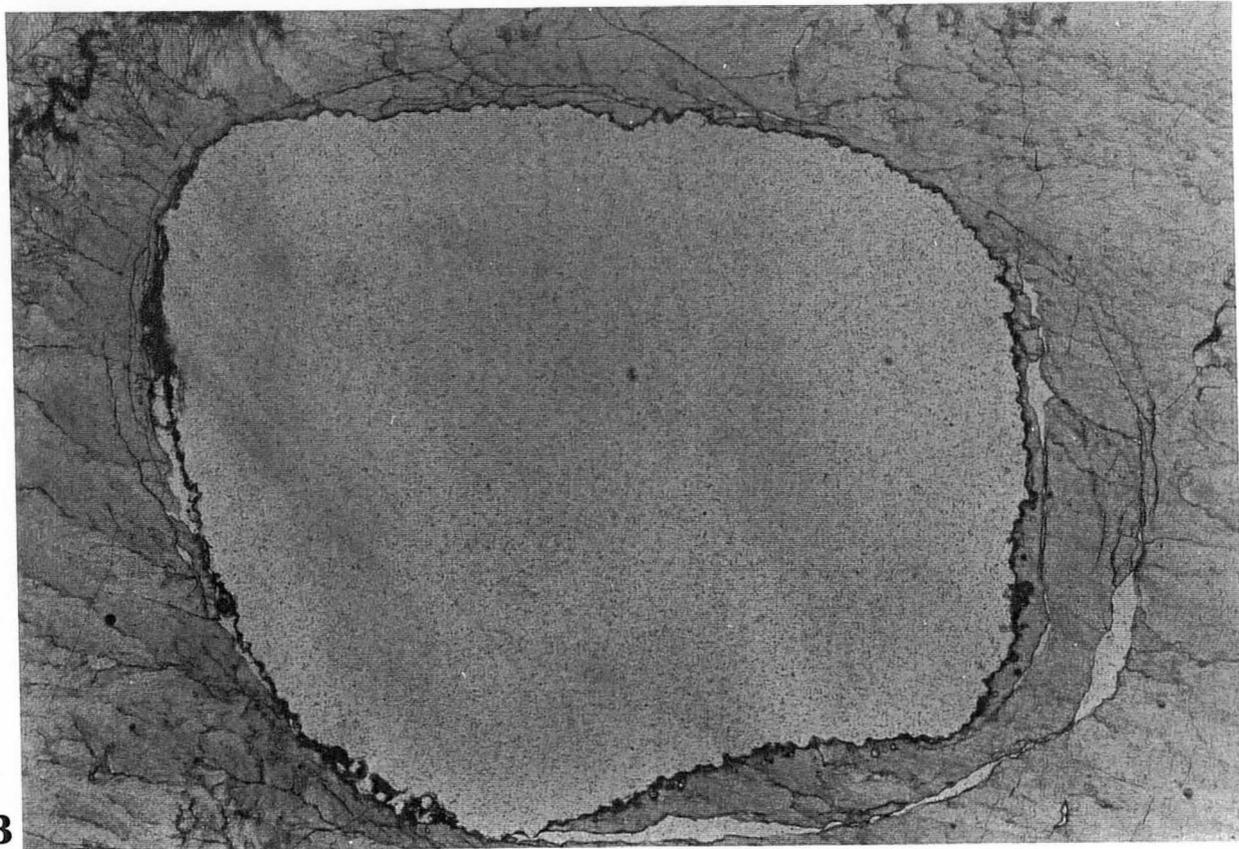
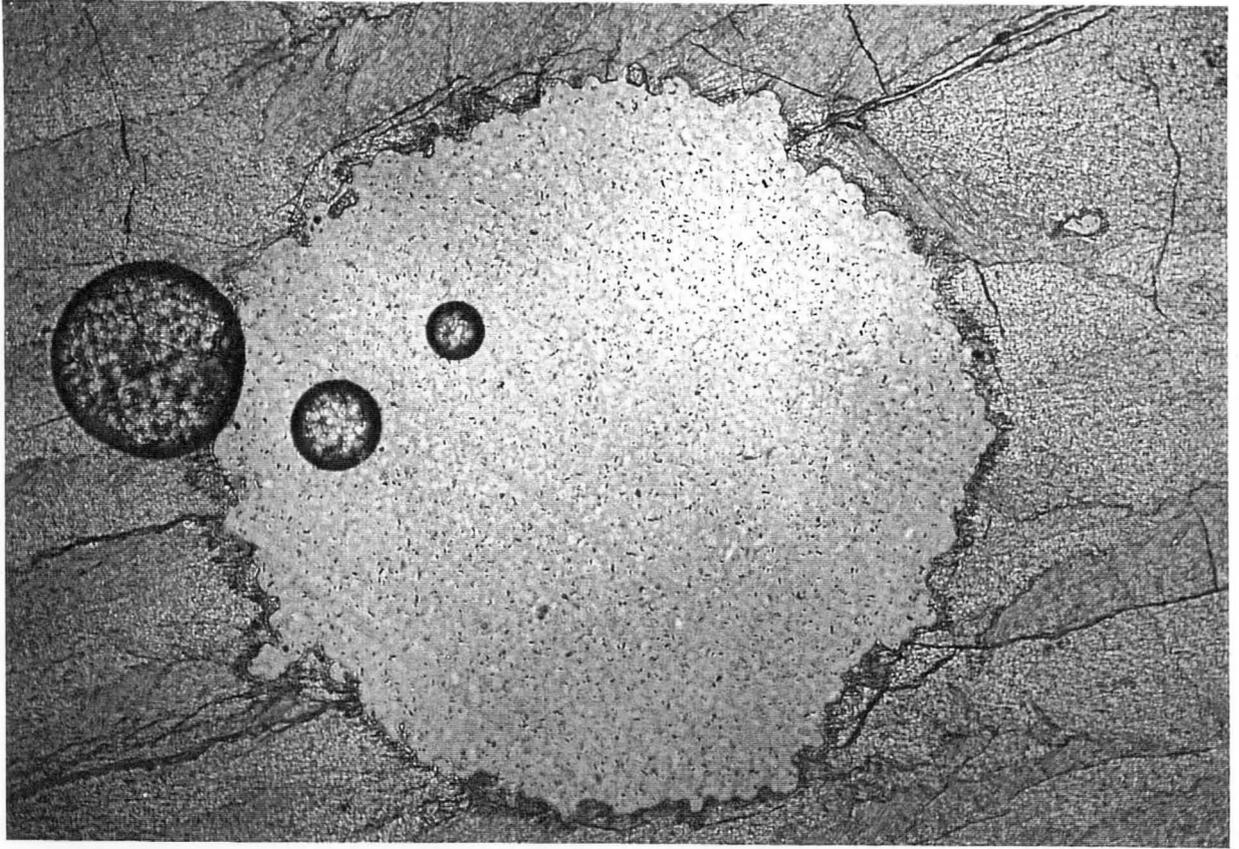
A



B

Plate X:

A,B Close up of sponge borings in Plate IX A. Dark micritic rims can also be seen around the inner walls of both sponge borings.



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