Distribution of Microborers within Planted Substrates along a Barrier Reef Transect, Carrie Bow Cay, Belize

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ABSTRACT

A diverse assemblage of endolithic microorganisms was identified in a series of carbonate substrate stations planted along a transect across the barrier reef near Carrie Bow Cay, Belize. These tropical endoliths at the sediment-water interface include the cyanophytes, *Hyella tenuior* Bornet and Flahault, *Mastigocoleus testarum* Lagerheim, and *Plectonema terebrans* Bornet and Flahault, the chlorophytes, *Ostreobium brabantium* Weber Van-Bosse and *Phaeophila engleri* Reinke, the rhodophyte *Porphyra* sp. (*Conchocelis*-phase), and various fungi. This assemblage was subdivided into an upper photic zone assemblage dominated by *Mastigocoleus*, *Hyella*, *Phaeophila*, and *Ostreobium* species, and a lower photic zone assemblage dominated by *Porphyra* sp.

Subsurface endolithic activity detected at the shallow lagoon station included filamentous irregular polygonal networks, irregular flattened masses, and regular crenulate discoids, which differed from and were less diverse than the assemblage at the sediment-water interface. Affinities of these subsurface microborings are unknown but they resemble endolithic traces and organic scars variously attributed to fungi, bacteria, and Actinomycetes. The regular discoids and irregular masses occurred only in association with the filamentous form, and therefore may be related reproductive bodies. For reasons not fully understood, microborings were not present in the second subsurface station, in fore-reef sand at a depth of 24 m.

Introduction

Endoliths are microorganisms (generally less than 1 μm to 100 μm in diameter) that penetrate calcareous substrates by chemical and/or mechanical means and that leave post-mortem microscopic networks. They are distinguished from "epiliths," which live only on a substrate's surface, and from "chasmoliths," which adhere to surfaces of fissures or cavities within the substrate (Golubic et al., 1975). Endoliths include cyanophytes, chlorophytes, rhodophytes, fungi, and possibly bacteria and sponges.

The most diverse and ecologically important microborers occur in the marine setting; their boring patterns—size, mode of branching, spatial arrangement, and growth directions—are taxonomically characteristic (Golubic, 1972). The marine endoliths have been subdivided on the basis of bathymetric and regional assemblage distributions, which are controlled by geographic, climatic, photic, and environmental factors (Perkins and Halsey, 1971; Perkins, 1972; Rooney and Perkins, 1972; Golubic et al., 1975; Green, 1975). Various studies of ancient and modern forms have indicated that endoliths may be used to interpret paleoclimatic conditions and to recon-

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struct depositional environments (for example, see Swinchatt, 1965; Gatrall and Golubic, 1970; Perkins and Tsentas, 1976). As well, microboring organisms have been used to establish the positions of relict shorelines (Perkins and Halsey, 1971; Edwards and Perkins, 1974) and to detect sediment transport (Rooney and Perkins, 1972).

Microborers modify both lithified and unlithified carbonate coasts (Purdy and Kornicker, 1958; Hodgkin, 1970; Schneider, 1976), in the colonization of shifting upper sublittoral substrates—where they create finer carbonate sediments, preferentially remove certain components, and initiate micrite rind formation (Bathurst, 1966; Golubic, 1969; Alexandersson, 1972; Rooney and Perkins, 1972; Perkins and Tsentas, 1976)—and in their alteration of the deep-sea sedimentary record (Zeff and Perkins, 1979). Endolithic algae not only dissolve carbonates, but also induce precipitation of calcium carbonate within shallow marine corals (Schroeder and Ginsburg, 1971; Schroeder, 1972a, b; Scherer, 1974). Furthermore, their biologically related physico-chemical processes may influence low-temperature sedimentary mineralization within boring networks (Taylor, 1971; Kobluk and Risk, 1977).

Recently, planted substrates have been used to identify modern microboring assemblages and to establish rates of infestation (Golubic, 1969; LeCampion-Alsumard, 1975; Perkins and Tsentas, 1976). The present investigation examined and identified endoliths within planted substrates in order to determine the distributional patterns of these organisms at the sediment-water interface along a reef transect. Two stations planted below the sediment surface allowed a cursory examination of subsurface microboring activity.

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Methods

This study examined two types of carbonate substrates planted at and below the sediment-water interface along a reef transect of Carrie Bow Cay (Figure 62): (1) crushed, fresh inner shell parts of the queen conch, *Strombus gigas* Linnaeus, and (2) cleaved calcite rhombohedra. Samples of each type were retained as controls. Fragments from 1 to 10 mm in size were attached to 15 cm^2 plexiglass plates (one type per plate) and 40 cm long polyvinyl chloride (PVC) pipes (types mixed) by a thin film of epoxy resin. Fourteen substrate-covered plexiglass plates were mounted on short lengths of protruding PVC pipe to maintain the samples above shifting substrata (Figure 63). These plates were placed in pairs at seven locations extending from the lagoonal *Thalassia* zone (depth 1.2 m) to the fore-reef slope (depth 27.4 m). One subsurface pipe station (consisting of one pipe) was inserted into the sea floor in the *Thalassia* zone (Figure 64) and another into the *Halimeda*-rich sand of the fore-reef sand trough (depth 24 m). Exposure time of substrates ranged from 21 to 24 months.

After being harvested, the planted substrates were preserved in 4 percent formaldehyde in 0.1 M phosphate neutral buffer. Fragments intended for light microscopic study were carefully scraped to remove epilithic organisms, then dissolved with 5 percent EDTA solution (van Reine and van den Hoek, 1966) at a pH of 6. Although the three-dimensional configuration of the microborers is lost because of their collapse, organic structure and color are not damaged by this slow-dissolving solution. Extracted tissues were then mounted on glass slides.

Scanning electron microscopic (SEM) analysis was based on the casting-embedding technique of Golubic et al. (1970). An alcohol dehydration series was followed by an infiltration series using Durcupan ACM Araldite Base Embedding Agent. After polymerization within plastic holders, the substrate fragments were exposed by means of a rotary grinding tool, then etched with 3 percent hydrochloric acid. This technique revealed plastic casts of the microboring networks,

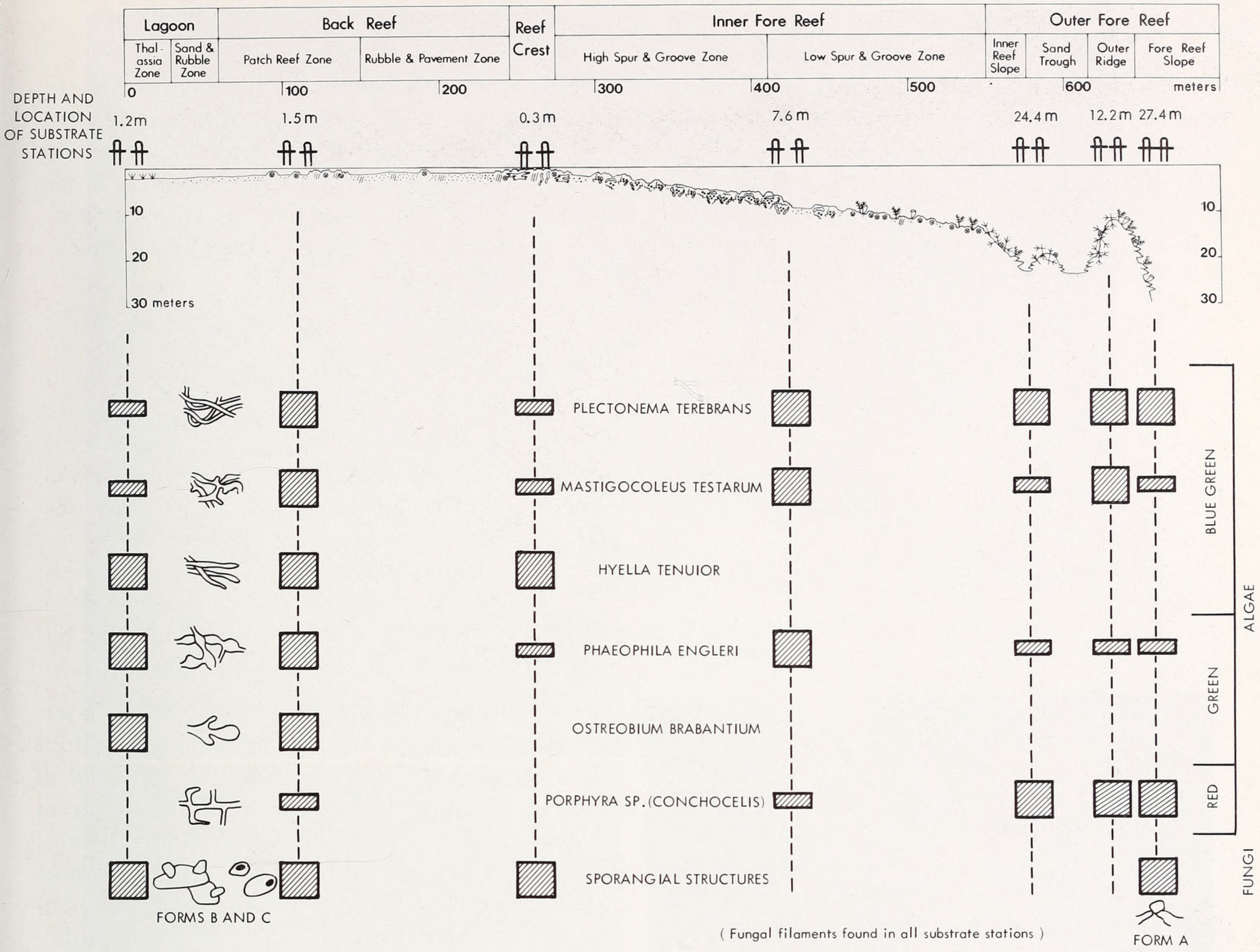


FIGURE 62.—Idealized cross section of Carrie Bow Cay transect showing locations of substrate stations planted at sediment-water interface and the distribution of endoliths collected from these plates (hatched squares = great abundance; hatched rectangles = presence observed).

which retained the original spatial relationships of the endoliths and their three-dimensional configurations. The mounted plastic blocks were scanned with an International Scientific Instruments Super II electron microscope after vacuum shadowing with gold-palladium alloy. Casts of boring networks were correlated with the endoliths isolated by acid dissolution.

Results

ENDOLITHS AT THE SEDIMENT-WATER INTERFACE.—Blue-green algae were ubiquitous and consisted of *Hyella tenuior* Bornet and Flahault, *Mastigocoleus testarum* Lagerheim, and *Plectonema terebrans* Bornet and Flahault. Green algal microborers, likewise abundant, included *Ostreobium brabantium* Weber Van-Bosse and *Phaeophila engleri* Reinke. Red algae were much less abundant and were represented only by the *Conchocelis*-stage of *Porphyra* sp. Fungal forms were found in almost all samples.

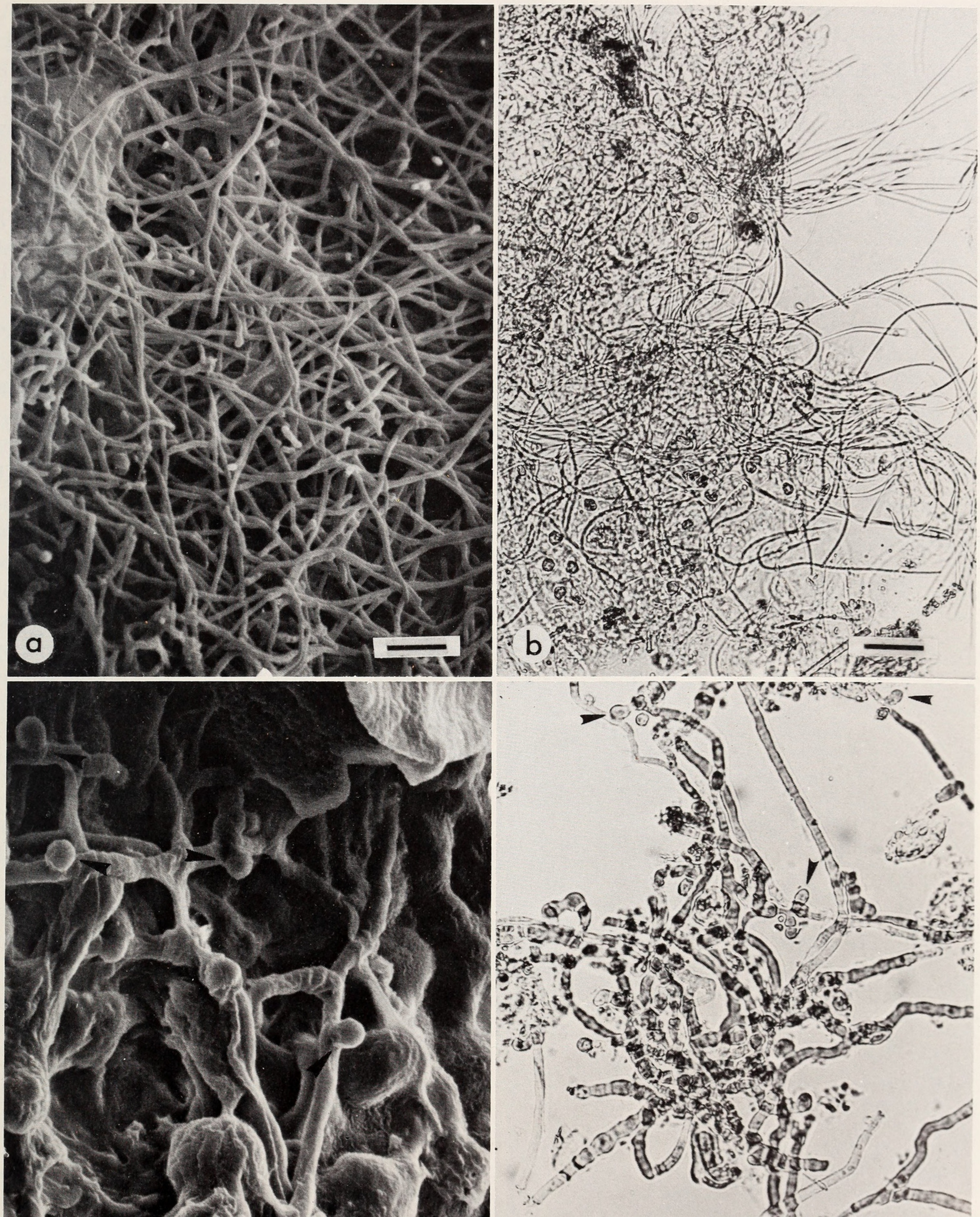
Plectonema terebrans was the most common cyanophyte at all stations. Diagnostic are its smooth, elongate, thread-like filaments 2 to 4 μm in diameter, which may run along the interior

FIGURE 63.—Patch reef zone substrate station, Carrie Bow Cay, showing location of plates above the sediment-water interface.

FIGURE 64.—*Thalassia*-zone subsurface substrate station, Carrie Bow Cay, showing a closeup of the buried substrate-covered 40 cm long PVC pipe. Note that only the protective collar and a small portion of the pipe protrude above the sediment-water interface.

surface of the substrate or may form dense, interwoven meshworks (Figure 65*a*,*b*). Also ubiquitous was *Mastigocoleus testarum*, which is composed of sharply curved to elongate filaments 5 to 8 µm in diameter that have numerous short lateral branches and heterocysts (Figure 65*c*,*d*). The morphology of *M. testarum* penetrating inorganic substrates is much more affected by the rhombohedral microstructure than is the morphology of *P. terebrans*; this observation corresponds with findings of LeCampion-Alsumard (1975). *Hyella tenuior*, which is less common, appears as a cluster of slender, elongate, relatively straight to bent filaments 5 to 8 µm in diameter (Figure 66*a*,*b*). These filaments grow subperpendicular to the surface of the substrate.

FIGURE 65.—Scanning electron and transmitted light photomicrographs of endolithic algae: *a*, *Plectonema terebrans* forming a typical dense network of filaments, acid-etched mollusk fragment, *Thalassia* zone (note the smooth, elongate, fine nature of the plastic casts); *b*, *P. terebrans* isolated by dissolution of a mollusk fragment, reef-crest zone; *c*, characteristic heterocyst development of *Mastigocoleus testarum* shown on plastic casts, acid-etched mollusk fragment, *Thalassia* zone; *d*, *M. testarum* isolated by dissolution of a mollusk fragment, Thalassia zone (note the heterocyst development marked by arrows). (Scale = 50 µm for *a*, *d*; 40 µm for *b*; 25 µm for *c*.)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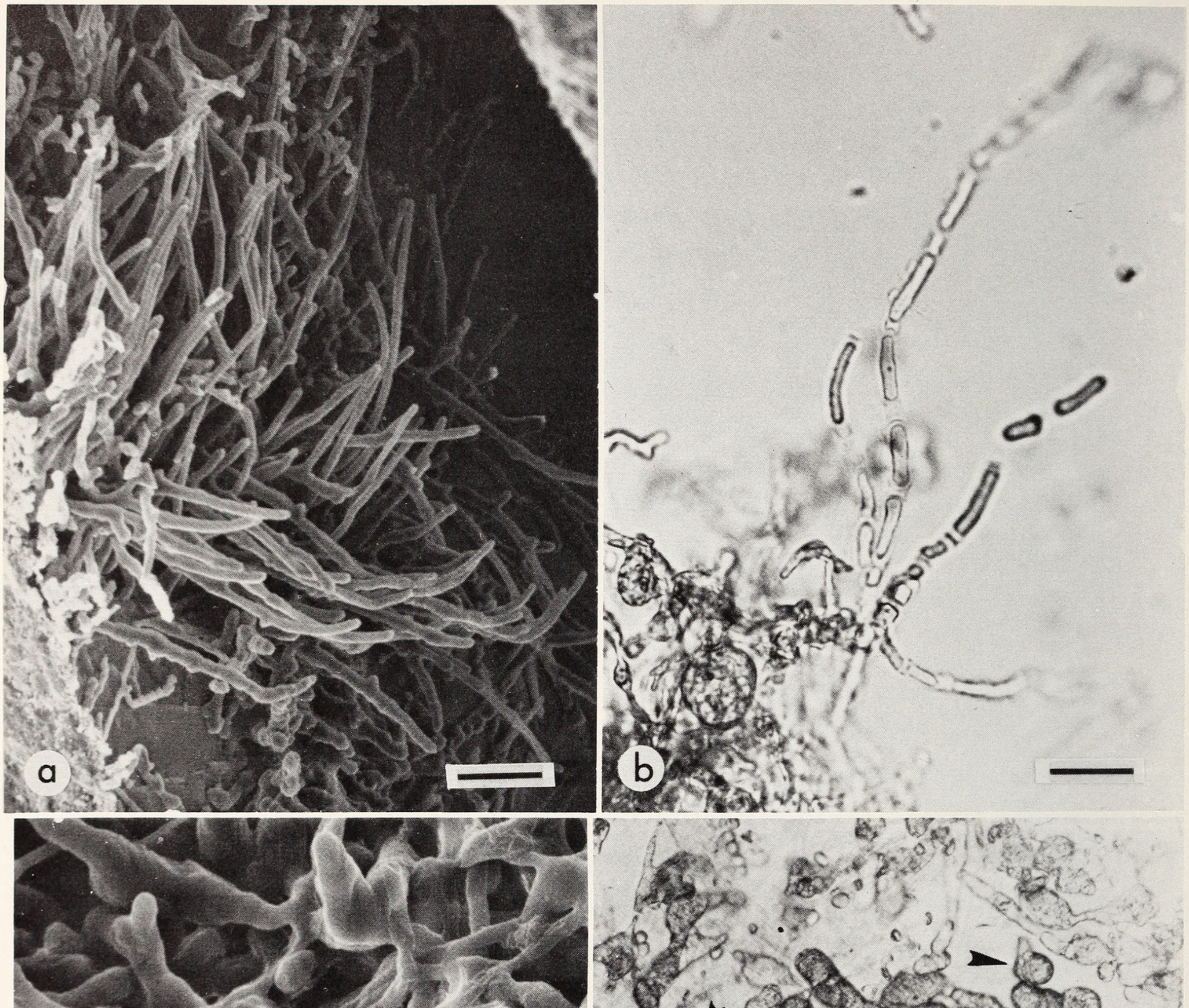
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Phaeophila engleri was the most abundant and widespread chlorophyte. This species is characterized by rectilinear branching and pronounced bulbous or irregularly ovoid, 15 to 20 μm swellings at points of branching or along the irregular 5 to 10 μm filaments (Figure 66*c*,*d*). The largest boring species detected, *Ostreobium brabantium* has digitate growths of single or bilobate branches (Figure 67*a*,*b*). Single plants up to 1 mm in length radiate into the substrate; individual branches of 40 to 60 μm may enlarge up to 120 μm before bifurcation. The *Conchocelis*-stage of the rhodophyte *Porphyra* sp. is characterized by rectilinear branching of long and fine, 2 to 3 μm filaments running along slightly beneath the substrate surface (Figure 67*c*,*d*).

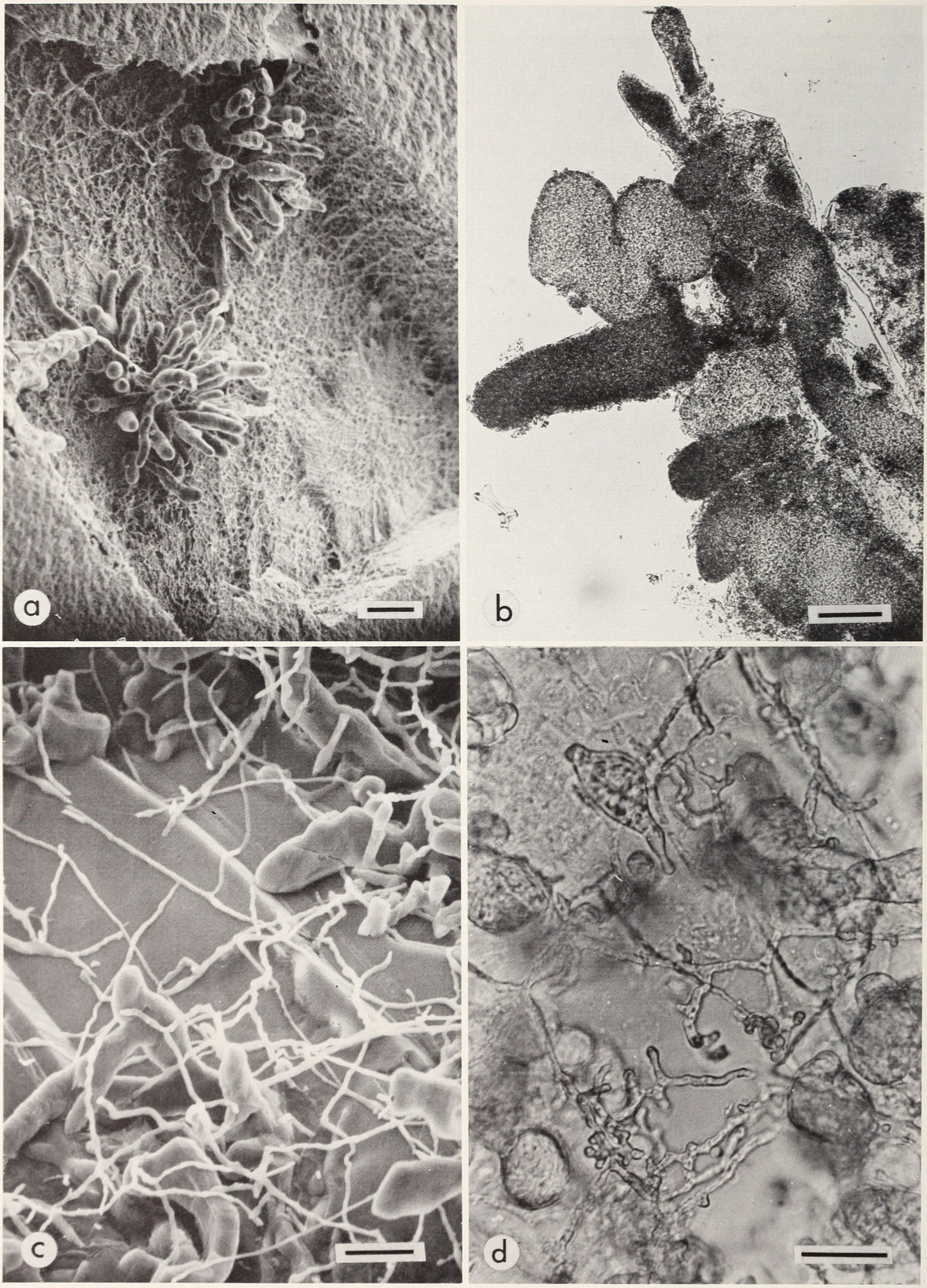
Extremely fine filaments from less than 1 up to 4 μm in diameter occur in a wide variety of forms, from non-branched to extensively branched and fused, sparse to massive networks (Figure 68*a*,*b*). These filaments probably represent fungal hyphae. The hyphae appear to be directed towards algae and can be observed penetrating these organisms, presumably in the act of feeding (Figure 68*b*). Three different types of structures observed with the scanning electron microscope were attributed to fungal spore cases. Form A has 5 to 15 μm ovoid to pyriform reproductive bodies, from the bases of which radiate long and threadlike, 1 to 2 μm hyphae (Figure 69*a*). These hyphae are typically unbranched and connect spore cases. Form B has 8 to 20 μm, globose to oblong fruiting bodies with connective hyphae attached at their sides, so that these spore cases appear positioned along filaments (Figure 69*b*). The irregular hyphae of less than 1 μm diameter become branched and fused, and form interconnected networks. Fungal form C has 5 to 15 μm globose to discoid sporangial bodies with indented ends that appear "doughnut-shaped" (Figure 68*c*). These bodies occur alone or in clusters directly upon the surface of endolithic algae; connective hyphae are lacking.

FIGURE 66.—Scanning electron and transmitted light photomicrographs of endolithic algae: *a*, elongate casts of the blue-green alga *Hyella tenuior* directed away from the substrate surface, some branching near their bases, plastic cast within an acid-etched calcite rhomb, *Thalassia* zone (very little control is exerted by the substrate microstructure); *b*, filaments of *H. tenuior* displaying elongate, somewhat rectangular cells, isolated by dissolution of the molluscan substrate, *Thalassia* zone; *c*, green alga *Phaeophila engleri* exhibiting characteristic ovoid swelling at points of branching and rectangular branching pattern, plastic cast of etched mollusk fragment, *Thalassia* zone; *d*, *P. engleri* demonstrating probable sporangia (arrows) and swellings at branching points, filaments isolated by dissolution of a molluscan substrate, *Thalassia* zone. (Scale = 50 μm for *a*; 25 μm for *b*, *c*; 40 μm for *d*.)

ENDOLITHS BELOW THE SEDIMENT-WATER INTERFACE.—In contrast to the diverse assemblage of microorganisms boring into the substrates planted at the sediment-water interface, only a few endolithic forms were found below the surface. These boring organisms were present only in the molluscan fragments planted within the lagoonal *Thalassia* zone. Classification is problematic as these forms have not previously been described. No microboring activity was recorded at the subsurface station in the fore-reef sand-trough zone.

An extremely irregular, polygonal network of variable and intermittent filaments 5 to 7 μm in diameter (Figure 70*a*,*b*) commonly crosses the regular and parallel lines representing remnants of the organic matrix that separated the inorganic crystals of the gastropod shell. This network of variously spaced filaments bores just below the surface of the molluscan substrates. The filaments are curvilinear, have a twisted appearance, and branch sideways. This form is recurrent in approximately 10 percent of the molluscan fragments throughout the pipe planted in the *Thallasia* zone, and was not found in the control samples or in samples from the sediment-water interface. Possibilities for taxonomic assignment include marine fungi (Phycomycetes, Ascomycetes, and Deuteromycetes) and filamentous bacteria (Actinomycetes).

Another group occurs as regular patches or regular crenulate discs associated only with the irregular polygonal networks described above (Figure 70*c*,*d*). These may be reproductive structures or separate endolithic forms; they range from 125 to 200 μm in diameter and average 2 μm in thickness. Although they may be remnants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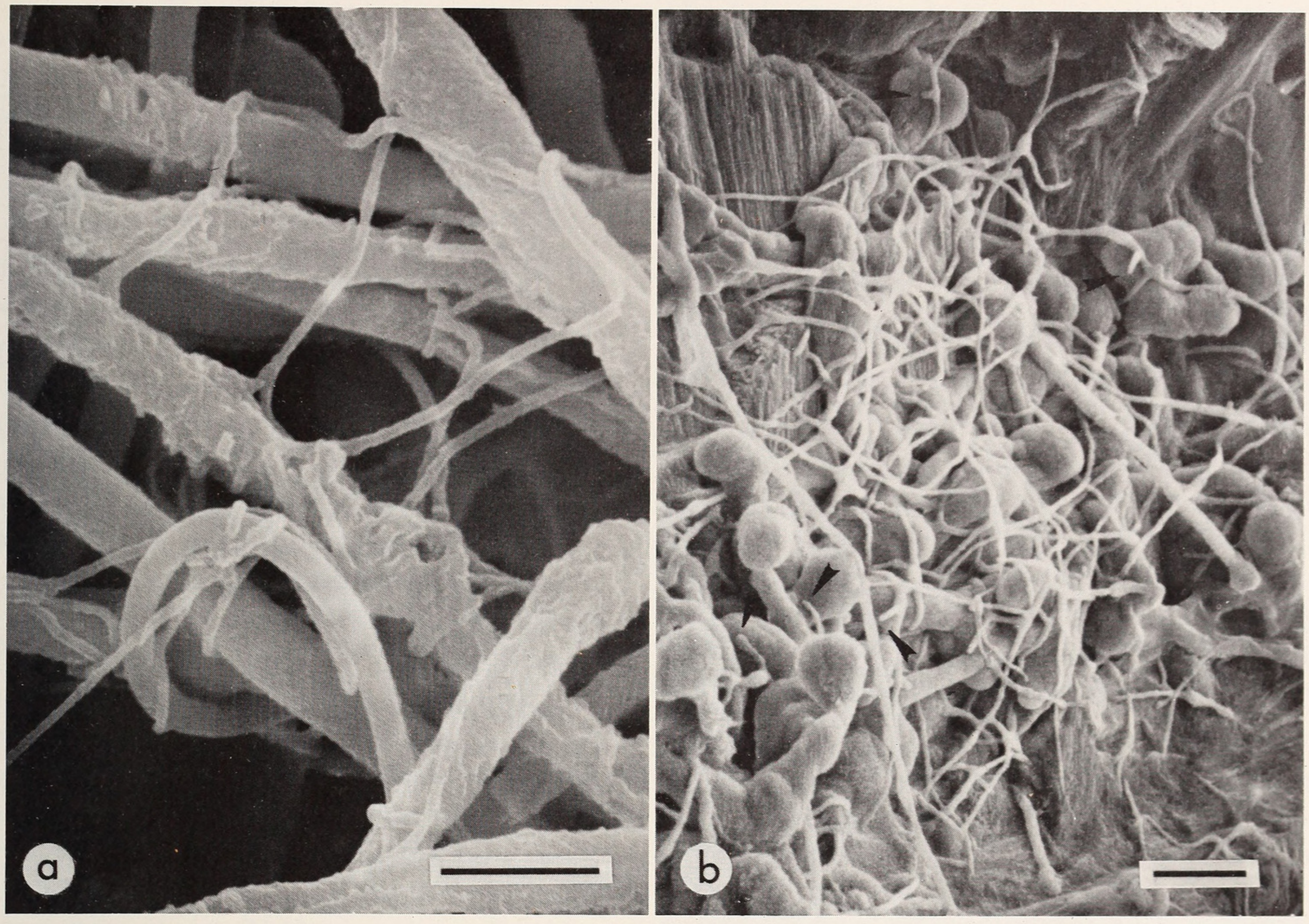


FIGURE 68.—Scanning electron photomicrographs of endolithic fungi: *a*, little-branched, thin plastic casts believed to be fungal hyphae, intertwined with the larger blue-green alga *Plectonema terebrans*, etched mollusk fragment, *Thalassia* zone; *b*, network of fine fungal borings covering and possibly feeding (arrows) upon the underlying alga, plastic casts within an etched mollusk substrate, *Thalassia* zone. (Scale = 5 μm for *a*; 25 μm for *b*.)

of the organic matrix, no analogous structures were found in any control sample or in any sample infested at the sediment-water interface.

FIGURE 67.—Scanning electron and transmitted light photomicrographs of endolithic algae; *a*, large, radiating growth form of the green alga *Ostreobium brabantium*, plastic cast within an acid-etched mollusk fragment, *Thalassia* zone (note both the single and bilobate branches, background forms are algae and fungi); *b*, *O. brabantium* filaments isolated by dissolution of a molluscan substrate, patch-reef zone; *c*, characteristic rectilinear pattern of the *Conchocelis*-stage of the red alga *Porphyra* sp., plastic cast, enhanced on a microscale by boring within a calcite rhomb, fore-reef slope zone (larger forms are an unidentified alga with strong microstructural control upon its boring pattern); *d*, *Conchocelis*-stage of *Porphyra* sp. displaying fine filaments in the typical rectilinear pattern, isolated by dissolution of a molluscan substrate, fore-reef slope zone. (Scale = 200 μm for *a*; 100 μm for *b*; 25 μm for *c*, *d*.)

Discussion

ENDOLITHS AT THE SEDIMENT-WATER INTERFACE.—The bathymetric distribution of Belizean endoliths was compared with similar tropical microboring assemblages recovered from artificial substrate stations planted in reefs off St. Croix and Jamaica (Green, 1975; Perkins and Tsentas, 1976). The distribution of autotrophic endolithic organisms is related to light penetration in the sea—both the intensity of illumination and spectral composition (Golubic et al., 1975). Although endolithic organisms cannot be assigned to absolute depths—owing to variations in water clarity, currents, and other environmental factors—Perkins and Tsentas (1976) pointed out that "clear-water" assemblages might be used to estimate maximum depths for endolithic algae. Their di-

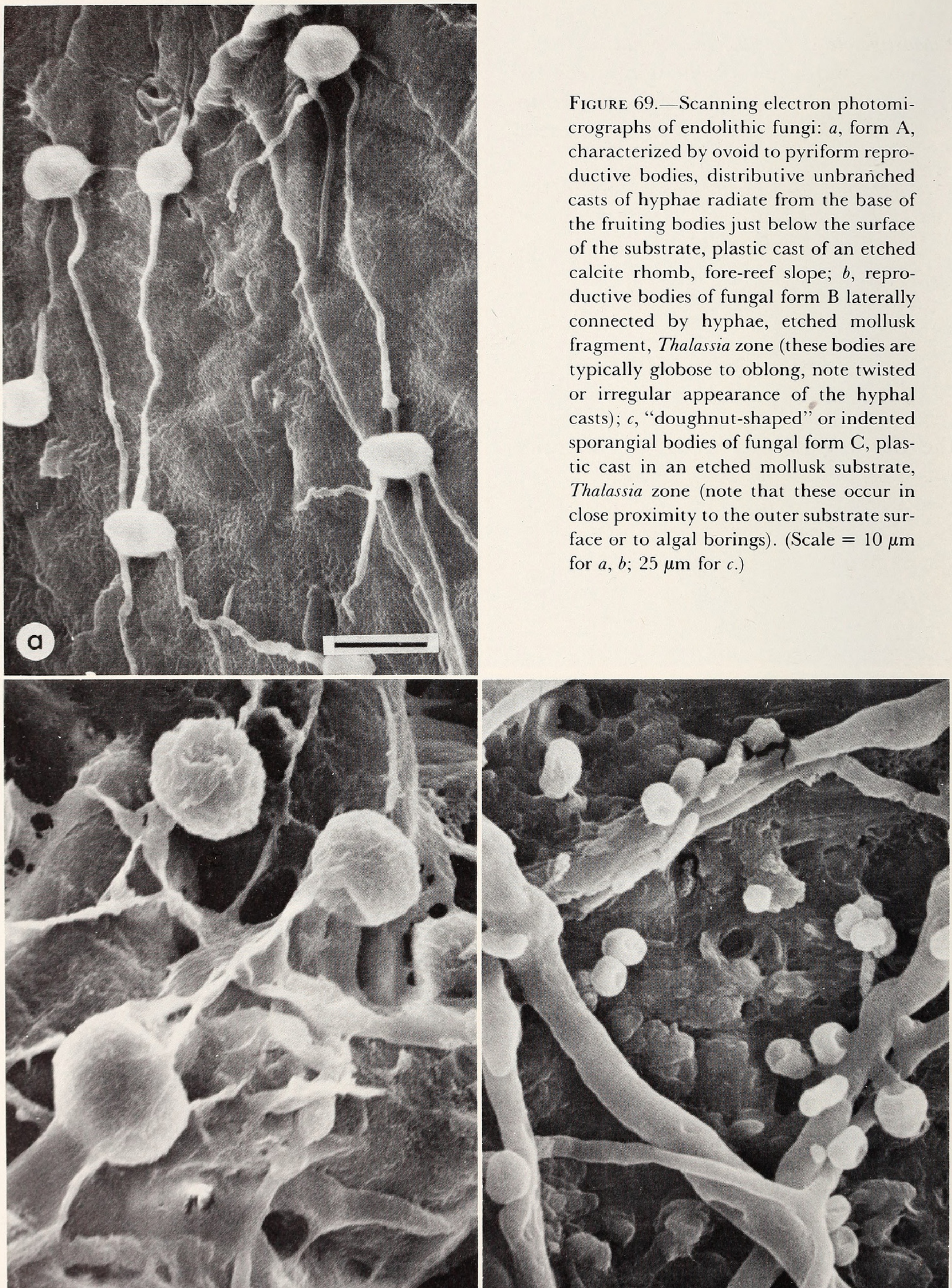


FIGURE 69.—Scanning electron photomicrographs of endolithic fungi: *a*, form A, characterized by ovoid to pyriform reproductive bodies, distributive unbranched casts of hyphae radiate from the base of the fruiting bodies just below the surface of the substrate, plastic cast of an etched calcite rhomb, fore-reef slope; *b*, reproductive bodies of fungal form B laterally connected by hyphae, etched mollusk fragment, *Thalassia* zone (these bodies are typically globose to oblong, note twisted or irregular appearance of the hyphal casts); *c*, "doughnut-shaped" or indented sporangial bodies of fungal form C, plastic cast in an etched mollusk substrate, *Thalassia* zone (note that these occur in close proximity to the outer substrate surface or to algal borings). (Scale = 10 μm for *a*, *b*; 25 μm for *c*.)

vision of such assemblages into an upper photic zone of *Mastigocoleus*, *Hyella*, *Phaeophila*, and *Ostreobium* species, and a lower zone dominated by *Porphyra* sp. in its *Conchocelis*-phase parallels, to some extent, the zonation found in the present study (Figure 62).

Ostreobium brabantium was observed only in the shallowest (1.2 and 1.5 m) sites of the *Thalassia* and patch-reef zones off Belize. In St. Croix, although present to 30 m, *O. brabantium* was predominant in depths less than 15 m (Perkins and Tsentas, 1976). Also, only the three shallowest sites off Belize contained *Hyella tenuior*, which was found down to 45 m in Jamaica (Green, 1975).

Four species of algae occurred at all depths along the Carrie Bow Cay transect. *Phaeophila engleri* was most abundant from 1.2 m to the 7.6 m spur and groove zone of the inner fore reef; similarly, this species is very common in the shallower zones of St. Croix and Jamaica. *Mastigocoleus testarum* was most abundant in the upper 12 m of the Belize sites, as was the case in St. Croix. Off Belize, however, it decreased slightly in the reef-crest and *Thalassia* zones. *Plectonema terebrans* was ubiquitous off Belize as well as Jamaica and St. Croix, except that in Belize it was less abundant in the *Thalassia* and reef-crest zones. Patchily distributed below 1.5 m, *Porphyra* sp. was most common in depths of 12 to 27 m, the deepest zone examined off Belize. This pattern has also been reported from the Australian Barrier Reef (Rooney and Perkins, 1972), the Puerto Rico shelf (Perkins, 1972), and Woods Hole, Massachusetts (Golubic et al., 1975), as well as Jamaica and St. Croix (Green, 1975; Perkins and Tsentas, 1976).

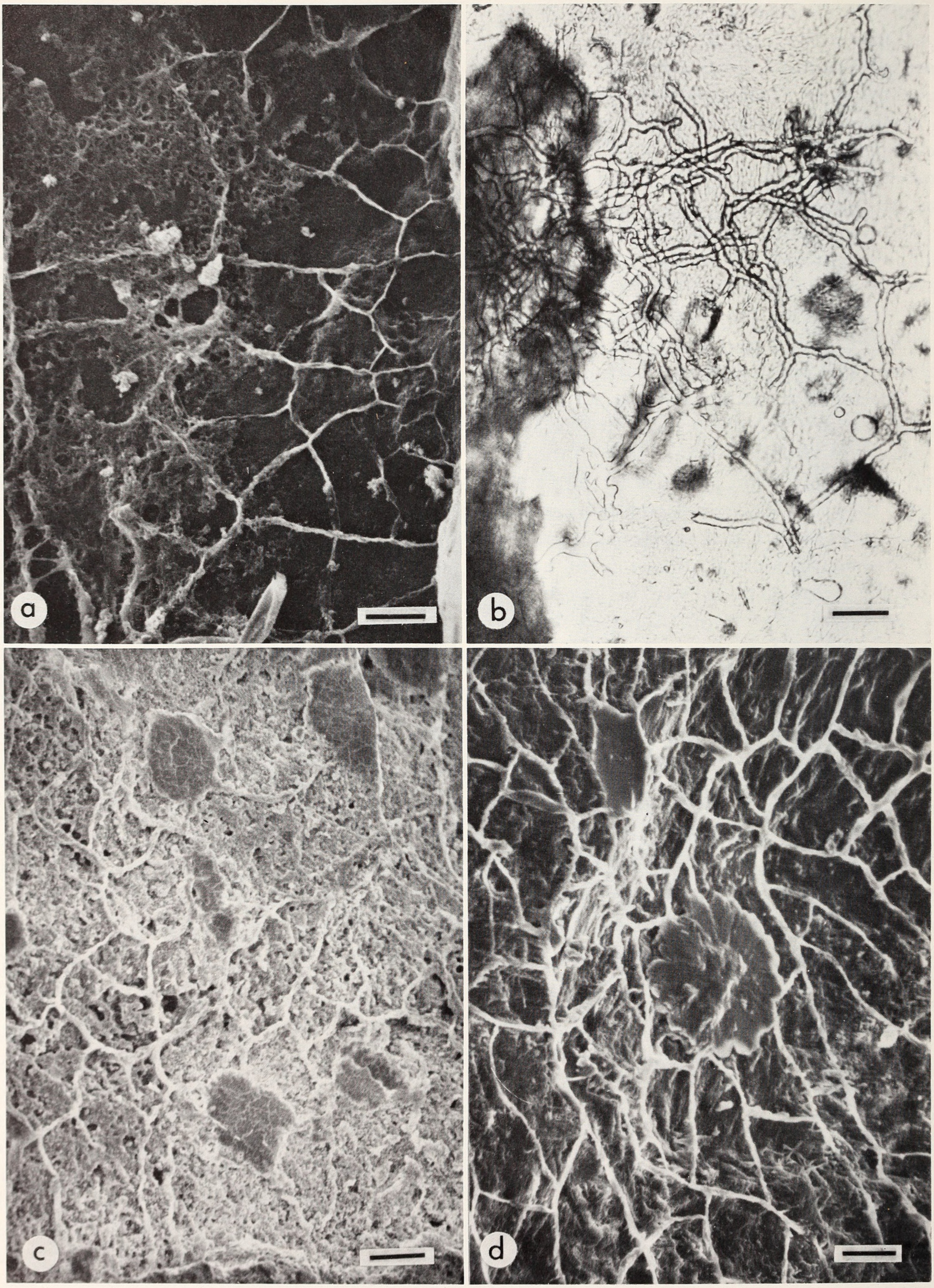
Although thin filaments believed to be fungal hyphae were present at all depths, the distribution of different sporangial structures was depth dependent. Fungal form A, with pyriform to ovoid bodies, from which basal hyphae radiate, was found only in the sample from 27 m on the fore-reef slope. Similarly, Perkins and Tsentas (1976) found a reticulate fungal form at 30 m in St. Croix. Forms B and C with laterally arranged globose spore cases and isolated "doughnut-shaped" bodies, respectively, were found only in the shallow reef-crest, patch-reef, and *Thalassia* zones off Belize.

ENDOLITHS BELOW THE SEDIMENT-WATER INTERFACE.—Fungi may be as important as bacteria in breaking down organic matter into a nutrient source for other organisms. Marine fungi may be as versatile and potent in their feeding activity as their terrestrial and fresh-water counterparts, and are probably able to attack the entire spectrum of plant and animal detritus (Johnson and Sparrow, 1961). Endolithic fungi in living and dead shells at the sediment-water interface produce intertwined, anastomosing, and branched networks, and are able to use the energy contained in organic conchiolin and chitin matrix and to parasitize algal microborers (Kohlmeyer, 1969; Calvaliere and Alberte, 1970; Green, 1975; Zeff and Perkins, 1979).

Although marine fungi are generally believed to be restricted to the aerobic surface layers of bottom sediments, the Thraustochytriacea and Chyritidiaceae commonly occur well below the sediment surface (Clokie, 1970; Bremer, 1976; Johnson, 1976). The similarity between irregular polygonal networks observed in this study and microborings attributed to fungi leaves little doubt that these polygonal networks are of fungal origin.

The associated irregular masses and crenulate discoids may be the reproductive bodies of these boring fungi. Kohlmeyer (1969) described irregular black peritheca and conidia 100 to 125 μm in diameter as fruiting bodies for endolithic marine Ascomycetes and Deuteromycetes. Alternatively, these masses may be separate endolithic fungal colonies, similar to irregular patches and to crenulate rosettes attributed to fungal colonies attacking spores, pollen, and other organic microfossils (Elsik, 1971).

In addition, two other groups of organisms, the bacteria and Actinomycetes, could produce endolithic scars resembling these forms. Similar scars on modern and ancient spores and pollen have also been attributed to bacteria and Actinomycetes (Moore, 1963; Elsik, 1966, 1971; Hav-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inga, 1971). Both groups are abundant at all levels within bottom sediments (ZoBell and Feltham, 1942) and at all depths sampled in lakes and the ocean (ZoBell and Rittenberg, 1938; Weyland, 1969; Willoughby, 1976). Boring by bacteria and Actinomycetes into carbonate substrates has not yet been investigated.

The heterotrophic or chemoautotrophic mode necessitated by endolithic life within buried sediments may explain the occurrence of these forms only in the molluscan shell fragments planted in the *Thalassia* zone. The lack of endoliths within inorganic calcite rhombs planted below the sediment-water interface may indicate parasitic or saprophytic requirements of these organisms. Boring might be an effort to obtain nutrients from the organic matrix of the molluscan substrates. No reasons are known for the lack of these endoliths in the deeper fore-reef sand-trough zone of Carrie Bow Cay. Although both this environment and the *Thalassia* zone consist of a carbonate sand bottom, the latter may contain more interstitial detrital organic matter or may be a more reducing environment. The availability of nutrients may control the distribution of these endoliths and therefore may explain the paucity of these forms within coarse sediments lacking necessary nutrient sources. Eh conditions within sediments may also be a controlling factor. Endolithic boring in this case may not be an "active" search for organic matrices in carbonate substrates, but a "passive" result of metabolic reaction or a form of protection from interstitial grazers.

FIGURE 70.—Scanning electron and transmitted light photomicrographs of unidentified microborings collected in subsurface station in the *Thalassia* zone: *a*, irregular polygonal network of varying intermittent borings, plastic cast within an etched mollusk fragment, 20 cm below the sediment-water interface; *b*, irregular polygonal endolithic network within molluscan substrate, collected 35 cm below the sediment-water interface; *c*, irregular, flattened aggregates associated with a polygonal network, these patches might be related reproductive bodies or separate colonial forms, plastic cast of acid-etched molluscan substrate; *d*, crenulate discoid associated with a polygonal network, this also might be a separate organism or related reproductive body, plastic cast of an etched mollusk fragment, 5 cm below the sediment-water interface. (Scale = 50 μm for *a*, *c*, *d*; 25 μm for *b*.)

PALEOECOLOGIC AND GEOLOGIC SIGNIFICANCE.—Endoliths and their borings found in carbonate sediments that are exposed on the sea floor may provide valuable information for the study of paleoecological conditions of carbonate sediments. The microborers and their distributional patterns at the sediment-water interface of Belize closely resemble those of assemblages previously examined in St. Croix, Jamaica, and Florida (Perkins and Tsentas, 1976). It thus becomes possible to identify endoliths typical of a tropical shallow marine setting and to establish their occurrence in upper photic and lower photic zones. Microborings commonly are preserved within ancient carbonates (Hessland, 1949; Gatrall and Golubic, 1970; Golubic et al, 1975), but they have not been examined in relation to recent zonations for the interpretation of paleoenvironmental conditions.

Conclusions

Carbonate substrates, both conch shell fragments and cleaved calcite, planted just at the sediment-water interface in various depths along the reef transect off Carrie Bow Cay, Belize, contained a diverse assemblage of microboring forms. The blue-green alga *Hyella tenuior* and the green alga *Ostreobium brabantium* were restricted to the shallowest sample sites of the upper photic zone, which is also characterized by the abundant blue-green alga *Mastigocoleus testarum* and the green alga *Phaeophila engleri* and very little of the *Conchocelis*-stage of the red alga *Porphyra* sp. The lower photic zone, below approximately 12 m, is characterized by abundant *Porphyra* sp. and considerably less *M. testarum* and *P. engleri*. The blue-green alga *Plectonema terebrans* was abundant at all depths examined. Hyphae of fungal endoliths were present at all sample sites, although different sporangial forms were bathymetrically restricted. This study of algal endoliths supports previous findings of a distinct tropical assemblage that may provide a basis for paleoecological studies of ancient assemblages.

Below the sediment-water interface off Belize, endoliths infested only the molluscan (conch) fragments in the *Thalassia*-zone station and were not present in material buried in a deeper fore-reef sand-trough station. Restriction of infestation to the molluscan shell fragments suggests that these subsurface endoliths require organic matrices as nutrient sources. Three types of endoliths occur below the sediment-water interface: (1) irregular filamentous networks, (2) irregular flattened amorphous masses, and (3) regular crenulate discoids. These microborers have unknown taxonomic affinities but they closely resemble endolithic traces and scars attributed to fungi, bacteria, and Actinomycetes. Further studies are needed to explain the origin and geological importance of these possible environmental indicators and post-depositional carbonate degraders.

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