

## Distribution, Taxonomy, and Boring Patterns of Marine Endolithic Algae

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**SYNOPSIS.** Penetration of calcareous substrates by algae involves different micro-environments. Endolithic algae include two different life forms: (1) algae colonizing existing spaces within the rock, and (2) algae actively boring within the carbonate substrate.

Two species of boring Cyanophyta were studied, and their borings were compared in exposed calcite (Island spar). The size and pattern of borings reflect the corresponding properties of the algae and show taxonomic distinctions. The direction of the tunnels and their wall sculpture are determined by the planes of crystal cleavage and twinning.

Algal boring is a dissolution process performed by the terminal cells of endolithic filaments. The space dissolved away by an alga has the shape of a miniature calcite crystal. Dissolution proceeds along the crystal twinning lines diagonally to the previous microcrystal space. The tunnel represents a sequence of such microcrystal-shaped spaces. Both biological and mineralogical determinants should be considered in the interpretation of algal boring patterns.

### DISTRIBUTION AND SIGNIFICANCE OF BORING ALGAE

Penetration of calcareous substrates by algae contributes to the formation of complex ecological habitats with different types of micro-environments. Endolithic algae are those which live within a hard rocky substratum as opposed to epilithic algae which cover the external surface of rock. Endolithic algae include two distinct life forms: algae which colonize the already existing spaces within substrates, such as fissures and structural cavities, and those which actively penetrate the substrates.

Colonization of endolithic cavities is frequent in porous carbonate as well as non-carbonate rocks. A distinct green band closely following the outline of the cracks is exposed when the rock is fractured. Algae in these cracks (most frequently

unicellular Cyanophyta) represent the colonizers of pre-existing fissures in the rock and are not actively boring forms. Although the presence of these algae may contribute to the gradual destruction of the rock, their influences are indirect and are exerted through retention of water, freezing and thawing, releasing metabolic products, and associated bacterial decomposition.

In contrast to the colonizing endolithic algae, boring algae possess specialized filaments which actively penetrate the substrate. Active penetration is limited to readily soluble rocks, most commonly calcium carbonate. Semantic difficulty arises from the fact that thalli of many boring algae can be morphologically and functionally distinguished into epilithic parts which spread over the surface of the rock and endolithic parts which penetrate the substrate. Clearly, in this case "endolithic" applies only to the part of the algal thallus within the rock.

Boring algae are predominantly marine. They invade a variety of carbonate substrates (*e.g.*, calcareous rocks, shells of molluscs, skeletal fragments, sand grains, and oolites). Generally the vertical distribution of endolithic algae ranges from the upper sublittoral zone into the spray zone. These

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algae are the main constituents of the dark-colored, intertidal-supratidal band along the carbonate coasts of the world. Several communities of boring algae have been studied in the Mediterranean Sea, subdividing the dark band into zones of different color shadings (Ercegovic, 1932). The capacity of these communities to invade extremely stressful habitats between the marine and terrestrial environment is of great ecological significance.

Algal boring contributes to the destruction of carbonate coasts (Purdy and Kornicker, 1958). This contribution becomes particularly significant in the supralittoral zone, where many rock-abrading plants and animals cannot survive (Neumann, 1966). In the upper sublittoral zone of tropical seas, boring algae invade sand and oolite shoals (Rusnak, 1960). Their geological importance here is due to their destruction of small carbonate grains and skeletal fragments. They are ecologically important because of their colonization of shifting substrata inaccessible to other primary producers such as higher algae and marine phanerogams.

Early literature concerning the biology of boring algae is summarized by Frémy (1936). Geological literature on boring algae is surveyed by Hessland (1949) and Bathurst (1966).

This paper is primarily concerned with the implications endolithic algae have for paleoecology. Recognition of algal boring patterns in the fossil record provides reliable criteria in determining the ancient photic zone in shallow-water environments. The following question appears to be of basic interest for interpretation of algal boring patterns: are algal boring patterns taxonomically specific, or are they determined by the mineralogical properties of the substrate?

#### METHODS

In an attempt to answer this question, crystals of Iceland spar (calcite), a mineralogically well-defined substrate, were exposed to the activity of boring algae in the upper intertidal zone at La Parguera on

the southern coast of Puerto Rico. After three years the crystals were heavily colonized and the boring patterns were well developed. This material was either dried, or fixed in 3% buffered formaldehyde solution. One part of it was treated with 2% HCl to remove calcium carbonate and free the endolithic algal filaments; the other part was saved for direct observations of boring patterns by light microscopy.

#### TAXONOMY OF ALGAL SPECIES COMPARED

Although boring algae have been found among several algal groups (Cyanophyta, Rhodophyta, Phaeophyta, and Chlorophyta) the upper intertidal and supratidal boring algal flora is composed exclusively of Cyanophyta. The ensuing discussion is based on comparison of two common cyanophytes found in the crystals: *Hormatonema paulocellulare* Ercegovic, and *Hyella caespitosa* Bornet and Flahault. The taxonomic interpretation of these algae by different authors varies considerably. Ercegovic, considers them distinct species belonging to two genera of the family Hyellaceae of the order Pleurocapsales. The Hyellaceae is composed of five genera with about 20 species (Ercegovic, 1932). Drouet and Daily (1956), on the other hand, attempted to unite the entire family Hyellaceae together with many other species as "ecophenes" of one single species, *Entophysalis deusta* (Meneghini) Drouet and Daily. The following direct comparison of the two morphs shows them to be distinct morphological entities. Given the fact that they were grown under identical conditions, they will be treated here as separate species.

Their common morphological characters are: both species have cells embedded in a thick gelatinous sheath and are loosely organized in rows or in filaments. When they are exposed to strong illumination, extracellular pigments are deposited in the gelatinous sheaths, staining the parts of the alga close to the surface of the rock. Both algae grow distinct epilithic and endolithic filaments. The cells in the epilithic filaments are closely packed together,

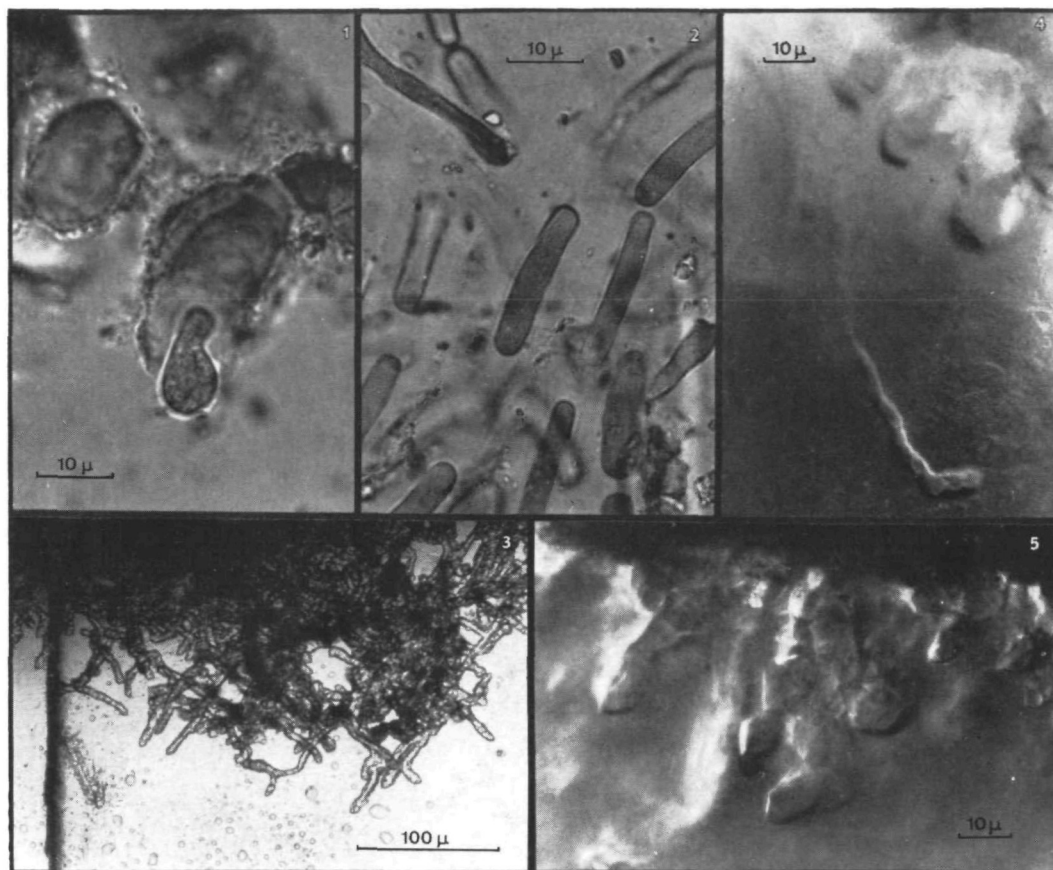


FIG. 1. *Hormatonema paulocellulare*. Terminal cells of the boring filaments after calcite crystal (Iceland spar) was dissolved in dilute HCl. Transmitted light.

FIG. 2. *Hyella caespitosa*. Rows of cells in the boring filaments. Preparation same as in Figure 1. Transmitted light.

FIG. 3. Algal boring pattern within a calcite crystal. Direction of filament growth is diagonal to the main cleavage lines (left) and coincides with the

lines of crystal twinning. Transmitted light.

FIG. 4. Bored algal tunnels within a calcite crystal. Upper right corner: three tunnels of *Hormatonema paulocellulare*. The thin, long, L-shaped tunnel belongs to *Hyella caespitosa*. Incident light.

FIG. 5. Bored algal tunnels of *Hormatonema paulocellulare* within a calcite crystal. The angular outlines at the inner end of the tunnels are concurrent with the main cleavage lines. Incident light.

while the ones in the endolithic filaments are separated by shorter or longer sections of gelatinous matter. The terminal cells of each endolithic filament are club-shaped. The blunt end of the terminal cell projects from the gelatinous sheath; it is frequently in direct contact with the calcareous substrate and presumably dissolves it.

The most prominent differences between the two species are: the epilithic filaments in *Hormatonema paulocellulare* are distinct, spread thinly over the rock surface, and contain few uniserially organized cells;

in *Hyella caespitosa* the filaments are densely compacted, containing multiserial, pseudoparenchymatous, cell masses. The extracellular pigment in *Hormatonema paulocellulare* is dark blue (which turns red at  $\text{pH} < 6$ ); in *Hyella caespitosa* it is yellow-brown (which turns green at low pH). Endolithic filaments of *Hormatonema paulocellulare* are thick ( $8\text{--}12\mu$ ) and short ( $< 50\mu$ ), seldom branched, and are composed of few (1-4) nearly isodiametric cells separated by long stalk-like gelatinous segments of the filament (Fig. 1).

Endolithic filaments of *Hyella caespitosa* are thinner ( $4\text{--}5\mu$ ) and several hundred microns long, frequently branched, and contain very elongated ( $10\text{--}30\mu$  long) proximate cells (Fig. 2). The apical enlargement of the club-shaped terminal cells in *Hormatonema* is more pronounced than in *Hyella*.

#### OBSERVED CHARACTERISTICS OF ALGAL BORING PATTERNS

Before exposure to the marine environment, the crystals had perfectly smooth surfaces. After exposure the surfaces were heavily bored showing a labyrinth of grooves and tunnels. The borings of *Hormatonema paulocellulare* were recognizable as a "carpet" of closely packed, parallel tunnels,  $8\text{--}15\mu$  in diameter, penetrating the crystal to a uniform depth of  $30\text{--}50\mu$  (Fig. 5). By transmitted light and at a magnification of  $\times 400$  the terminal cells of the alga were visible within the slightly expanded inner ends of the tunnels. The borings of *Hyella caespitosa* were less common. They penetrated more deeply ( $120\text{--}300\mu$ ), as laterally or dichotomously branched tufts; the individual tunnels were  $4\text{--}6\mu$  in diameter, significantly narrower than those of *Hormatonema paulocellulare*.

Before exposure to algal boring activity, two sets of cleavage lines were visible within the crystals, related to each other as the main cleavage lines to the lines of the crystal twinning. The main growth orientation of the endolithic filaments of both algae within the crystal was diagonal to the main cleavage lines, following the lines of crystal twinning (Fig. 3).

The inner walls of the tunnels frequently showed angular surface sculpture resembling stepwise-arranged arrowheads or chevrons. Similar outlines are often found at the inner ends of the tunnels (Fig. 5). These outlines are coincident with the main planes of crystal cleavage. The space dissolved away by the terminal cell has the shape of an oriented, miniature, calcite crystal. Due to growth of the filament, the

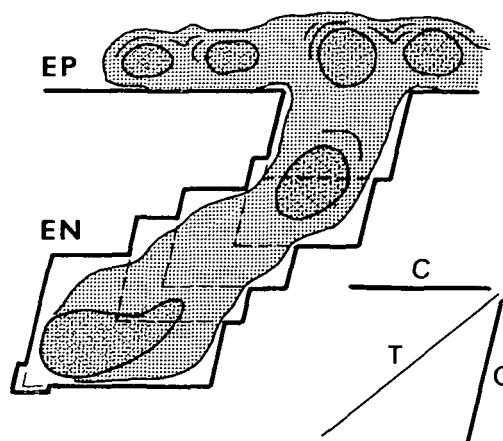


FIG. 6. Diagrammatic presentation of the relationship between algal filaments (*Hormatonema*) and calcitic substrate (Iceland spar). Bold lines represent the actual outlines of the crystal surface along the tunnel. Thin dashed lines indicate the outlines of micro-crystal spaces dissolved at different stages of penetration. EP, epilithic filament; EN, endolithic (boring) filament; C, directions of main cleavage lines in the crystal; T, direction of twinning lines coincident with the direction of growth of the boring algal filament.

terminal cell advances into this space directing the further course of dissolution (Fig. 6). The next crystal-shaped space is usually dissolved in a diagonal direction relative to the previous one, following a twinning line of the crystal. The bored tunnel thus represents a diagonally oriented sequence of microcrystal-shaped spaces, where the matrix is replaced by algal filaments.

#### CONCLUSIONS

Taxonomically distinct boring algae produce specific boring patterns which can be recognized in the absence of the algae. This property opens the possibility of interpretation of fossil boring patterns. The size of the bored tunnels is determined by the size of the algal filaments; similarly the pattern and frequency of tunnel branching is determined by the corresponding properties of the endolithic algal filaments. The directions of growth, on the other hand, as well as the fine sculpture of the inner surface of the bored tunnels, are controlled by the mineralogical properties

of the substrate. In characterizing algal boring patterns, both biological and mineralogical determinants should be considered.

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