REEFAL MICROBIAL CRUSTS

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Introduction

Fine-grained, non-skeletal crusts, variously described as laminar micrite crusts, cements, stromatolites, and microbialites, are locally common in late Quaternary coral reefs. They occur on wave-swept margins in dark or low-light habitats, such as cavities and deep fore-reef slope surfaces. They have often been regarded as cements, but are now widely interpreted as microbial carbonates produced by heterotrophic bacterial communities. The crusts typically form at the end of active reef development, as late stage veneers on framework skeletons. They can be up to 20 cm thick, and locally constitute 80% of the reef structure. Crusts are particularly important in strengthening cavernous reef frameworks. Their development in poorly illuminated cavity and deepwater habitats suggests eukaryote competition for substrates. Their preferential development at wave-swept reef margins probably indicates the effect of increased carbonate saturation state by intense seawater flushing. Reefal microbial crusts appear to be more common in Late Pleistocene and Early Holocene reefs than in those of the past 6,000 years. Similar crusts are also present in much older reefs. Many questions remain concerning the factors that have controlled their formation and uneven distributions in space and time.

Recognition

In important papers, Ian Macintyre (e.g., Macintyre, 1977, 1984) drew attention to fine-grained crusts in Holocene Caribbean reefs and reef caves. Their non-skeletal fabrics are evidently precipitated, and these examples, together with others in the Great Barrier Reef (Marshall and Davies, 1981), attracted attention as examples of submarine lithification. Outcrops of Late Miocene reefs in the western Mediterranean revealed their variable distribution and local importance. In *Porites* reefs of Messinian (~6 Myr) age in southern Spain, crust volume can far exceed that of coral. Their clotted-peloidal fabrics can be interpreted as calcified bacterial organic matter, and grains trapped in the crusts on steep or overhanging surfaces suggest adhesive biofilm (Riding et al., 1991). Following recognition of similar features in crusts in cores through late Quaternary reefs at Tahiti (Montaggioni and Camoin, 1993) and in reef caves at St Croix (Zankl, 1993), recognition and interpretation of the crusts as microbial stromatolites and thrombolites became common. They have been particularly well described by Gilbert Camoin and colleagues at Tahiti, where they were among the targets of IODP Expedition 310 in 2005 (Camoin et al., 2007).

Structure and fabric

Reefal microbial crusts range from millimeters to decimeters in thickness (Figure 1). Their external surfaces can be irregular, smoothly domical, or patterned by 'knobby' dendritic columns (Figure 2). Internally, smooth domes are usually relatively well layered (stromatolitic), whereas the columns are usually more weakly layered.

Crusts exhibit complex internal fine-grained microfabrics, with subordinate allochthonous grains and microencrusting skeletons. Silt-size grains made of fine-grained $CaCO_3$ (peloids) are characteristic components of crusts (Macintyre and Marshall, 1988) (Figure 3). These grains, generally <50 μm across, are relatively evenly spaced, and often 'float' in lighter colored microspar that includes irregular sinuous fenestrae up to 250 μm across. Similar aggregates form geopetal fills in small cavities, and it appears that peloids occur both in situ precipitated crusts and as allochthonous (although probably quasi-autochthonous) fills.

Origin

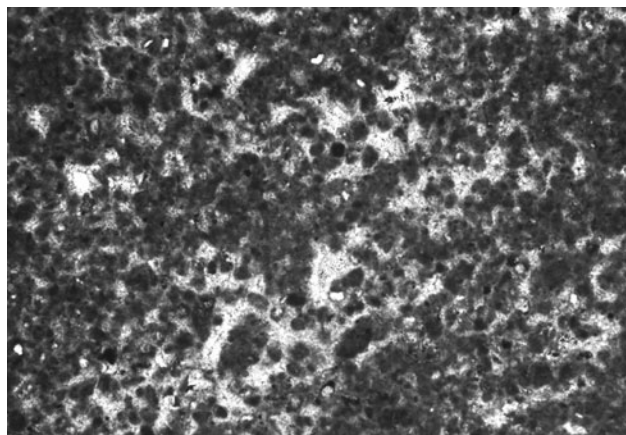Even studies that described crusts as cements often invoked bacterial processes, such as decay of organic

Reefal Microbial Crusts, Figure 1 Fine-grained crusts (*light*) on dissolved vertical *Porites* branches (*dark*). Late Messinian (~5.5 Ma), Mesa de Roldán, Almería, SE Spain. The crusts have smooth external surfaces and range in thickess from ~3 mm to 3 cm.
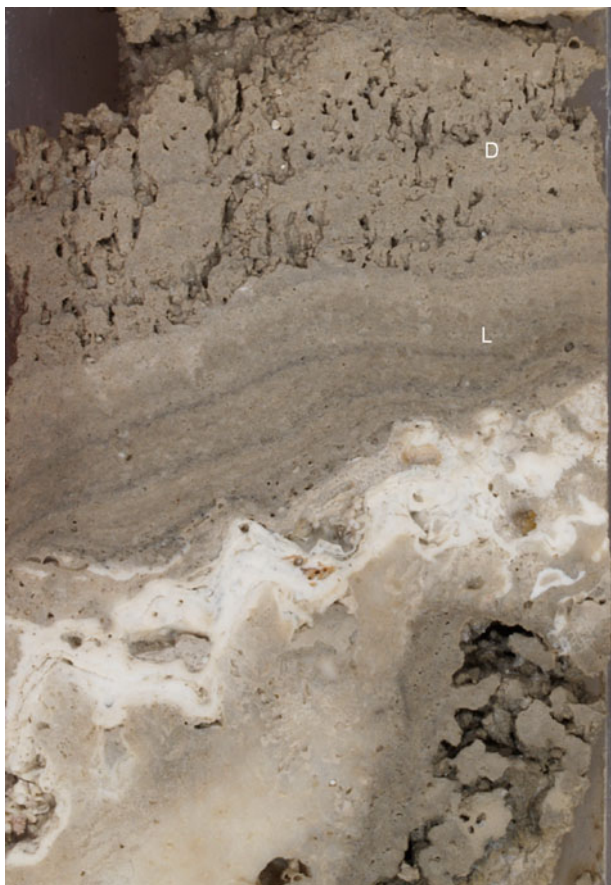
Reefal Microbial Crusts, Figure 2 Coralgal-microbialite reef framework with ∼5 cm of fine-grained crust, showing laminated (L) lower part and dendritic (D) upper part. The crust overlies coralline algae (*white*) and other skeletal encrusters, which in turn overlie *Acropora* (bottom of picture). Core through late Pleistocene–early Holocene reef, SW Tahiti, IODP 310, Maraa eastern transect, Hole M0015B, Last Deglacial Sequence, Subunit 1B, interval 310-M0015B-19R-01, 59–67 cm (Camoin et al., 2007, p. 4, Figure F16). Visual core description and core images of Hole 310-M0015B. doi:10.1594/PANGAEA.499787. Width of view, 6 cm. © IODP/ECORD.

Reefal Microbial Crusts, Figure 3 Peloid microspar microfabric, showing irregularly amalgamated dark peloidal masses in a light microspar, locally fenestral, matrix. Sample T302-R34, provided by Jody Webster; −988 m drowned reef, Kohala, NW Hawaii; approx. age 375,000–400,000 years. Width of view 1.4 mm.

matter, to account for their formation (Macintyre, 1984, p. 232; Macintyre and Marshall, 1988). Chafetz (1986) proposed that peloids could form in semi-isolated cavities in present-day reefs by bacterially induced precipitation around suspended bacterial colonies. The presence of similar peloids, together with other microfabric comparisons (Riding et al., 1991; Montaggioni and Camoin, 1993; Zankl, 1993), and also the local presence of microbial filaments have all been used to infer a bacterial origin for the crusts. More specifically, their typically magnesian calcite composition, stable isotope values, and biomarkers provide evidence for sulfate-reduction: (a) Reefal peloidal crusts are typically magnesian calcites in the range 12–18 mole% Mg. Difficulties in obtaining such high Mg-calcite compositions inorganically suggest biological involvement such as bacterial sulfate reduction (Malone et al., 2001, p. 891, and Figure 10). (b) Bacterial processes, specifically sulfate reduction, have been inferred from carbon and oxygen isotope values of peloidal crusts and fills (Land and Goreau, 1970; Pigott and Land, 1986, Figures 9–11; Reitner et al., 2000, p. 153). (c) Reitner et al. (2000, pp. 158–159) found biomarker evidence for anaerobic heterotrophs in Lizard Island and St Croix peloidal crusts. In Tahiti reef crusts, Camoin et al. (1999, p. 297) found muramic and diaminopimelic acid, characteristic of bacterial cell walls, and Heindel et al. (2009) found fatty acids typical of sulfate reducers.

Living examples

Living microbialites in reef caves are potential analogues for older crusts. Examples are centimetric crusts at Lizard Island and St Croix. These are forming in association with invertebrate and algal encrusters. Their surface microbial mucus can trap sediment and provide a medium for peloid precipitation (Reitner et al., 2000, pp. 154, 156). Chafetz's (1986) proposal that cavity peloids can be calcified bacterial aggregates is supported by the observation of organic remains in the cores of peloids forming in 'degraded microbial organic substances' within microbial films in St Croix caves (Reitner et al., 2000, p. 156, and Figure 5). Raised alkalinity in organic matrices associated with calcification in decaying sponges is 'believed to be largely a result of heavy sulfate reduction' (Reitner et al., 2000, p. 153).

Sedimentological role

Thick crusts strengthen reef skeletons and reduce cavity volume, especially in branching or platy frameworks. In Messinian reefs of SE Spain, crusts up to 15 cm thick coat vertical *Porites* branches that are 1–3 cm wide and are linked horizontally by thinner platelike connections.

The crusts are therefore often thicker than the corals and locally constitute 80% of the reef volume. Crusts fused the otherwise delicate coral frame into a solid mass while the reef was still forming. The crust-welded reef rock occurs as cuboidal blocks up to 5 m across on the fore-reef slope (Riding et al., 1991). Crusts up to 20 cm thick occur in Late Pleistocene reefs in Tahiti (Camoin et al., 1999).

Distribution and controls

Crusts occur on wave-swept reef margins in enclosed framework cavities and on deep fore-reef slope surfaces. This is well documented from studies of Late Pleistocene–Holocene reefs (Macintyre, 1977, p. 513; Camoin and Montaggioni, 1994). Their formation in the closing stage of framework growth is reflected by their position between sciaphilic encrusters (e.g., corallines, foraminifers) and overlying reef or pelagic sediment. As light diminishes, reef surfaces are colonized by a succession of increasingly sciaphilic (shade-loving) skeletal organisms: coralline algae, bryozoans, sclerosponges, foraminifers, and serpulids. The corallines can include shallower and deeper water communities (Braga et al., 2005; Webster et al., 2009, Figure 8). Fine-grained crusts typically overlie this sequence (Montaggioni and Camoin, 1993) (Figure 4). Crusts are preferentially developed on wave-swept margins, relative to lagoon and platform interior sediments, both in shallow reef crest zones (e.g., Macintyre, 1977) and on deeper foreslopes.

Ability to grow in dark environments is consistent with interpretation of the crusts as products of essentially heterotrophic bacterial communities. It also suggests contest for substrate in which crusts were outcompeted by eukaryote skeletal encrusts (see Eukaryote competition). Preference for wave-swept reef margins suggests the effect of seawater flushing on precipitation. This too is not inconsistent with a microbial origin for reefal crusts since bacterial calcification is strongly dependent on environmental factors that promote precipitation.

Late Quaternary crusts were common during deglacial sea level rise but declined ~6,000 years ago. This secular pattern of late Holocene decline was recognized in Tahiti and other Pacific reefs. A possible explanation is that crust formation was promoted by increases in alkalinity and nutrients in reef waters due to enhanced oceanic upwelling and terrestrial runoff during deglacial sea-level rise, and that these effects declined as sea level stabilized in the mid- Holocene (Camoin et al., 1999, p. 300).

Eukaryote competition

The restriction of crusts to cryptic environments and deep foreslope habitats suggests competition for space with photophilic eukaryote reef builders. Such competition has long been considered a key factor in the geological decline of stromatolites in marine environments. Applying this view to reefal microbial crusts suggests that they were outcompeted for substrate by algal and invertebrate
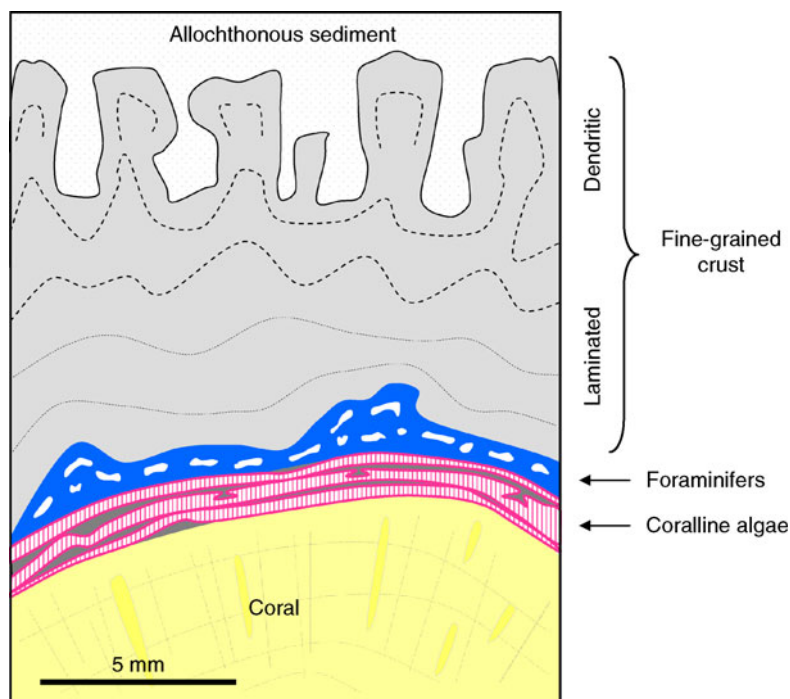
Reefal Microbial Crusts, Figure 4 Succession from coral to fine-grained crust: coral, coralline algae, foraminifers, crust. Variations are common; omitting some components and including additional skeletal encrusters. Based on Figure 2, and Riding et al. (1991, Figure 15), Riding and Tomás (2006, Figure 5), and Webster et al. (2009, Figure 8).

encrusters such as corallines and foraminifers. Only as decreasing illumination excluded even these shade-loving competitors did microbial crusts develop extensively. Relegation to dark habitats thus helps to account for crust development at the end of reef-growth. It also indicates independence of illumination, supporting an essentially heterotrophic interpretation of microbial crust communities.

Fore-slope drowning

The formation of crusts in deepening sequences at the end of reef growth has been emphasized in studies of deep and drowned late Quaternary reefs. Late Pleistocene–Holocene crusts occur on reef foreslopes at depths of ∼80–200 m in widespread locations, e.g., Jamaica, Belize, the Red Sea, Huon Gulf, Papua New Guinea, Tahiti and the Marquesas Islands, and Hawaii (Webster et al., 2009). It is not known whether these deposits are still forming. Presumably, they began to form during deglacial sea-level rise and are now at much greater depths than when they started. These deep 'slope microbialites' occupy a position between low-light framework encrusters, such as deep water corallines, and overlying pelagic sediments. Camoin et al. (2006, p. 289) suggested that crusts at Tahiti and the Marquesas Islands formed below 100 m because they overlie deep water assemblages of corallines and foraminifers, are partly contemporaneous with phosphate–FeMg crusts, and are overlain by plankic carbonates. Fore-slope crusts have therefore been regarded as signatures of sea-level rise (Camoin et al., 2006) and, in some cases, of reef drowning (Webster et al., 2009). The drowned reef at −150 m around Hawaii shows shallow-water *Porites* overlain by sciaphilic skeletal encrusters, followed by microbial crusts (Webster et al., 2009, Figures 6, 8). The microbial crust is estimated to have formed at depths of ∼120–150 m or more (Webster et al., 2009, 136–137). The sea-level rise that terminated reef development at this location can be connected to a deglacial meltwater pulse ∼14,700 years ago (Webster et al., 2009, Figures 10, 11).

Older examples

Fine-grained clotted-peloidal crusts are not restricted to geologically young reef corals. Similar examples have been widely recognized in skeletal reefs throughout the Palaeozoic and Mesozoic. Present-day reefal crusts can therefore shed light on the origin and development of much older examples. Early Cretaceous (120 million year) peloidal crusts on scleractinian corals have been interpreted as heterotrophic bacterial carbonates (Riding and Tomás, 2006).

Stromatolites and scleractinian corals can in several respects be regarded as end members of reef construction (Riding et al., 1991). Their locally intimate association in the Quaternary has implications for reef development and environmental change during this interval. The distribution of reefal microbial crusts in space and time, and the factors that have determined their development, are significant research questions. Living examples need to be related in detail to Quaternary examples, and also to much older ones in the geological record.

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Cross-references

Microbes

REEFAL SEDIMENTS

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Definition

A coral reef involves frame-building and frame-binding organisms, unconsolidated sediment fill, and the living veneer, which is an expression of the interactions between environmental and organic activities. Under normal conditions of stable sea level, the reef reflects a balance between the forces of construction (organic growth) and the forces of destruction (erosion, dispersal by transportation, and deposition).

Sediment production processes involve the mechanical and biological erosion of the cemented reef material and the decay/disintegration of the biogenic organisms in which the form of the skeletal material can be either segmented (*Halimeda*), tabular (red algae), or spicular (gorgonians, sponges, and holothurians), and the direct postmortem contribution of primary grains including whole tests of organisms such as foraminifera, small mollusks, and planktic calcareous or siliceous organisms, and the chemical and biochemical precipitation of discrete carbonate particles and cement.

The agents/controls are physical (waves) and currents, abrasion during transport, or biological such as rasping or burrowing organisms. Also, the decomposition of organic tissue may be assisted by bacteria and fungi. In several instances, growth characteristics dictate the skeletal particle size, e.g., benthic foraminifera. Population productivity may determine the initial distribution of the skeletal detritus, e.g., benthic foraminifera, coral, diurnal cycles in pH, dissolved CO_2, and carbonate saturation may result in precipitation of calcium carbonate either as aragonite, high Mg-calcite, or calcite.

The result of the sediment production either remains in situ or undergoes transportation across the reef top to the site of deposition. Large coral heads descend down the seaward slope or are thrown up onto the reef rim or reef flat. Coarse rubbles form prominent boulder zones, or coral sticks form conspicuous shingle ridges. Flat *Halimeda* plates form gravel deposits and benthic foraminifera concentrate in ponds or hollows. The sand-sized skeletal fragments are removed from the source area by currents of removal and are transported as bed load to be deposited in the sand wedge adjacent to the lagoon, and the finer sand and silt-sized material is transported in suspension to finally be deposited in the lagoon or carried to the leeward reef slope.

The processes of sediment breakdown can be differentiated into biological (disintegration), physical (attrition which is mechanical and disintegration through impact), mechanical breakdown into individual skeletal microarchitecture, or chemical/biochemical corrosion/solution and bacterial action. The agents/controls are the various organisms such as bottom feeders (sediment ingesters), raspers, grazers, crushers, and borers. The skeletal material thus produced is subjected to the variable energy experienced in the environment related to the strength and frequency of the waves and currents. In addition, the type, size, density, abundance of particles, and the mode of transportation (traction, saltation, and suspension) and the microarchitectural control further influence the relative abundance of particular particle sizes (Stoddart, 1969).

There is a continuous reduction of particle size. Discrete grain-size populations are produced either as skeletal modes or by discontinuous breakdown of the skeletal materials. There is greater fragmentation taking place in the traction load than in suspension. Also, there may be some degree of corrosion of the skeletal particles during passage through the gut of various organisms. In the high energy environments of the Great Barrier Reef, it is rare for fecal pellets to remain intact, and the finer-sized material within the pellets is dispersed by the currents and wave activity. Discontinuous size reduction of the skeletal material will finally produce very fine-grained sedimentary material, which takes the form of carbonate mud (finer than 0.03 mm). These muddy facies are restricted to the central part of the lagoons on the platform reefs, or the sediment wedge to leeward of the reef top.

The processes of transport are either biological (e.g., grazing by fish and turtles) or physical, which involves a winnowing process whereby sedimentary particles are moved in response to the normal physical transportation processes. In addition, very high energy but low frequency cyclonic activity provides an overprinting of the low energy, high frequency translatory waves and tidal currents. The sediments may be differentiated on the basis of particle size, shape, surface texture, and bulk density, and the interrelationship between roughness, threshold velocity, and settling velocity influences the relative importance of different transportation modes.

The effect/product of sediment transportation processes is that lag deposits remain in the high energy zone