Environmental control of the genesis of Tahitian reef-microbialites during the last deglacial sea-level rise

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Katrin Heindel
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Gutachter der Dissertation
PD Dr. Hildegard Westphal
Prof. Dr. Jörn Peckmann

Prüfer
Prof. Dr. Eberhard Gischler
Prof. Dr. Helmut Willems

Weitere Mitglieder des Prüfungsausschusses
Dr. Thomas Felis
Markus Eisele
ERKLÄRUNG


Anschrift: Kirchbachstraße 209, 28211 Bremen

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ABSTRACT

During IODP Expedition 310 “Tahiti Sea-Level”, drowned Pleistocene to Holocene barrier reef terraces have been drilled on the slope of the volcanic island Tahiti (French Polynesia, central Pacific). The main motivation for the expedition to Tahiti was the assumption that the last deglacial sea-level rise is precisely recorded in the coral reefs of this far-field site (far from active plate boundaries and influences by ice sheets). Three sites around Tahiti were drilled: Tiarei in the North, Faa’a in the West, and Mara’a in the South. This thesis focuses on the cores of the post-Last Glacial Maximum (LGM) reef sequence. The Tahitian deglacial reef succession typically consists of zooxanthellate corals, which are encrusted by coralline red algae and subsequently by microbialites. These microbialites (microbial carbonate crusts) are composed of high-magnesium-calcite and show two growth patterns. An initially laminated pattern changes partly to a dendritic pattern during progressive microbialite growth. The large volume of microbialites (up to 80 vol. % of the cores) is uncommon for modern shallow-water coral reefs. This study aims in the investigation of the still poorly understood genesis of these voluminous Tahitian microbialites.

In corals, coralline algae, and microbialites, microbioerosion patterns (ichnocoenoses) dominate, which are typical for deeper euphotic to dysphotic zones. This is highly unusual for a tropical, light-flooded setting. The scarcely detected ichnotaxa (traces of bioeroders) typical for the shallow euphotic zone are restricted to the base (oldest sequence) of the deglacial reefs. This indicates shallower relative water depths at the base compared to the upper (younger) ranges of the deglacial sequence. Hence, reflecting the deepening-upwards as a result of the deglacial sea-level rise. Moreover, at the base of the deglacial reef-succession, the ichnocoenoses present in the corals indicate shallower bathymetries (euphotic conditions) than those in the encrusting microbialites (dysphotic conditions). This correlates with radiocarbon data that indicate a time gap of more than 600 years between coral growth and microbialite formation. With respect to the rising sea-level, the time gap explains the change to deeper bathymetries from coral growth to microbialite development. In contrast, at the middle and top ranges of the deglacial reefs, the microbioerosion patterns in all framework components reveal dysphotic conditions, which indicate a uniform palaeobathymetry. Along with similar radiocarbon ages, it is demonstrated that the encrustation by microbialites was almost coeval to coral growth.

The encrustation of the corals took place within the photic zone, which is demonstrated by the dominance of traces produced by phototrophic microbioeroders in corals and microbialites, mainly low-light specialists. This implies an encrustation horizon (microbialite growth layer) shortly below the reef-top. The “cementation” of the reef framework by microbialite encrustation almost simultaneous to coral growth would explain the rarely observed reef debris in the drilled cores as a result of an exceptional
stability of the Tahitian fossil reefs against reworking storms.

An enigma arises from the fact that the ichnocoenoses are representative for mostly deeper euphotic to dysphotic conditions, which seems very deep for zooxanthellate coral growth. The elemental composition of the microbial carbonates (relative high contents of Al, Si, Fe, and Ba) and the detected clay- and basalt-derived minerals in the microbialites (mainly phyllosilicates, pyroxene, plagioclase, and magnetite) point to a strong terrigeneous influx from the volcanic island. That could be an explanation for increased nutrient levels, which intensified the primary productivity during the last deglacial sea-level rise. The higher primary productivity is thought to have reduced the light availability (illumination), which finally resulted in a condensation of the photic zones (“telescoping effect”), giving the impression of deeper water depths.

For the identification of microbes in the reef-microbialites of Tahiti, lipid biomarkers have been successfully used. In the microbialites, terminally-branched fatty acids (iso-/anteiso-C\textsubscript{15} and iso-/anteiso-C\textsubscript{17}) were detected in uncommonly high concentrations for coral reefs. Iso- and anteiso C\textsubscript{15/17} fatty acids are typical biomarkers for sulphate-reducing bacteria. The slight shift from the carbon isotopic values of the bulk organic matter to the carbon isotopic values of the iso- and anteiso C\textsubscript{15/17} fatty acids shows insignificant enzymatic fractionation, which corroborate the heterotrophic sulphate reducers as source of these biomarkers.

The increased nutrient supply (dissolved inorganic nutrients) and the intensified primary productivity were assumed to have forced the development of marine snow, which, deposited on coral heads, initiated the increased production of coral mucus (“slime” secretion of the polyps to remove sediment). The marine snow-mucus-mixture probably provided the anoxic habitat and the organic matter for sulphate-reducing bacteria, which produced high amounts of extracellular polymeric substances (EPS) as reaction on environmental stress. Since clear indications for cyanobacteria or other phototrophic microbes were not found, the chemical and/or bacterial degradation of the EPS might have initiated the carbonate precipitation. The results of this study demonstrated that sulphate reducers might have dominated the deglacial microbial community and probably activated the major processes which induced the precipitation of the outstanding volume of microbialites in the post-LGM coral reefs off Tahiti.
ZUSAMMENFASSUNG


Die Inkrustierung der Korallen erfolgte im photischen Bereich. Das beweist die Spurendominanz lichtabhängiger Bioerodierer in Korallen und Mikrobialithen (hauptsächlich Schwachlicht-Spezialisten). Folglich muss sich der Inkrustierungs-Horizont

Die Mikrobioerosionsergebnisse implizieren meist tiefere euphotische bis dysphotische Bedingungen, was zu tief für zooxanthellate Korallen und dadurch rätselhaft erscheint. Die Elementzusammensetzung der Mikrobialithe (relativ hohe Gehalte an Al, Si, Fe und Ba), enthaltene Tone und basaltische Minerale (hauptsächlich Schichtsilikate, Pyroxene, Plagioklase und Magnetit) weisen auf einen erhöhten Sedimenteintrag vom vulkanischen Hinterland hin. Dadurch könnte der Nährstoffgehalt in den Riffen angestiegen sein und zu einer Intensivierung der Primärproduktion während der letzten Abschmelzphase geführt haben. Die Trübung der Wassersäule und die dadurch reduzierte Intensität der Sonneneinstrahlung resultierten vermutlich in einer vertikalen Komprimierung der photischen Zonierung (Teleskopeffekt), wodurch der Eindruck tieferer relativer Wassertiefen entstand.

Lipid Biomarker wurden erfolgreich zur Identifikation von Mikroben in den Riff-Mikrobialithen von Tahiti eingesetzt. Endständig verzweigte Fettsäuren (iso-/anteiso C_{15/17}) wurden in ungewöhnlich hohen Konzentrationen für Riff-Mikrobialithe gefunden. Iso- und anteiso-C_{15/17} Fettsäuren sind typische Biomarker für sulfatreduzierende Bakterien. Die geringe Varianz der organischen Kohlenstoffisotopien vom mikrobiellen Karbonat zu den Kohlenstoffisotopien der iso- und anteiso C_{15/17} Fettsäuren zeigt eine sehr geringe enzymatische Fraktionierung. Das bestätigt die Theorie der Sulfatreduzierer als Quelle der spezifischen endständig verzweigten Fettsäuren.

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1 INTRODUCTION

1.1 IODP Expedition 310 “Tahiti Sea-Level” to Tahiti

The tropical Pacific Ocean is known to play an important role in driving and modulating the
global climate variability and change, on a wide range of timescales (Bjerknes, 1969;
Pickard and Emery, 1990). Currently under discussion is the role of the tropical Pacific in
Glacial-interglacial climate changes. Additional information is needed for a better under-
standing of climate changes. The determination of the progression of the last deglaciation
(19,000–6,000 years BP) is essential to unravel the dynamics of large ice sheets (Lindstrom
and MacAyeal, 1993) and their effects on the Earth’s isostasy (Nakada and Lambeck, 1989;
Lambeck, 1993; Peltier, 1994). Moreover, the reconstruction of the last sea-level rise is
important to understand the complex relationships between freshwater fluxes into the
ocean, thermohaline circulation, and finally the global climate during the Late Pleistocene
and the Holocene. Hence, the last deglaciation is exceptionally appropriate for the study of
environmental changes and their global impact, particularly with respect to the future
climatic alterations and melting of the polar and alpine ice sheets, as a result of the
greenhouse effect.

Tahiti is located in the central Pacific Ocean (French Polynesia, Society archipelago) at
17°50’S and 149°20’W in a tectonically stable region and far from the isostatic effects
induced by deglaciation – a so called far-field site (Mix et al., 2001; Clark and Mix, 2002;
Camoin et al., 2007). Tahiti is a volcanic island on top of a hot spot that has been active
during the last million years (e.g., Duncan and McDougall, 1976; Searle et al., 1995). The
subsidence rates are uniform within the range between 0.15 mm/yr (Pirazolli and
Montaggioni, 1988; Le Roy, 1994) and 0.25 mm/yr (Bard et al., 1996). Tahiti is therefore
considered as a ideal location for a reliable reconstruction of the last sea-level rise on coral
reefs (Bard et al., 1996; Camoin et al., 2007).

Coral reefs are highly sensitive for changes in past climates and environments. This is
especially reflected in the skeletal geochemistry of annually-banded massive
zooxanthellate corals, which record sea surface temperatures and sea surface salinities; for
instance, Porites sp. that dominate the deglacial coral association in the reefs off Tahiti. The
investigation of shallow tropical coral reefs helps to identify and understand the glacial-
interglacial cycles and the mechanisms driving those (Camoin et al., 2007). Accordingly,
coral reefs are considered ideal for reconstructing past sea-level changes as they reliably
follow the sea-level (e.g., Chappell, 1974; Bloom et al., 1974; Pomar, 1991; Bard et al.,
1996). However, the exact course of the sea-level rise following the Last Glacial Maximum
(LGM) is still far from understood.

Three of the four published sea-level curves, which were reconstructed with drilled cores
from coral reefs were derived from settings situated near active subduction zones at
Barbados in the Caribbean Sea (19,000 – 8,000 yr BP; Fairbanks, 1989; Bard et al., 1990),
Papua New Guinea in the equatorial West Pacific (13,000 – 6,000 yr BP; Chapell and Polach, 1991; Edwards et al., 1993;), and Vanuatu in the North of New Caledonia, South-West Pacific (23,000 – today yr BP; Cabioch et al., 2003; Cutler et al., 2004). At Barbados and Vanuatu, the coral reefs that comprise the LGM were drilled. The fourth curve was reconstructed on drilled cores of coral reefs from Tahiti, but this record does not extend to the LGM (13,850 – 3,000 yr BP; Bard et al., 1996); (Fig. 1).

![Fig. 1](image1.png)

**Fig. 1** The sea-level history, reconstructed using drill cores from Tahiti (yellow and blue squares), Barbados (yellow and green circles), and New Guinea (black dots and red triangles); (slightly modified after Bard et al. 1996). MWP = meltwater pulse

During the IODP Expedition 310 “Tahiti sea-level” some drowned Pleistocene to Holocene barrier reef terraces (Fig. 2) were drilled seaward from the modern fringing reefs off Tahiti in order to:

A) extend the Tahiti sea-level record down to the LGM,
B) reconstruct the exact pattern of the post-LGM sea-level rise,
C) define variations in sea surface temperatures and sea surface salinities during the last deglaciation, when solar insolation, sea-level, and atmospheric CO₂ levels differed from today,
D) analyse the impact of the sea-level and environmental changes (nutrient concentrations, palaeoproductivity, terrigeneous and freshwater input) on the reef development during the last deglaciation,

E) investigate the geomicrobiology of the microbialites and identify the microbial communities that were involved in the formation of the microbialites in order to understand the environmental significance of these microbialites that are major structural and volumetric framework elements of the last deglacial coral reef sequence of Tahiti (Camoin et al., 2007).

Fig. 2  Development of the coral reef terraces during the last 200 kyr on the slope of Tahiti based on the reef growth model SEALEX (Kölling et al., accept.). Above: Sea-level curve for the last 200 ka of Waelbroeck et al. (2002). Middle: Model of a fossil Tahitian coral reef. Below: Zoomed view of the seaward coral reef part without vertical exaggeration. The white numbers show the minimum age of the internal reef structure in ka. The arrow indicates the modelled position of the post-LGM reef terraces, which were drilled during IODP expedition 310 (modified after Kölling et al., accept.).
1.2 Study area and samples

Three sites were drilled: Tiarei in the North, Faa’a in the West, and Marā’a in the South of Tahiti (Fig. 3). The entire recovery of IODP 310 comprised more than 600 m of core material that represent a major part of the Tahitian post-LGM reef sequence. U-series dating of selected corals demonstrated that the drilled deglacial reef sequence covered the deglacial time interval between 16,000 and 8,000 yr BP (Camoin et al., 2007). This thesis focus on the post-LGM interval of the drilled reef cores. Samples from the core sections of 18 bore holes from the three sites were investigated: samples from 10 bore holes at Tiarei, samples from seven bore holes at Marā’a, and one sample from one bore hole at Faa’a (Fig. 2; for exact positions of the sites and samples studied, see tables 2 (Chapter 4.1), 6 (Chapter 4.2), and 10 (Chapter 4.3). Today, the fluvial supply of eroded basaltic material from the volcanic island is strongest in the discharge area of the Papenoo River, near the site Tiarei in the North of Tahiti (Fig. 3). Probably, the Papenoo River already drained next to the site Tiarei during the late Pleistocene (Hildenbrand et al., 2004; 2006).

![Map of Tahiti](image)

**Fig. 3** Map of Tahiti, which is located in the central Pacific Ocean (French Polynesia), with all studied bore holes indicated. Tiarei in the North (Papenoo River; bore holes: 25A, 25B, 24A, 23A, 23B, 21A, 21B, 9B, 9D, 9E), Faa’a in the West (bore hole: 19A), and Marā’a in the South (bore holes: 18A, 17A, 16A, 16B, 15A, 7B, 5B). Right-hand side: core sections (1.2 m in length and 7 cm in diameter) from Marā’a (left) and Tiarei (right).
1.3 The Tahiti special: dominant post-glacial reef-microbialites

Other than the typical shallow-water barrier reefs of the World’s oceans, the drilled coral reef sites of Tahiti contain large volumes of microbialites. The microbialites encrusted up to 80 vol.% of the primary porosity of the coral framework in the cores (Camoin et al. 2007; Fig. 3). The basis of the typical ‘encrustation succession’ of the Tahitian post-glacial coral reef sequence is formed by zooxanthellate corals (mainly massive Porites sp., Pocillopora sp. and Acropora sp.), which successively are encrusted by coralline algae (Hydrolithon sp., Lithoporella sp., Lithothamnium sp., and occasionally Mesophyllum sp.) and microbialites (Fig. 6, Fig. 7). Storm deposits, which are usually indicated by reworked reef debris were rarely observed in the reef cores. The reef framework is mostly preserved in situ because of the massive microbialite encrustation, which gives the impression of a “reef in aspic” (Westphal et al., in prep.).

Up to date, in the modern Tahitian reefs, an occurrence or development of microbialites with similar characteristics and volumes were not found. The dominance of those thick microbial carbonate crusts in the post-LGM coral reefs off Tahiti might be a result of environmental changes during the last deglaciation and seem to be influenced by the volcanic hinterland (Camoin et al., 1999, 2007; Cabioch et al., 2006).

1.4 What are microbialites? Definition and history

The definition of the term microbialite is still under discussion in the geological and biological literature. Initially, the term stromatolite described laminated organo-sedimentary structures, where each laminae represents the lithified layers of a former microbial mat characterised by different types of microorganisms with distinct metabolic activities (Kalkowsky, 1908; Krumbein, 1983; Van Gemen, 1993). However, the term stromatolite was used to refer to products of microbial sedimentation in general, to describe laminated structures of probable microbial origin, or to describe discrete laminated lithified bodies. Burne and Moore (1987) recommended that the term stromatolite should be restricted for refering to microbialites with an internal structure of fine, more or less planar laminations (sensu Kalkowsky, 1908). Currently, the term stromatolite is mainly used for laminated modern shallow-water carbonates, which are precipitated due to chemical and microbial processes in cyanobacteria-dominated microbial mats (cf., stromatolites from the Bahamas and the Australian Shark Bay; e.g., Golubic et al., 1982; Reid et al., 2000; 2003a; b; Riding et al., 2000; Dupraz and Visscher, 2005). Burne and Moore (1987) defined microbialites “as organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation”. In this presented research, the term microbialite is strictly used to describe the diverse patterns of the Tahitian grey carbonate crusts (laminated and dendritic microbialites).

Microbialites, including stromatolites, are of crucial importance because they are the fossil
evidence of first life on Earth and they flourish for almost 85% of the Earth’s history (Grotzinger and Knoll, 1999). Since the Precambrian, microbialites are known to show a large diversity in morphology, mineralogy, and ecology, while appearing in a wide variety of settings, such as lacustrine, lagoonal, brackish, and marine environments (e.g., Riding, 2000; 2006; Murphy and Sumner, 2008; Gischler et al., 2008a; b; c). During the Precambrian, the reefal structures were built by microbialites themselves (Grotzinger and Knoll, 1999), while during the Phanerozoic, the microbialites were found to be associated with algal-metazoan reef frameworks (Webb, 1996; Kiessling, 2002; Riding, 2005). Since the early Phanerozoic, the fossil record indicated a decline in microbialite occurrences and volumes (Kiessling, 2002; Kiessling and Flügel, 2002).

Microbialites in coral reefs are known through large periods of the Earth’s history (Kiessling, 2002). For instance, microbial carbonate crusts in Mesozoic coral and sponge reefs played an important role by cementing the reefal framework, which increased the stability against storms and the fossilization potential (Dupraz and Strasser, 2002). In many cases the development of reef-microbialites was interpreted as a result of shifts in environmental and ecological conditions, which interrupted coral growth and led to an encrustation (overgrowth) of the dead or dying coral frameworks by microbialites (e.g., Shen and Xu, 2005; Camoin et al., 2006). In Jurassic coral reefs, moderate reef-microbialite development was observed coeval to coral growth (Dupraz and Strasser, 2002; Olivier et al., 2004). While modern stromatolites were studied since the 1980s (e.g., Dravis, 1983; Golubic et al., 1982; Reid et al., 1995), more recently the scientific interest has been directed to Pleistocene and Holocene reef-microbialites, which were found to be volumetrically and structurally important components in coral reef frameworks (Gischler et al., 2008b; c; and references therein). Since then, Pleistocene to modern reefal microbial crusts have been reported from a wide range of settings and with a wide range of characteristics. For instance, microbialites in minor occurrences were observed in cryptic habitats (reef caves) in tropical shallow-water barrier and atoll reefs offshore of Australia (Great barrier reef), Belize, the Bahamas, and the Maldives (Macintyre, 1984; Reitner, 1993; 2000; Zankl, 1993; Reid et al., 1995; Macintyre, 1996; Camoin et al., 1997; Webb et al., 1999; Gischler et al., 2008b; c). Microbialites were also observed in the coral framework of deeper fore-reef slopes in the Red Sea region, (James and Ginsburg, 1979; Land and Moore, 1980; Brachert and Dullo, 1991; Dullo et al., 1998), and in lagoonal to intertidal settings (Jones and Hunter, 1991). Quaternary microbialites, which encrust the coralgal associations in large volumes were described first from coral reefs off Tahiti (Montaggioni and Camoin, 1993) and Vanuatu (Cabajo et al., 1999).

The coral reefs off Vanuatu (North of New Caledonia, South-West Pacific) show post-glacial reef-microbialites with volume, microstructure, and geochemistry similar to the reef-microbialites of Tahiti (Cabajo et al., 1999; 2006). The microbialites from Vanuatu encrusted the primary porosity of the coral framework similarly to that of Tahiti. At the Rasdhoo Atoll (Maldives, Indian Ocean), non-laminated cryptic reef-microbialites were
found, which developed also during the last deglaciation, but in less volumes compared to Tahiti and Vanuatu (Gischler et al., 2008b). The Vanuatu site is influenced by a volcanic hinterland, similar to Tahiti, whereas the Rasdhoo Atoll is far from any volcanic basement. However, the geo- and organic-chemistry of the microbialites from the Rasdhoo Atoll is still less investigated and therefore it is hardly possible to compare it with the microbialites from Tahiti and Vanuatu at this stage of knowledge. However, the research of the last decades indicated that the development of large volumes of microbialites encrusting coral reefs seem to be linked to the environmental conditions of the last deglaciation and to locations with a volcanic hinterland (Camoin et al., 1999, 2007; Cabioch et al., 2006).

1.5 Formation of microbialites

In general, carbonate accumulation in microbial mats requires that the precipitation of minerals outweighs the dissolution (Dupraz and Visscher, 2005). Cyanobacterial photosynthesis, anoxic bacterial photosynthesis, and sulphate reduction account for carbonate formation by inducing precipitation, while aerobic respiration and aerobic sulphide oxidation dissolve carbonate (e.g. Visscher et al., 1998) (Fig. 4). Cyanobacteria were mainly thought to be responsible for carbonate precipitation and therefore for the formation of ancient and modern stromatolites or microbialites, respectively (e.g., Golubic et al., 1983; Awramik, 1992). Contrary, more recent studies demonstrated that cyanobacterial carbonate precipitation does not dominate the lithification process in marine microbial mats because of the nearly entire dissolution of the carbonate by aerobic respiration/oxidation; a balance of these processes results in less or no lithification at the surface of the mat (e.g., Visscher et al., 1998; Visscher and Stolz, 2005). Carbonate precipitation within the aphytic zone mediated by anaerobic heterotrophy is assumed to be considerably higher than the carbonate precipitation by living cyanobacteria (oxygenic photosynthesis) and exceeds the amount that can be dissolved by respiration and sulphide oxidation (Paerl et al., 2001). Moreover, laboratory experiments with heterotrophic bacterial cultures showed that the precipitated carbonate has nearly an identical morphology than that precipitated in nature in microbial mats containing cyanobacteria in the surface layer (Chafetz and Buczynski, 1992). Other experiments have shown that bacterial sulphate reduction can be responsible for the formation of carbonates enriched with Mg, such as dolomite or high-Mg-calcite (Vasconcelos et al., 1995; Castanier et al., 1999; Sagemann et al., 1999, van Lith et al., 2003a).

The relevant pathways for microbial and/or chemical carbonate precipitation in the Tahitian post-LGM coral reefs will shortly be introduced in the following. Cyanobacteria and anoxygenic phototrophic bacteria, for example, increase the alkalinity due to photosynthetic processes, which induce carbonate precipitation (Konhauser, 2000; Visscher and Stolz, 2005). The study of Lower Cretaceous carbonate mud mounds (Albian, North Spain) revealed that carbonate was formed on non-living organic substrates (Neuweiler et al., 1999). In modern microbialites from the lagoon of the Tikehau atoll
(French Polynesia), carbonate precipitation was observed on living cyanobacterial filaments and on dead organic substrate. In the latter case, authigenic carbonate formation was initiated by heterotrophic degradation processes of organic matter (Sprachta and Camoin, 2001). Carbonate precipitation is induced by sulphate reduction, increasing the alkalinity, or by microbial and/or chemical alteration of extracellular polymeric substances (EPS; e.g., Trichet and Défarge 1995; Défarge et al. 1996; Reid et al. 2000, 2003b; Dupraz et al. 2004; Hendry et al. 2006). EPS represents an extension of the microbial cells and is highly hydrated mucilage composed of a wide variety of molecules, such as polysaccharides and amino acids (Costerton et al., 1995; Decho, 2000), in which the microbial cells are embedded (Decho, 1990). The progressive replacement of EPS with calcite generates micropeloidal structures, the so called clotted microfabrics (Dupraz et al., 2004).

**Fig. 4** Metabolic pathways and geochemical gradients in a lithifying microbial mat. Five major groups of microbes composing a microbial mat community, which induce calcium carbonate precipitation and dissolution. Combined metabolic activities determine the net precipitation potential and also the vertical geochemical gradients (left and right panels). Note the dissolution of the carbonate (Ca²⁺) by aerobic respiration; a balance of these processes results in less lithification at the surface of the mat (e.g., Visscher et al., 1998; Visscher and Stolz, 2005) and the extreme fluctuations during day and night of oxygen, sulphide and pH depending on photosynthesis. Carbon cycling (bottom part of figure) is coupled to element cycles of O, S and N. Similarly, excess carbon fixation enables, for example, EPS build-up, whereas excess anaerobic respiration favours precipitation through an increased saturation index (modified after Dupraz and Visscher, 2005).
EPS has a high binding/adsorption capability for cations (Ca^{2+}, Mg^{2+}) due to negatively charged carboxyl-groups, which initially inhibit the precipitation process of the carbonate (Hartley et al., 1996; Dupraz and Visscher 2005). In this introduction, three of various pathways are proposed, which enable the carbonate to be precipitated via microbial and/or chemical alteration of EPS (Fig. 5):

1. The heterotrophic bacterial degradation of EPS leads to the release of cations, which increase the saturation index and therefore the calcium carbonate is precipitated by replacing the decaying EPS polymers (Dupraz et al., 2004, Decho et al., 2005; Visscher and Stolz, 2005).

2. Alteration of EPS causes the reorganization of the carboxyl groups and creates a molecular template at the mucus surface initiating carbonate precipitation (Trichet and Défarge, 1995). This process is known as organomineralization.

3. The saturation of the binding capacity of the EPS mucus terminates the inhibition of precipitation, thereby causing a local super saturation, which allows for carbonate precipitation on the EPS matrix (Arp et al., 2003).

![Model for carbonate precipitation through production and consumption of exopolymeric substances (EPS). EPS is produced by various microbes (e.g., sulphate-reducing bacteria), binds cations, including Ca^{2+} and Mg^{2+}, which inhibits initially the carbonate precipitation. The carbonate precipitation is activated by microbial and/or chemical alteration of EPS via the three different pathways (modified after Dupraz and Visscher 2005). SI – saturation index.](image)
1.6 Major groups of microbes associated in mats

Microbial mats are planar structures, which can consist of very diverse microbial populations (Ley et al., 2006) organized in up to five layers that extend between micrometers and centimetres, depending on light penetration depth (e.g., Garcia-Pichel et al., 1994). Hence, the microbial processes hosted in mats can enclose many different types of microbial metabolisms. This introduction will cover selected groups of bacteria, which can populate different types of microbial mats (e.g., cyanobacterial mats). The top layer of the modelled microbial mat is the oxic zone, commonly colonised by filamentous photosynthetic cyanobacteria. The deeper layers consist of the aerobic respirers, anoxygenic phototrophic bacteria, and sulphide oxidizers. Sulphate-reducing bacteria commonly colonise the deepest layer (Fig. 4). Out of these groups of bacteria, the cyanobacteria, the anoxic phototrophic bacteria, and the sulphate-reducing bacteria are pertinent to the topic of this thesis, because they are capable to induce the processes leading to carbonate precipitation.

1.6.1 Cyanobacteria

Well-known cyanobacteria belong to the genera *Schizothrix*, *Spirulina*, and *Oscillatoria*. In general, the photoautotrophically growth of cyanobacteria is limited to 1% of the surface irradiance. Some species of the genera *Fischerella* and *Calothrix* are able to grow photoheterotrophically at low light levels (< 1% surface irradiance) or even chemoheterotrophic in the dark (Rippka et al., 1979). The photosynthetic activity of cyanobacteria generates $O_2$, along with an alkalinity increase, which induces carbonate precipitation (Equation 1a; Fig. 4).

$$2HCO_3^- + Ca^{2+} \rightarrow CH_2O + CaCO_3 + O_2$$

(1a)

However, aerobic respiration processes (Equation 1b; Fig. 4), which are active in the layers below the cyanobacteria dissolve the carbonate.

$$CH_2O + CaCO_3 + O_2 \rightarrow 2HCO_3^- + Ca^{2+}$$

(1b)

1.6.2 Anoxygenic phototrophic bacteria

All other known photosynthesizing bacteria are anoxygenic phototrophic bacteria. These bacteria depend on reduced chemical environments and therefore are restricted to deeper layers within a microbial mat. These group of bacteria are highly metabolic flexible and can grow photoautotrophically, photoheterotrophically, and heterotrophically. Anoxygenic phototrophs include the green sulphur bacteria (e.g., *Chlorobium* sp.), the green non-sulphur bacteria (e.g., *Chloroflexus* sp. and *Heliothrix* sp.), the purple sulphur bacteria (e.g., *Chromatium* sp. and *Thiocapsa* sp.), and the purple non-sulphur bacteria (e.g., *Rhodopseudomonas* sp. and *Rhodobacter* sp.). Anoxygenic phototrophs can survive with low light conditions. Mostly, they utilize inorganic compounds, $H_2$, and sulphide ($H_2S$, HS$^\cdot$). Anoxygenic phototrophs oxidize sulphide to sulphur ($S^0$) or sulphate ($SO_4^{2-}$) and thereby
activate carbonate precipitation (van Gemen, 1986); (Equation 2; Fig. 4). Anaerobic phototrophic bacteria can not utilize organic macromolecules (such as cellulose, lipids, or proteins). Consequently, these bacteria act together with fermentative/chemoheterotrophic bacteria, for example sulphate-reducing bacteria.

\[
3\text{HCO}_3^- + \text{Ca}^{2+} + \text{HS}^- \rightarrow \text{CH}_2\text{O} + \text{CaCO}_3 + \text{SO}_4^{2-}
\]  

(2)

### 1.6.3 Sulphate-reducing bacteria

The deepest layer mostly contains anaerobic (chemo-) heterotrophs; these are usually the sulphate reducers. Sulphate-reducing bacteria require the complete absence of O₂, but are able to survive short exposures to oxygen and recover when anoxic conditions return. The most common and well investigated sulphate-reducing bacteria belong to the genera *Desulfovibrio, Desulfotomaculum, Desulfobacter, and Desulfobacterium*. Sulphate reducers can use a wide variety of organic molecular substrates, e.g., acetate, fumarate, pyruvate, and glycolate, which is produced by cyanobacteria (e.g., Teske et al., 1998); as well as inorganic compounds. They typically oxidize organic matter through sulphate reduction to sulphide, which increases the alkalinity inducing carbonate precipitation (Equation 3; Fig. 4).

\[
2\text{CH}_2\text{O} + \text{SO}_4^{2-} + \text{OH}^- + \text{Ca}^{2+} \rightarrow \text{CaCO}_3 + \text{CO}_2 + 2\text{H}_2\text{O} + \text{HS}^-
\]  

(3)

Alternatively, carbonate precipitation can be initiated by chemical alterations and/or microbial degradation (e.g., via sulphate reduction) of EPS, which is produced by various bacteria (see above; Fig. 5).
2 DESCRIPTION OF THE TAHITIAN REEF-MICROBIALITES

2.1 Macroscopic and microscopic descriptions

The Tahitian microbialites are described in detail by Westphal et al. (in prep), which is outlined as abstract in Chapter 4.4. Herein, the characteristics of the Tahitian microbialites are shortly introduced. The microbialites occur in two growth patterns: An initial laminated microbialite, which encrusts the zooxanthellate corals and/or coralline algae, that is succeeded by a dendritic microbialite (Fig. 7; cf., Camoin et al., 1999, 2006). The main growth direction of the microbialites is upwards, whereas encrustations on the bottom and the sides of the coral is also present, but less pronounced. The contact zone, where upward and downward growing microbialites join is usually dendritic (Fig. 6B, F). The mean thickness of the Tahitian microbialite crusts is between 2 and 8 cm; but thicknesses of up to 15 cm also occur. At the Mara’a sites, the typical microbial carbonate is laminated and consists of relatively light-coloured carbonate, which is denser (less porous) and more homogeneous than that of the dendritic microbialites. The microbialites of the sites from Tiarei consists mainly of dark coloured dendritic to laminated carbonates (Fig. 6), which show strongly variable porosity. The microbialites of the site Faa’a are macroscopically similar to the samples from the site Tiarei. At all sites, the coralline algal crusts are up to 5 mm thick and usually encrust the corals. Light microscopy studies revealed that coralline algal crusts are intercalated in microbialites in some samples (Westphal et al., in prep.; Fig. 7A, B, C). The typical coralline algae, which were found, belong to the genera Hydrolithon, Lithoporella, Lithothamnium, and less abundant Mesophyllum. Mainly at Mara’a, Halimeda (green algae) plates were trapped in lows of upward-growing microbialites, and it seems that the sedimentation of those Halimeda fragments took place coeval with the carbonate precipitation, while the microbialite surrounded the Halimeda plates during upward growth (Westphal et al., in prep.; Fig. 6E). At the contact zone of the coral to the microbialite, the microporosity of the coral is usually encrusted by microbialites (Fig. 7C, D; Fig. 8A). The microbialite crusts are clearly more fluorescent than the coral skeleton (Fig. 8A, B). The microfabric of the micritic carbonate is composed of clotted to cloudy peloidal textures (Fig. 7E, F; Fig. 8C), which imply a microbial origin (Gerdes et al. 1994; Reitner et al., 1995; Kazmierczak et al., 1996; Dupraz et al., 2004) and is described in detail in Westphal et al. (in prep.). At all sites, the lamination occurs in variable intervals and always parallel to the encrusted surface. With plane-polarized light it reveals that the dark laminae seem to be developed because of horizontal enrichments of mostly dark clasts and/or basalt-derived minerals proportional to carbonate precipitation (Fig. 8E). With UV-light, the dark laminae are less fluorescent than the light carbonate intervals (Fig. 8F). Single laminae are up to 2 mm in thickness, but usually reach less than 1 mm in cross sectional dimension.
Fig. 6  The different types of microbialites, which occur at the sites Tiarei (A, B, D) and Mara’a (C, E, F). The microbialites from the site Fa’a are similar to those of Tiarei. Generally, the microbialites from Tiarei are darker coloured A. Branching corals encrusted partly by coralline algae (whitish layers) and by laminated microbialites, which change to the dendritic pattern with progressive encrustation process of the primary coral framework porosity. B. Upwards and downwards growth of a laminated microbialite (arrows) with a dendritic contact zone. C. Coral, coralline algae and a faintly laminated microbialite. D. Coral encrusted initially by a laminated microbialite, which change on top to the dendritic pattern. E. The laminated microbialite shows a "pocket" or low, which is filled with Halimeda plates (arrow). F. This sample from Mara’a shows similarly to A the encrustation process of the coral framework. The microbial carbonate crusts occlude almost the entire pore space. The change from the laminated to the dendritic pattern of the upward grown microbialite before reaching the downward grown microbialite is clearly visible (arrows).
Fig. 7  Photomicrographs (plane polarized light) of cross-sections through the typical deglacial reef succession of Tahiti. A. and B. Coral (C) encrusted by coralline algae (CA) and microbialite (M). The coralline algal crusts alternate with the microbialite crusts, P - pore. C. Coral (white) and coralline algae (brown) providing the substrate for the microbial crust on top. D. The microporosity of the coral skeleton is partly encrusted by microbialite. E. and F. Clotted to cloudy peloidal microfabric.
Fig. 8  Photomicrographs of microbialites. A. Microbialite encrusting the microporosity (dark areas) of the coral (light areas); (plane-polarized light). B. The coral skeleton is less fluorescent than the microbial crust (fluorescent micrograph). C. The microfabric of the microbial carbonate (high-magnesium-calcite) is composed of clotted to cloudy peloidal textures (plane-polarized light). D. The clotted peloidal microfabric is highly fluorescent (fluorescent micrograph). E. Horizontal enrichments of dark basaltic minerals creating the lamination (plane-polarized light). F. The lighter carbonate is more fluorescent and contains less abundant dark minerals (fluorescent micrograph).
2.2 Scanning Electron Microscopy observations

Scanning Electron Microscopy (SEM) showed that abundant *Cliona* chips of coral skeletons (produced by clionaid boring sponges) are incorporated in the microbialites (Fig. 9A; Fig. 10D). At the sites of Mara’a and Tiarei, observed peloidal aggregates comprise irregular dog-tooth-calcites (Fig. 9E, F; Fig. 10A, B). Calcitic spherical shapes with ~20 μm in diameter (Fig. 10E, F) and can be surrounded by syntaxial cement (Fig. 9D); (Westphal et al., in prep.). These spheres and hollows appear to be products of microbial metabolism (cf., Chafetz, 1986; Kazmierczak et al., 1996; Dupraz et al., 2004). Other “corn flake-shaped” carbonate aggregates on the surface of the spherical hollows and in micropors are composed of clay minerals (Fig. 9G, H; Fig. 10G). Energy dispersive X-ray analysis of these “corn flake-shaped” aggregates confirmed by Al detection clay minerals as source (Westphal et al., in prep.). The macroscopical observation that coralline algae partly grew intercalated in the microbialites was confirmed (Fig. 10C). It is a common feature in all samples from both sites, that the microbialites encrusted the primary porosity of the corals (Fig. 9C) and also the borings inside the coral skeletons at the contact zone of microbialites and corals. In all samples, the internal texture is heterogeneous and the porosity of the carbonate is infilled with micritic cements. The microfabric of the Tiarei microbialites is more heterogeneous and the content of basalt-derived clasts from Tahiti is more abundant than in those from the site Mara’a (cf., Fig. 9B and Fig. 10B). This is consistent with the darker colour of the microbialites at the Tiarei site (Fig. 6). The microbial carbonates from the site Mara’a contain more abundant aragonitic *Cliona* chips and more abundant frambooidal pyrite (Fig. 10H), which is rare in the samples from Tiarei. Conversely, the “corn flake-shaped” aggregates of authigenic clay minerals were detected more abundant in the Tiarei microbialites (Westphal et al., in prep.). These findings were confirmed by powder X-ray diffraction analysis (Table 11).
Fig. 9  SEM images of laminated microbialites from Tiarei. The cutted surfaces were polished (A-D) and etched with 0.5% HCl for 20 sec; the grown surfaces (E-H) were etched without polishing. A. Contact zone of coral and microbialite (micritic cement) with an incorporated *Cliona* chip (arrow). B. Microbialite with incorporated basalt-derived clasts (arrows) and *Cliona* chips (triangles). C. Coral microporosity infilled by microbialite and unknown round aggregates (arrow). D. Cemented calcitic spherical shapes with syntaxial cements (arrow) surrounded by micritic cements. E. The grown surfaces are composed of peloidal aggregates. F. Irregular dog-tooth calcite. G. Flake-shaped aggregates. H. Spherical hollow with flake-shaped aggregates on the surface.
Fig. 10 SEM images of laminated microbialites from Mara’a. The cutted surfaces were polished and etched with 0.5% HCl for 20 sec. A. Peloidal and micritic microtexture, micropors show dog-tooth shaped calcite. B. Peloids with dog-tooth shaped calcites and basalt-derived clasts (arrow). C. Coralline algal thalli (arrow) interlayered in the microbialite. D. Abundant Cliona chips (arrows) incorporated in micritic cements. E. and F. Cemented calcitic spherical shapes (in E middle; in F arrows). G. Corn-flake shaped clay minerals in a micropor. H. Framboidal pyrite surrounded by irregular dog-tooth calcite.
3  THESIS OUTLINE

A better understanding of the last deglacial environmental changes are required to allow a more precise reconstruction of the last sea-level rise on coral reefs off Tahiti. Currently, the coralgal assemblages, the taxonomy of corals, and the geochemical tracers in their skeletons are used to reconstruct the exact deglacial sea-level curve and to evaluate the development of sea surface temperatures and sea surface salinities. However, the environmental changes that accompanied the last sea-level rise might have influenced the zooxanthellate corals. Accordingly, the deglacial fluctuations in water energy, light intensities, erosion of the volcanic hinterland, and nutrient levels might have strongly impacted the evolution of the reef biology, geometry and accretion. For a tropical shallow-water reef, an unusual voluminous part of the post-glacial coral reef framework off Tahiti is encrusted by microbialites. They seem to have played an important role in the coral reef environment during the last deglaciation; in the modern reefs, the formation of this thick and voluminous type of microbialite is not observed. Therefore, the aim of this study was to unravel the scarcely understood environmental significance of the microbialites and the processes that led to their formation in the post-LGM coral reefs of Tahiti.

A multi-proxy approach is applied to answer these objectives. The approach includes the investigation of microbioerosion patterns in corals, coralline algae, and microbialites as a mean for studying the light availability during coral growth and subsequent microbial encrustation. That is in order to constrain palaeobathymetries and the timing of encrustation along with radiocarbon dating. Additionally, microbioerosion patterns allow for evaluating changes in trophic conditions during the deglacial sea-level rise (Chapter 4.1 and 4.2).

Lipid biomarker analysis and lipid-specific isotopic measurements are applied as main tools for the identification of the microbial communities and the processes, which were involved in the microbialite formation. The investigation of the elemental composition of the microbialites (X-ray diffractometry and Laser-ablation ICP-MS) and the measurements of total organic carbon contents, carbonate contents, carbon and oxygen stable isotopes are used for unravelling the last deglacial environmental conditions (Chapter 4.3).

The results of these studies are presented in three manuscripts (Chapters 4.1, 4.2, and 4.3.). Additionally, I will contribute to a future publication, which focuses on petrographic analyses of the three principal Tahitian framework components in order to strengthen the understanding of the environmental significance of microbialites and the chronology of encrustation. The abstract which is presented in Chapter 4.4 outlines the preliminary results.

Following sections introduce each manuscript, the aims, methods, major conclusions, and importance for the entire study.
Chapter 4.1: Microbioerosion in Tahitian reefs: A record of environmental change during the last deglacial sea-level rise (IODP 310)

Katrin Heindel, Max Wisshak, Hildegard Westphal


The microbioerosion patterns, which were found in three principal post-glacial framework components (corals, coralline algae, and microbialites) of Tahiti are presented in this manuscript. Generally, a dominance of low-light (dysphotic) indicators among the traces of bioeroders (ichnotaxa) was observed. The radiocarbon data and the microbioerosion patterns in the corals and encrusting microbialites reveal almost similar ages, which indicates an encrustation coeval or shortly after coral growth. Surprisingly, the traces of the endolithic cyanobacteria communities typical for the shallow euphotic zones I and II were rarely detected. In this light-flooded tropical setting, the dominance of the ichnotaxa indicating dysphotic conditions was interpreted as a reflection of an increased primary productivity caused by higher nutrient-levels. This reduced the illumination and consequently condensed the photic zonation (telescoping-effect). Intensified primary productivity would have enhanced the growth of heterotrophic bacteria, which could have mediated the carbonate precipitation.

This hypothesis gained in importance during this thesis. The microbialite formation “model” is introduced and discussed in the third manuscript (Chapter 4.3). The successful application of microbioerosion analysis on reef-microbialites in relation to changing trophic conditions is unique, to our knowledge, and might be considered as pilot study.

Chapter 4.2: Data report: Bioerosion in the reef framework, IODP Expedition 310 off Tahiti (Tiarei, Mara’a, and Faa’a sites)

Katrin Heindel, Hildegard Westphal, Max Wisshak


The taxonomic descriptions of the ichnotaxa, which were presented in the previous manuscript (Chapter 4.1), and the descriptions of other yet unknown boring traces in open nomenclature are in the focus of the second manuscript. Additionally, the sample- and data-set was extended in order to confirm previous results. The interpretation of the largely absence of the endolithic boring cyanobacteria which usually dominate the shallowest euphotic zones in tropical coral reefs is herein directed to three different possibilities or their combination. First, the rapid sea-level rise reduced the illumination and therefore suppressed the development of the shallowest microborer community. Second, the microbialites developed mostly in cryptic habitats, but within the photic zone of the coral reef, which explains the dominance of the low-light (dysphotic) indicators
among the microborers. Third, the reduced light availability is interpreted as a result of enhanced nutrient-rich terrigeneous input, which pushed the primary productivity and thereby condensed the photic zonation.

**Chapter 4.3: Formation of deglacial Tahitian coral reef-microbialites (IODP 310) involving sulphate-reducing bacteria**

Katrin Heindel, Daniel Birgel, Henning Kuhnert, Jörn Peckmann, Hildegard Westphal

In preparation for *Palaios*

This manuscript focuses on lipid biomarker analysis, which was successfully performed for the first time on the deglacial reef-microbialites from Tahiti. In addition, the analysed elemental composition of the microbialites (LA-ICP-MS and X-ray diffraction) implies a strong terrigeneous influx of basalt-derived minerals, which would have intensified the nutrient levels and consequently the primary productivity during the last sea-level rise. These findings corroborate the results of the study of the microbiocerosion patterns which were highlighted in the first and second manuscripts (Chapter 4.1 and 4.2). In the microbialites, specific lipid biomarkers were identified that can be assigned to sulphate-reducing bacteria. The proposed habitat for microbialite formation is the cryptic reef-environment within the photic zone (indicated by photic microbiocerosers, Chapters 4.1 and 4.2). Intensified primary productivity might have increased coral mucus excretion and bacterial EPS production, inducing the development of anoxic microenvironments.

**Chapter 4.4: Microbialites as contemporaneous framework components of coral reefs – the trophic paradox (deglacial of Tahiti, IODP 310) (abstract)**

Hildegard Westphal, Katrin Heindel, Marco Brandano, Jörn Peckmann, Guy Cabioch

In preparation for *Journal of Sedimentary Research*

This study clearly demonstrates that microbialite encrustation has taken place within the photic zone and almost at the same time as coral growth. The photic conditions are indicated by microbiocerosion (Chapter 4.1, 4.2) and coralline algal crusts, which are intercalated in microbialites, even though cyanobacteria appear not to play a role in the microbialite precipitation, which was indicated by lipid biomarker analysis (Chapter 4.3). That implies an encrustation horizon (microbialite growth layer) shortly below the reef-top, which also confirms the findings of the previous manuscripts. This coeval encrustation to coral growth has stabilized the post-glacial coral reefs against destructions by storms, which explains the rarely observed reef debris in the drilled reef cores. The development of the reef-microbialites from Tahiti represents a continuous process that appears to have been normal for the ecosystem during the last deglaciation at Tahiti.
4 MANUSCRIPTS

4.1 Microbioerosion in Tahitian reefs: A record of environmental change during the last deglacial sea-level rise (IODP 310)

Katrin Heindel¹, Max Wisshak², Hildegard Westphal¹

1) Geosciences Department, MARUM Building, University of Bremen, Leobener Straße, 28359 Bremen, Germany, kheindel@uni-bremen.de
2) GeoZentrum Nordbayern, Erlangen University, Loewenichstr. 28, 91054 Erlangen, Germany

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Abstract. – The main motivation for IODP Expedition 310 to the Tahitian Archipelago was the assumption that the last deglacial sea-level rise is precisely recorded in the coral reefs of this far-field site. The Tahitian deglacial succession typically consists of coral framework subsequently encrusted by coralline algae and microbialites. The high abundance of microbialites is uncommon for shallow-water coral reefs, and the environmental conditions favoring their development are still poorly understood. Microbioerosion patterns in the three principal framework components (corals, coralline algae, microbialites) are studied with respect to relative light availability during coral growth and subsequent encrustation, in order to constrain the palaeobathymetry and the relative timing of the encrustation. Unexpectedly for a tropical, light-flooded setting, ichnotaxa typical for the deep-euphotic to dysphotic zone dominate. The key ichnotaxa for the shallow euphotic zone are scarce in the analysed sample-set, and are restricted to the base of the deglacial succession, thus reflecting the deglacial sea-level rise. At the base of the deglacial reef-succession, the ichnocoenoses present in the corals indicate shallower bathymetries than those in the encrusting microbialites. This is in agreement with radiocarbon data that indicate a time gap of more than 600 years between coral death and microbialite formation. At the top of the deglacial reef-succession, in contrast, the microbioerosion patterns in the three framework components indicate a uniform palaeobathymetry, and radiocarbon ages imply that encrustation took place shortly after coral demise. An enigma arises from the fact that the ichnocoenoses imply photic conditions that appear very deep for zooxanthellate coral-growth. During the deglacial sea-level rise increased nutrients and fluvial influx may have led to (seasonal?) eutrophication, condensing the photic zonation. This would have exerted stress on the coral ecosystem and played a significant role in initiating microbialite development.

Keywords: Microbioerosion, microendoliths, microbialites, coral reefs, last deglacial sea-level rise, palaeobathymetry, DP Hunter, Expedition 310, Tahiti Sea-Level
4.1.1 Introduction

Zooxanthellate coral reefs are considered ideal for reconstructing past sea-level change because they faithfully follow the sea-level (e.g., Chappell, 1974; Bloom et al., 1974; Pomar, 1991; Bard et al., 1996). However, reconstructions of the sea-level rise following the Last Glacial Maximum (LGM) are still far from being beyond doubt. Three of the four published sea-level curves based on coral reefs are derived from settings situated near the active subduction zones at Barbados (19,000-8,000 yr BP; Fairbanks, 1989; Bard et al., 1990), Papua New Guinea (13,000-6,000 yr BP; Chapell and Polach 1991; Edwards et al., 1993), and Vanuatu (New Caledonia); (23,000-today yr BP; Cabioch et al., 2003; Cutler et al., 2004). At Barbados and at Vanuatu the coral reef cores reach the Last Glacial Maximum (LGM). The fourth curve is reconstructed for the volcanic island of Tahiti that is situated far from active plate boundaries and isostatic effects induced by deglaciation (Mix et al., 2001; Clark and Mix, 2002; Camoin et al., 2007), but this record does not extend back to the LGM (13,850-3,000 yr BP; Bard et al., 1996). Tahiti is located at 17°50'S and 149°20'W in the central Pacific Ocean (French Polynesia, Society Archipelago) on top of a mantle plume (Searle et al., 1995) with uniform subsidence rates in the range of 0.15 mm / yr (Pirazzoli and Montaggioni 1988; Le Roy 1994) to 0.25 mm/yr (Bard et al., 1996). It is therefore considered as a prime location for reliable sea-level reconstructions of the last deglaciation (Bard et al., 1996; Camoin et al., 2007). Thus, Tahiti was targeted by IODP-Expedition 310 in order to extend the sea-level record back to the LGM (Camoin et al., 2007). Further, it aimed at identification of short-term palaeoclimatic and palaeoceanographic changes associated with the last deglacial sea-level rise and corresponding changes in reef growth and geometry. The expedition took place in October/November 2005, and more than 600 m of core material were recovered comprising the major part of the Tahitian post-LGM reef sequence. U-series dating of selected corals demonstrate that the drilled deglacial reef succession covers the time interval between 16,000 and 8,000 yr BP (Camoin et al., 2007).

Zooxanthellate corals (dominated by the genera Porites, Pocillopora, Acropora, and Montipora) encrusted by coralline algae and subsequently by microbial crusts represent the typical growth succession of the Tahitian deglacial reefs (Camoin et al., 2007; Fig. 11). The Tahitian microbialites show two dominant growth habits: an initial laminated microbialite encrusting zooxanthellate corals and/or coralline algae, and a subsequent dendritic growth pattern (cf., Montaggioni and Camoin, 1993; Camoin et al., 1999, 2006; Fig. 11). While the definition of the term microbialite is still under discussion (e.g., Burne and Moore, 1987; Van Gennep, 1993; Riding, 2000; Dupraz, 2004), we here use the term strictly to describe laminated and dendritic grey calcareous crusts.

The post-LGM reef succession on the slopes of Tahiti differs from its modern counterpart by its unusual and outstanding quantity of microbial crusts (up to 80 vol. %) largely occluding the primary porosity of the coral reef. This abundance of microbialites is thought to be a result of environmental change accompanying the rapid last deglacial sea-level rise
(Camoin et al., 1999, 2006). For reconstructing the exact course of the deglacial sea-level rise and for evaluating the development of sea-surface temperature, the taxonomy of corals, the coralgal assemblages, and geochemical tracers in their skeletons are currently studied by Science Party members of the IODP Expedition 310. These parameters have to be distinguished from those influencing coral growth, including water energy, nutrient levels, light intensity, wave-base levels, and erosion of the hinterland. In this paper, we apply microbioerosion analysis as a mean for characterising the palaeobathymetric development of the Tahitian deglacial reef setting and for evaluating potential changes in trophic conditions during the deglacial sea-level rise.

![Fig. 11 Vertical core sections of the repetitive Tahitian deglacial reef-succession with zooxanthellate corals (1: dominated by the genera *Porites*, *Pocillopora*, *Acropora*, and *Montipora*) partly encrusted by coralline algae (2; whitish layers) followed by encrusting microbialites with laminated (3) or dendritic (4) growth pattern. A. Pockets in the laminated microbialite are filled with pieces of *Halimeda* (calcareous green algae). B. This sample represents two sequences. At the top the laminated microbialite clearly changes in dendrites. C. Heavily sponge-bored coral (*Porites*) barely encrusted by coralline algae. The laminated microbialite changes in a dendritic growth pattern. D. The branching corals (*Acropora*) are entirely encrusted by microbialites whereas coralline algae partly encrust the tops of the coral branches.

Bioerosion is the main process of carbonate degradation in marine environments and in most settings exceeds pure physicochemical dissolution and mechanical destruction (e.g.,
Bioerosive agents are organisms that penetrate or abrade solid substrates in different ways (e.g., mechanical and/or chemical boring, scraping, biting, crushing and gnawing) and for different reasons (e.g., habitat, protection, feeding, grazing, attachment, parasitism and predation; Bromley 1994). They are divided into three major groups: grazers (gastropods, chitons, echinoids, etc.), macroborers (trace diameters >100 μm; sponges, bryozoans, worms, etc.) and microborers (traces diameters <100 μm; mainly bacteria, algae and fungi; e.g., Golubic et al., 1975; Warme, 1975). Their boring traces have a fossilisation potential that is far superior to that of their producers. Trace fossils are highly sensitive palaeoenvironmental indicators that can be traced as far back as the Proterozoic (Bromley, 2004; Glaub and Vogel, 2004). Microbioeroders are evolutionary conservative organisms in terms of morphology and palaeobiology, turning them into particularly reliable palaeoenvironmental proxies (Vogel and Glaub, 2004). They record information on light availability (and hence relative water depths), trophic conditions, and water temperatures in modern and ancient environments.

Typical communities of microbioerosion traces form so-called index ichnocoenoses that indicate specific photic zones: the shallow euphotic zones I, II, and III, the deep euphotic zone, the dysphotic zone, and the aphotic zone (Glaub, 1994, 1999; Vogel et al., 1995, 1999; Glaub et al., 2002; Vogel and Marincovich, 2004; Table 1). Index ichnocoenoses for the shallow euphotic zone I and the dysphotic zone are yet to be defined, but there are several traces of microendoliths that are typical for these zones. Borings of the shallower euphotic zones are typically vertically oriented (e.g., *Fascichnus* isp. produced mainly by the cyanobacteria *Hyella* spp.), whereas the microborers of deeper euphotic and dysphotic zones tend to create horizontal borings (e.g., *Ichnoreticulina elegans* produced by the chlorophyte *Ostreobium quekettii*). The base of the euphotic zone is delineated at a light intensity of 1% of the surface illumination and the base of the dysphotic zone at the limit of photoautotrophic algae (~0.001 to 0.01% of the surface illumination), respectively (Table 1).

| **Table 1**: The photic zonation is reflected by specific index ichnocoenoses and general microborer characteristics (after Wisshak, 2006, modified after Glaub, 1994; 1999 and Vogel and Marincovich, 2004). | **Photic zonation** | **Index ichnocoenoses** | **General characteristics** |
|---|---|---|
| **Euphotic zone (>1% surface illumination)** | Shallow I (supralittoral) | Not yet defined | Dominance of cyanobacteria with sheath pigmentation |
| | Shallow II (eulittoral) | *Fascichnus acinosus* / *Fascichnus dactylus* ichnoconosis | Dominance of cyanobacteria; vertical orientation of borings |
| | Shallow III (sublittoral) | *Fascichnus dactylus* / *Palaeoconchochelis starmachii* ichnoconosis | Cyanobacteria abundant and eukaryotes; change from vertical to horizontal orientation |
| | Deep | *Palaeoconchochelis starmachii* / *Ichnoreticulina elegans* ichnoconosis | Dominance of eukaryotes: mainly rhodophytes and chlorophytes; horizontal orientation; heterotrophs increasing; maximum diversity |
| **Dysphotic zone (0.01-1% surface illumination)** | Not yet defined | Dominance of heterotrophs; additionally *Ichnoreticulina elegans* and/or *Scolecia filosa* |
| **Aphotic zone (<0.01% surface illumination)** | *Saccocoma phyla* / *Orthogonum lineare* ichnoconosis | Only heterotrophs |
Fig. 12 Tahiti with the three study sites Tiarei, Faa’a, and Mara’a and the location of the 13 bore holes: Faa’a - 19A, Mara’a (from W to E) - 7B, 18A, 16A, 15A, 17A, and Tiarei (from W to E) - 25A, 25B, 24A, 9B, 9D, 9E, 23A (slightly modified after Camoin et al. 2003).
4.1.2 Materials and methods

During IODP Expedition 310, the Pleistocene to early Holocene Tahitian reef terraces that are located seaward of the modern fringing reef have been drilled in order to recover the deglacial reef sequence. Based on high-resolution seismic and multibeam bathymetric data acquired during the SISMITA cruise, boreholes along bathymetric transects were drilled in water depth between 41.6 to 117.5 m (Camoin et al., 2003, 2007). Samples of all three sites were examined for the present study (Tiarei in the North, Mara’a in the South, Faa’a in the West of the island of Tahiti; Fig. 12).

Sample selection

For microbioerosion analysis, a total of 18 samples were selected and prepared in two different ways (Table 2):

1. The first set of samples was cut vertically in growth direction, thus covering the entire succession from corals to coralline algal crusts to microbialites. They were analysed with respect to the vertical extension of microborings in the substrate, potential changes in the composition of the microbioeroding communities with progressive penetration depths, and substrate dependence of the microborer communities.

2. The second sample set was taken from the upper surfaces of the various substrates (coral, coralline algae, microbialite) in order to study superficial microbioerosion patterns, and the horizontal extension of microbioerosion patterns.

Seven samples were taken as close as possible to the base of the deglacial (post-LGM) reef-suc-cession from Faa’a, Mara’a and Tiarei, seven samples represent the middle part of the post-LGM reef from Mara’a and Tiarei, and four samples represent the upper deglacial succession (Table 2). This way the samples span the entire deglacial succession covered in the IODP 310 cores (16,000-8,000 yr BP; Camoin et al., 2007).

Sample preparation and analysis

The vacuum cast-embedding technique modified after Golubic et al. (1970, 1983) as described by Beuck and Freiwald (2005) and Wisshak (2006) was applied to produce casts for examination under the scanning electron microscope (SEM). First, samples were treated with hydrogen peroxide to remove organic matter and cleaned in an ultrasonic bath. They were then impregnated with epoxy resin under vacuum conditions. After curing, the samples from the first sample set were etched superficially in hydrochloric acid (∼5%) for 20 seconds, thereby removing only the uppermost ~100 m of the calcium carbonate matrix (coral, coralline algae, microbialite). This partial etching produces casts of traces that can be studied in relationship to the calcium carbonate matrix. The samples of the second set were trimmed to the uppermost few millimetres after impregnation and before etching with hydrochloric acid in order to limit overlap of collapsing traces. The casts were sputter-coated with gold and analysed using scanning electron microscope. The quantities
of the various microendolithic traces in corals, coralline algae, and microbialites were determined semi-quantitatively using three classes of abundance: rare (few specimens), common (few to many specimens), and abundant (very many specimens).

| Hole | Core | Section | Top Depths [cm] | Bottom Depths [cm] | Study sample code | Depth below sea-level [m] | Sample position in deglacial reef-succe$$
| M0023A | 2R | 1W | 40 | 47 | T10t | 71 | top |
| M0023A | 3R | 1W | 10 | 12 | T9t | 72 | top |
| M0023A | 8R | 1W | 5 | 41 | T8m | 79 | middle |
| M0024A | 1R | 1W | 3 | 6 | T7m | 91 | middle |
| M0009E | 3R | 1W | 99 | 110 | T6m | 96 | middle |
| M0009B | 1R | 1W | 33 | 46 | T5m | 100 | middle |
| M0024A | 11R | 2W | 73 | 89 | T4b | 111 | base |
| M0009D | 9R | 1W | 108 | 114 | T3b | 114 | base |
| M0025B | 10R | 1W | 62 | 69 | T2b | 115 | base |
| M0025A | 9R | 1W | 22 | 29 | T1b | 117 | base |
| M0017A | 5R | 1W | 28 | 32 | M7t | 64 | top |
| M0007B | 11R | 1W | 54 | 60 | M6t | 56 | top |
| M0015A | 9R | 1W | 6 | 10 | M5m | 81 | middle |
| M0018A | 1R | 1W | 41 | 47 | M4m | 82 | middle |
| M0018A | 6R | 1W | 6 | 10 | M3m | 89 | middle |
| M0007B | 26R | 1W | 77 | 92 | M2b | 75 | base |
| M0016A | 35R | 1W | 23 | 27 | M1b | 116 | base |
| M0019A | 9R | 1W | 65 | 70 | F1b | 78 | base |

Table 2: This table gives the IODP 310 sample codes (area, site, hole, core, section, top depths and bottom depths in m of the samples) and the study sample codes (T = Tiarei, M = Mara’a, F = Faa’a, b = base of succession, m = middle range of succession, t = top of succession). Additionally, the water depths (mbsl), and the stratigraphical position in the reef-succe$$

Radiocarbon dating

In order to evaluate potential age differences between the coral framework and the microbialite encrustation, four sample pairs of corals (upper surfaces) and encrusting microbialite (lowermost layers) from the Mara’a and Tiarei cores were dated using the AMS $^{14}$C method (Czernik and Goslar, 2001). The analyses were carried out at the Poznań Radiocarbon Laboratory (Poland). The calibration of the AMS $^{14}$C ages to calendar years was done with the software CALIB REV 5.0.1 (Stuiver and Reimer, 1993) using the marine calibration dataset marine04.14c (Hughen et al., 2004) with adjustment to the regional reservoir age $\Delta R = 82 \pm 42$ ($\Delta R = deviation$ from the average global reservoir age of $\approx 400$ years; Stuiver and Braziumas, 1993). The regional reservoir age of Moorea, French Polynesia is 409 years (CHRONO marine reservoir database).
4.1.3 Results

The microbioerosion inventory

In all three framework elements (corals, coralline algae, and microbialites) a wide range of microbioerosion traces have been identified (Fig. 13). Macrobioerosion features are limited to sponge borings (ichnogenus Entobia) and polychaete domiciles (Caulostrepsis and Maeandropolydora) because most macrobioerosion patterns are too large to be studied via SEM and therefore are not further considered here.

Traces produced by phototrophic microborers (Fig. 14, Fig. 15) comprise ichnotaxa produced by cyanobacteria, such as Fascichnus dactylus (biotaxon e.g., Hyella caespitosa), Eurygonum nodosum (biotaxon Mastigocoleus testarum), and Scolecia filosa (biotaxon Plectonema terebrans), and traces of chlorophytes (green algae), as there are Rhopalia catenata (biotaxon Phaeophila sp.) and Ichnoreticulina elegans (biotaxon Ostreobium quekettii). Traces of heterotrophic microborers (Fig. 16) are represented by the fungal traces Saccomorpha clava (biotaxon Dogdella priscus), Orthogonum fusiferum (biotaxon Ostracobable implexa), and traces of unknown organisms such as Scolecia serrata (bacterium?) and Orthogonum lineare (fungus?).

Relative abundances and substrate affinities

Fa’a’a. – The ichnotaxa Fascichnus dactylus, Eurygonum nodosum and Scolecia filosa were common in the basal part (encoded as ‘b’ in the sample code; Table 2) of the deglacial reef-succession in the coral substrates of sample F1b from Fa’a’a while Orthogonum lineare appeared only rarely. The traces found inside the microbial and coralline algae crust of this sample could not be identified with confidence.

Mara’a. – The trace F. dactylus was identified in rare quantities exclusively inside the coral of sample M2b and common in M1b. Both samples are from the base of the deglacial succession. The trace E. nodosum is abundant exclusively in the coral of sample M1b. S. filosa is abundant in the coral of sample M2b and common in the coral of M4m from the middle range (encoded as ‘m’ in the sample code; Table 2) of the deglacial reef complex. Rhopalia catenata is abundant in the coral skeleton of one single sample: M2b. The ichnotaxon Ichnoreticulina elegans was identified abundantly in the coral sections of the samples M1b and M2b, and in sample M7t from the top (encoded as ‘t’ in the sample code; Table 2) of the deglacial reef-succession. The coralline algal crusts of these samples show no borings of this chlorophyte except from rare traces in M2b; the microbialites contain rare I. elegans. In addition, I. elegans was found commonly in corals and microbialites of the samples M3m and M5m but again not in the algal crusts. Rare occurrences of I. elegans were typical for all three framework components of the sample M4m. The ichnotaxon Saccomorpha clava was abundant in all components of sample M3m and rarely observed in corals and microbialites, and absent in coralline algae crusts of the samples M5m, M6t, and M7t. Scolecia serrata is abundant in the sample M7t, common in the samples M2b, M4m,
and M5m, and rare in M3m. There, *S. serrata* was most abundant in the corals and microbialite crusts, and only present in some coralline algae crusts. *O. lineare* was observed commonly in M5m and M7t in coral substrates and rarely in microbialites.

**Tiarei.** - *E. nodosum* occurs exclusively inside the coral skeletons in samples T3b and T4b where it is common. The trace *S. filosa* is abundant in sample T5m and common in samples T3b, T4b, T7m, and T10t, whereas it was observed rarely in T6m and in T8m. *S. filosa* is present in all three substrates but less abundant in algae and microbial crusts compared to coral skeletons. *R. catenata* is restricted to occurrences inside the coral-skeleton in sample T3b. *I. elegans* was found abundantly in the middle (T5m, T7m) and top parts of the succession (T9t, T10t), commonly in sample T3b and T6m, and only rarely in sample T4b and T8m. Generally, *I. elegans* is present in all three substrates with lower abundance in coralline algae and slightly lower abundance in microbial crusts compared to coral skeletons (absent in coralline algae crusts in T2b, T5m, T8m and in microbialite in T5m). The ichnotaxon *S. clava* is abundant in sample T1b and T8m, common in samples T2b, T5m, T6m, and T9t, and rare in T10t. This fungal trace is abundant in corals, entirely absent in coralline algae crusts, and is rare to common in microbialites (absent in T5m). *Orthogonum fusiferum* was observed in only two samples from Tiarei with rare abundances exclusively in corals of sample T5m and T8m. *S. serrata* is common in the sample T7m and rare in T2b, T4b, T6m, T8t, T9t, and T10t in corals, coralline algae and microbialites. The ichnotaxon *O. lineare* was observed commonly in all substrates in the samples T1b, T5m and rarely in T2b, T6m, and T10t. All results are summarised in Figure Fig. 13Fig. 13.

In summary, *Ichnoreticulina elegans* is the most abundant ichnotaxon with a presence in 78% of the samples, followed by *Scolecia serrata* with 67%. *Saccomorpha clava* shows a presence of 61%, *Scolecia filosa* of 56%, *Orthogonum lineare* of 44%, *Eurygonum nodosum* of 22%, and *Fascichnus dactylus* of 17%. *Rhopalia catenata* and *Orthogonum fusiferum* are less abundant with only 11%.

**Affinity to substrates and penetration depths**

*F. dactylus, E. nodosum, R. catenata,* and *O. fusiferum* are absent in microbial crusts while on average *S. filosa, I. elegans, S. clava, S. serrata,* and *O. lineare* are rare, demonstrating that this substrate is rather unattractive for microbioeroders (Fig. 13, Fig. 17). The same applies for coralline algae where *F. dactylus, E. nodosum, R. catenata, S. clava,* and *O. fusiferum* are absent, and *S. filosa, I. elegans, S. serrata* and *O. lineare* are rare (Fig. 13, Fig. 17). All identified microborers have the highest affinity to coral skeletons compared to microbialite and coralline algal crusts (Fig. 13, Fig. 17) with mean rare *F. dactylus, E. nodosum, R. catenata, S. serrata, O. lineare,* and *O. fusiferum,* and common *S. filosa, I. elegans,* and *S. clava.*

Within coral skeletons, the different microborers show a range of penetration depths. In general, the microbioerosion patterns of the light-dependent endolithic species show the highest densities in the upper millimetre of the coral skeletons (chiefly *Porites lobata*). *I.
**elegans** and less commonly *S. filosa* reach penetration depths of 1-4 mm. In samples from the base of the succession *I. elegans* can reach a maximum depth of penetration of 10 mm, while *E. nodosum* and *R. catenata* reach penetration depths of up to 5 mm. The direction of penetration for these microborers is from the surface into the skeleton. Boring directions of *I. elegans* from the inside out – as indication for *syn vivo* infestation – were observed only in sample T9t (Fig. 16C).

### Radiocarbon dates

At the Mar’a and Tiarei sites, the calibrated and corrected $^{14}$C ages show almost identical ages for the pairs of corals and encrusting microbialites from the top of the succession (maximum time lag of ~170 years when considering the maximum 1σ age range). In contrast, the corals from the base of succession are 600 to 700 years older than the encrusting microbialites (maximum time lag of ~1000 years when considering the maximum 1σ age range; Table 3).

<table>
<thead>
<tr>
<th>Site</th>
<th>IODP 310 sample code</th>
<th>$^{14}$C age (yr BP)$^1$</th>
<th>1σ cal. age ranges (cal. BP)$^2$</th>
<th>Calendar years (BP)$^3$</th>
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</thead>
<tbody>
<tr>
<td>Mar’a</td>
<td>M0007B 11R 1W (top of reef-succeision)</td>
<td>microbialite coral 8700 ± 40</td>
<td>9218-9388</td>
<td>9280</td>
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<td></td>
<td>M0007A 32R 1W (base of reef-succeision)</td>
<td>microbialite coral 8690 ± 50</td>
<td>9190-9383</td>
<td>9280</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10500 ± 50</td>
<td>11331-11642</td>
<td>11500</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10870 ± 50</td>
<td>12074-12364</td>
<td>12200</td>
</tr>
<tr>
<td>Tiarei</td>
<td>M0023B 4R 1W (top of reef-succeision)</td>
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<td>11122-11211</td>
<td>11160</td>
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<tr>
<td></td>
<td>M0024A 11R 2W 73-89 (base of reef-succeision)</td>
<td>microbialite coral 10270 ± 50</td>
<td>11139-11226</td>
<td>11180</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12860 ± 70</td>
<td>14150-14580</td>
<td>14200</td>
</tr>
<tr>
<td></td>
<td></td>
<td>13050 ± 70</td>
<td>14500-14980</td>
<td>14800</td>
</tr>
</tbody>
</table>

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1. AMS $^{14}$C ages in radiocarbon years BP.

2. Radiocarbon ages were calibrated using calib rev 5.0.1 (Stuiver and Reimer, 1993) and the marine04.14c dataset (Hughen et al, 2004) with a further adjustment of a regional reservoir age $\Delta R = 82 \pm 42$ ($\Delta R$ = deviation from the average global reservoir age of ~400 years). The extremes of 1σ cal. age ranges are given.

3. Intercept points of the calibrated age ranges (1σ) with the calibration dataset marine04.14c.

**Table 3:** AMS $^{14}$C data of corals and microbialites from the top and the base of the Tahitian deglacial reef-succession at Mar’a and Tiarei. At the top of the succession the ages of corals and microbialites are largely identical whereas at the base the time gap is more significant.
Fig. 13 Semi-quantitative analysis of the microendolithic traces observed by scanning electron microscopy in corals, coralline algal crusts and microbialites from the Tahitian deglacial coral reef-sequence, including the overall presence of each ichnotaxon, its substrate affinities, and the palaeobathymetric interpretation derived from the ichnocoenosis in each sample. (eu II = shallow euphotic zone II, eu III = shallow euphotic zone III, d eu = deep euphotic zone, dys = dysphotic zone, heterotrophs = heterotrophic microborders, mid = middle)
Fig. 14 SEM images of epoxy resin casts of traces produced by boring phototrophs recorded in coral skeletons from Tahiti deglacial coral reefs: **A-B** Fascichnus dactylus colonies produced by the cyanobacterium *Hyella caespitosa* and related species. **C-D** Eurygonum nodosum with characteristic swellings (heterocysts; arrows) produced by the cyanobacterium *Mastigocoleus testarum*. **E-F** Dense meshworks of *Scolecia filosa* produced by the cyanobacterium *Plectonema terebrans*. **G-H** Rhopalia catenata produced by the chlorophyte *Phaeophila dendroides* with typical swellings and appendices (arrows).
4.1.4 Discussion

**Palaeobathymetric implications**

The dominantly vertical oriented cyanobacterial traces of the shallow euphotic zones I and II (e.g., Glaub, 1994; Vogel and Marincovich, 2004; Table 2) are absent in the analysed samples of Tiarei. Solely at Faa’a and in two samples from Mar’a’a, *Fascichnus dactylus*, a key-ichnotaxon of the shallow euphotic zones II and III, was found. The horizontally orientated traces *Eurygonum nodosum* (cyanobacterium trace) and *Rhopalia catenata* (chlorophyte trace) on the other hand were present in several samples and are known to be typical components of ichnocoenoses in the shallow euphotic zone III and in the deeper euphotic zone (Vogel and Marincovich 2004). Hence, *F. dactylus, E. nodosum* and *R. catenata* are the ichnotaxa that give the shallowest photic indication amongst the observed traces and were found exclusively in coral samples from the base of the deglacial reef-succession, suggesting a shallow eulittoral/sublittoral (shallow euphotic zone II/III) to somewhat deeper sublittoral palaeobathymetry (deep euphotic zone) during the time of early post-glacial reef framework development (Table 4).
Fig. 16 Traces produced by boring heterotrophs (SEM of epoxy resin casts) recorded in coral-skeletons and microbial crusts from Tahiti deglacial coral reefs: **A** *Saccomorpha clava* produced by the fungus *Dodgella priscus* inside a coral-skeleton. **B** Sporangial chamber (a) and hyphae (b) of *S. clava* on the sponge boring *Entobia* (c), exhibiting typical boring cells inside a coral-skeleton. **C-D** *Orthogonum fusiferum* produced by the fungus *Ostracoblabe implexa* inside the coral-skeleton with diagnostic swellings (arrows). **E** The small and verrucose *Scolecia serrata* produced by an unknown bacterium together with *Ichnoreticulina elegans* penetrating the coral-skeleton. **F** Dens carpet of *S. serrata* in a coral-skeleton. **G** *Orthogonum lineare* produced by an unknown heterotrophic organism inside a microbial crust and **H** on *Entobia* inside a coral-skeleton.
**Fig. 17** SEM images of the three substrate types coral skeleton, coralline alga, and microbialite, which represent the repetitive Tahitian deglacial succession. The epoxy resin casts display the porosity inside the substrates. **A** Overview of the coral substrate (right), coralline alga (middle), and microbial crust (left). Inside the coral skeleton boring traces are abundant whereas they are rare in the coralline alga and microbialite. The sponge macroboring *Entobia* intersects all substrates. **B** Close up of the middle part of A (square) with the coralline algae crust. **C** Microbial crust with rare boring traces (arrows). **D** Microbialite with common *I. elegans* network. **E** Coralline alga cells with common *I. elegans*. **F** Coralline alga cells with common *S. serrata*. **G-H** Abundant *I. elegans* and *Entobia* isp. inside the coral skeleton.
The cyanobacterial trace *Scolecia filosa* and the chlorophyte trace *Ichnoreticulina elegans* are known from all euphotic zones but it is only in the dysphotic zone that they occur as the sole phototroph traces (Vogel and Marinovich, 2004; Wisshak et al., 2005). Here, both were found throughout the entire deglacial reef-sequence and in all three framework elements, thus indicating that at least dysphotic conditions prevailed during the deposition of the middle and upper part of the deglacial reef-sequence (Table 4). All other recorded ichnotaxa, as there are *Scolecia serrata, Orthogonum lineare, Orthogonum fusiferum* and *Saccomorpha clava* were produced by heterotrophic bioeroders and are of no direct palaeobathymetric significance.

In conclusion, the overall trend of the ichnocoenoses present in the deglacial reef succession suggests deepening-upwards (Fig. 18), thus reflecting the rising sea-level leading to the progressive drowning of the drilled deglacial reefs.

As outlined above, the microboring assemblage and in particular the bathymetrically relevant index ichnocoenoses allow a (palaeo)bathymetrical interpretation with respect to the photic zones. These photic zones are, however, not directly translatable into absolute water depths. The reason is that the extent of the photic zones is governed by a number of factors such as turbidity and wave action, and may thus vary considerable with time as well as along the same geographical latitude (e.g., Glaub et al., 2002; Perry and Macdonald, 2002). Today the Central Pacific waters surrounding Tahiti are classified as optical water type IA after Jerlov (1976: fig. 72), which translates to ~90 m water depth for the euphotic/dysphotic boundary (1% surface illumination at 350-700 nm wavelength; Jerlov 1976: fig. 132) and ~180 m for the dysphotic/aphotic delineation (0.01% surface illumination).

These water depths are maximum estimates for the modern Tahitian case with highly transparent waters and are definitely too large for the deglacial setting. During deglacial times, the photic zones are assumed to have been condensed as a result of a nutrient-driven reduction of sea-water clarity (see below).

**‘Cryptophotic microbialites’**

In the entire deglacial reef-succession, the microbial crusts have developed in a photic environment as indicated by the presence of microbioerosion produced by phototrophic organisms, which are specialised to low-light conditions (*Ostreobium quekettelii*, ichnotaxon *Ichnoreticulina elegans; Plectonema terebrans*, ichnotaxon *Scolecia filosa*). However in some cases, we have to consider the possibility that the strong representation of low-light boring specialists next to heterotrophic microborers in the microbialites could reflect the dysphotic conditions in the inner reef framework rather than as a result of larger water depths. The term ‘cryptophotic habitat’ in the reef framework is thus used here to describe the possibility of shaded but not necessarily entirely aphotic niches in otherwise euphotic environments. Such habitats provide substrate for extremists among photosynthetic microbioeroders, e.g., at the dead underside of corals and other hard substrates, in small
cavities, shaded crevices, etc. (Golubic et al., 1975; Jackson, 1984; Taylor and Wilson, 2003).

The rare samples that exclusively show microborings of heterotrophs in the microbial crusts and/or corals (S. clava, O. fusiferum, O. lineare, and S. serrata; samples M6t, T1b, and T2b; Fig. 13, Fig. 18) represent microavases, e.g., created by boring sponges (Fig. 16), independent from water depths. Therefore they are also interpreted as ‘cryptophotic’ (apparently aphytic) ichnocoenosis.

<table>
<thead>
<tr>
<th></th>
<th>Photic zonation</th>
<th>Index traces / Tahitian deglacial reefs</th>
<th>Substrate</th>
<th>Reef succession</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cryptic and shaded</td>
<td>Shallow I (supralittoral)</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Scolecia filosa, Ichnoreticulina elegans, Saccomorpha clava, Orthogonum fusiferum, Scolecia serrata, Orthogonum lineare</td>
<td>Shallow II (eulittoral)</td>
<td>Fascichnus dactylus</td>
<td>Coral</td>
<td>Base</td>
</tr>
<tr>
<td>Cryptophotic habitat</td>
<td>Shallow III (sublittoral)</td>
<td>Fascichnus dactylus, Eurygonum nodosum, Rhopalia catenata</td>
<td>Coral</td>
<td>Base</td>
</tr>
<tr>
<td>in all substrates</td>
<td>Deep</td>
<td>Eurygonum nodosum, Rhopalia catenata</td>
<td>Coral</td>
<td>Base, middle, top</td>
</tr>
<tr>
<td>entire deglacial reef succession</td>
<td>Dysphotic zone (0.01-1% surface illumination)</td>
<td>Scolecia filosa, Ichnoreticulina elegans</td>
<td>Coral, coralline algae, microbialite</td>
<td>Base, middle, top</td>
</tr>
<tr>
<td>Aphotic zone (&lt;0.01% surface illumination)</td>
<td>Saccomorpha clava, Orthogonum fusiferum, Scolecia serrata, Orthogonum lineare</td>
<td>Coral, coralline algae, microbialite</td>
<td>Base, middle, top</td>
<td></td>
</tr>
</tbody>
</table>

Table 4: The photic zonation of the deglacial Tahitian reef-succession (base, middle, top) is reflected by the specific index traces and their affinity to the three main deglacial framework components (coral, coralline algae, microbialite). The herein established ‘cryptophotic habitat’ is characterised by low light conditions in cryptic/shaded habitats (cavities, shaded crevices, dead underside of corals), partly developed throughout the entire deglacial reef-succession.

**Substrate affinity**

Generally, microbore communities are influenced by the microstructure, porosity and mineralogy of the carbonate substrate (Perry, 1998; Chacón et al., 2006). Independent of the ichnotaxa involved, the diversity and abundance of microbore erosion in the coral skeletons is noticeably higher than in microbial as well as in coralline algal crusts through the entire deglacial sequence. This is interpreted as an effect of the higher porosity of coralline algal crusts and clotted microfabric of the microbial crusts compared to the coral skeleton, rendering these substrates less favourable for penetration by microboreoders. This interpretation is in agreement with Perry (1998) who also found a higher endolithic infestation in corals compared to crustose coralline algae. Nevertheless, coralline algae are known in some cases to show abundant bioerosion (red alga *Hydrolithon onkodes* from Moorea, French Polynesia; Tribollet and Payri, 2001) with similar ichnotaxa as found in the current study, including *S. filosa, I. elegans, E. nodosum* and *F. dactylus*. Unfortunately the abundances between red algae and coral skeletons are not given by Tribollet and Payri (2001).
**Depth of penetration**

The depth of penetration of microborers into the substrate roughly corresponds to their bathymetric distribution (Tribollet, 2008). Phototrophic microendoliths penetrate the substrate to depths where photosynthesis equals respiration. This critical depth of penetration is 1 mm (e.g., *Mastigocoleus testarum*) to 2-4 mm (*Plectonema terebrans, Ostreobium quekettii*), and thus depends on the species involved and on the intensity of light (Chazottes et al., 1995).

Experiments in shallow tropical environments have shown that microborers start to penetrate calcium carbonate surfaces rapidly (4-9 days) after the death of the host organism (e.g., Perkins and Tsentas, 1976; Tudhope and Risk, 1985; Carreiro-Silva et al., 2005). However, infestation of living corals by microbioeroders is also possible but is significantly less intense and less diverse than for dead coral skeletons (Tribollet and Payri 2001). *Ostreobium quekettii* is one of the very few boring organisms known to infest live *Porites lobata* from Moorea, French Polynesia (LeCampion-Alsumard et al., 1995). Indication for *syn vivo* infestation of *O. quekettii*, which has to keep pace with the skeletal accretion of the polyp is a boring direction of its trace *Ichnoreticulina elegans* from the inside out without reaching the surface (LeCampion-Alsumard et al., 1995). The trace patterns of *I. elegans* in the analysed *Porites lobata* fragments, in contrast, show dense meshworks mainly in the upper 1-4 mm of the skeleton and a direction of penetration from the surface into the skeleton. In the samples from the base of the post-glacial succession when sea-level was shallowest, they reach a maximum depth of penetration of around 10 mm were *O. quekettii* must have still been able to photosynthesise. The decreasing penetration depths towards the top of the deglacial succession (1-4 mm) support the palaeobathymetric deepening-upward trend seen in the ichnocoenosis composition. Similarly, *E. nodosum* and *R. catenata* were found up to 5 mm deep inside the coral-skeleton at the base of the deglacial succession.

**Timing of microbialite genesis**

For the middle and upper parts of the deglacial reef succession, similar microbioerosion patterns found inside all three framework components imply that encrustation of the corals by coralline algae and microbialites took place soon after coral demise. The indications of constant photic conditions during coral growth and later encrustation as indicated by bieroerosion patterns is supported by radiocarbon dating, which yields almost identical ages for the corals and the encrusting microbialites of the upper sample pairs (Table 3). This is also in accordance with a moderate rate of sea-level rise of ~10 m/1000 yr (Bard et al., 1996) for the time span in question (9,200 – 11,200 cal. yr BP; maximum 1σ age range; Table 3; Fig. 16Fig. 18).

In contrast, at the base of the deglacial succession distinctly different microbioerosion patterns were observed in the various substrates. Here, microbioerosion in the corals
indicates shallow euphotic II to deep euphotic conditions, whereas microbioeroders in the red algal crusts and the microbialites imply dysphotic conditions (Fig. 13, Fig. 18). The corresponding calibrated AMS $^{14}$C ages corroborate these findings. They indicate a significant time delay between coral growth and microbialite development of ~700 years between 11,300 and 12,400 cal. yr BP (maximum 1σ age range) at the deglacial base of the Mara’a site. This time span, during which the sea-level rose at a rate of ~10 m/1000 yr (Bard et al., 1996), seems too short for a pure sea-level driven shift to dysphotic conditions. In contrast, at Tiarei, the age difference of ~600 years falls within the Meltwater Pulse 1A between ~14,000 and 14,500 cal. yr BP with the most rapid sea-level rise of ~50 m/1000 yr (Bard et al., 1996; Table 3; Fig. 18).

**The role of nutrients**

Other factors to address when evaluating photic conditions and palaeobathymetry are the nutrient regime and the particle load of the seawater, both of which significantly influence light penetration. An increase in terrestrial sediment influx and related eutrophication due to increased river runoff, flooding of the nutrient-rich volcanic slopes, might have played a significant role during the Tahitian deglacial sea-level rise.

Another mechanism potentially contributing to elevated trophic conditions is enrichment of seawater by interaction with the basement basalt of the island of Tahiti. For the modern Tahiti barrier reef, internal fluid circulation is known to be highly variable (Steinmann and Déjardin, 2004). Upward fluid migration from the volcanic basement leads to enrichment in nutrients by basalt–seawater interaction, whereas the repeated interruption of the upward fluid migration from the basement due to enhanced lateral admixture of seawater reduces nutrient levels (Steinmann and Déjardin, 2004). More intensive basalt–seawater interaction during the last deglacial might thus have contributed to the formation of microbial carbonates (cf., microbialites in Indo-Pacific Reefs; Reitner et al., 1996).

Independent of these potential processes, the recorded microbioerosiion patterns at the base of the deglacial succession with slightly shallower photic conditions (shallow euphotic II to deep euphotic zone; presence of *Fascichnus dactylus*) at Faa’a and Mara’a than at Tiarei (shallow euphotic III to deep euphotic zone) may indicate a superior water transparency owing to a lower input of nutrients by river runoff compared to Tiarei that is close to the main drainage of the island (Papenoo River). In turbid eutrophic or mesotrophic conditions the shallow euphotic zone is known to condense considerably (e.g., Hallock and Schlager 1986; Wisshak et al., 2005). Hence, a nutrient-driven telescoping effect could be reflected in the entire deglacial succession of Tahiti suppressing the development of the shallowest euphotic ichnocoenoses. An increasing telescoping effect appears to have intensified the sea-level driven shift from euphotic to dysphotic conditions along the deglacial succession.

Eutrophication leading to elevated abundances of plankton offers an alternative explanation for the larger time lag at the base of the succession (> 500 years) compared to
the middle and the top of the sequence (< 100 years). Microbial growth and encrustation by coralline algae are strongly promoted by elevated nutrient fluxes (Hallock 1988; Dade et al., 1996; Riding 2000; Chazottes et al., 2008), whereas corals suffer from reduced light availability and overfeeding stress (Hallock 1988; Hallock and Schlager 1986). This environmental stress leads to increased production of coral mucus containing active bacterial populations, which might eventually kill the corals (cf., Mitchell and Chet, 1975; Meile et al., 1988; Fabricius, 2005; Weber et al., 2006). This coral mucus could be responsible to initiate microbial carbonate precipitation via organomineralisation (cf., Dade et al., 1996; Reitner et al., 1996; Dupraz et al., 2004; Hendry et al., 2006). We speculate that these stressful conditions finally might have contributed to the fact that the drilled reefs could not keep pace with the rising sea-level and finally drowned.

Additionally, the rates of microbioerosion and macrobioerosion increase with high nutrient levels and in turbid water (Pari et al., 1998; Chazottes et al., 2002; Zubia and Peyrot-Clausade, 2001). In modern reefs, healthy areas with abundant grazing and macrorboring on dead coral substrates are clearly distinct from nutrient-enriched areas associated with high microboring activity (Chazottes et al., 2002). Fertiliser experiments demonstrate that inorganic nutrients have a rapid and strong positive impact on microbioerosion (Carreiro-Silva et al., 2005). Increased trophic conditions appear to favour particularly *S. filosa*, *E. nodosum* and *I. elegans* in coral skeletons (Zubia and Peyrot-Clausade, 2001; Chazottes et al., 2002) – all of which have been identified in the present study. Increased bioerosion may have built up additional stress for the coral ecosystem, further promoting the development of microbial crusts and contributing to the drowning of the drilled post-LGM reefs.

**The coral-microbialite paradox in Tahitian reefs**

In summary, the postulated enriched nutrient and particle flux are providing a model for the paradox co-occurrence of oligotrophic zoanthellate corals growing ‘side by side’ with microbial mats that tend to develop in eutrophic conditions (cf., Dade et al., 1996; Riding, 2000). Elevated nutrient levels may have lead to photic conditions that were sufficient for the stressed corals to survive but insufficient for the development of the shallowest euphotic ichnocoenosia. This interpretation offers an explanation of the apparent contradiction of such dominant endolithic low-light specialists in a tropical coral reef with light dependant zoanthellate corals (with a minimum demand of light irradiance on the order of 2-8% of the surface irradiance; Cooper et al., 2007; Titlyanov and Latypov, 1991) usually bearing ichnocoenosises with a much higher dominance of shallow euphotic boring cyanobacteria and chlorophytes (e.g., Vogel et al., 1995, 1999; Vogel and Marincovich, 2004). At the same time, enhanced nutrient levels might have triggered the establishment of microbial mats that induced carbonate precipitation and microbialite genesis. Consequently, the deglacial environment caused limiting environmental conditions for both corals as well as microbes that might have been permanently close to their coping range. Relatively short-term (seasonal?) shifts in trophic conditions might have played an
important role in the balance of coral reef growth and microbial encrustation. In addition, lowered tropical water temperatures (Beck et al., 1997) might have contributed to the stress acting on the coral reef ecosystem.

Fig. 18 The deepening-up sequence with final drowning of the deglacial reef as indicated by microbioerosion patterns in the various reef cores. Ichnofosses at the base of the deglacial reef indicate euhptic conditions (Faa’a and Mara’a: shallow euhptic zone II, III, and deep euhptic zone; Tiarei: shallow euhptic zone III and deep euhptic zone). Traces of exclusively heterotrophic organisms were identified in locally developed shaded niches (‘cryptophobic habitat’) within the photic zone (cores 7B, 25A, and 25B). Towards the top of the deglacial reef the euhptic indications give way to dysphotic ichnofosses, thereby tracing the post-LGM sea-level rise. Additionally, the calibrated AMS $^{14}$C ages (cal yr BP) of the four dated samples are indicated (MB = microbialite).
4.1.5 Conclusions and outlook

The post-LGM deglacial sea-level rise and corresponding deepening-upwards is reflected in the microbioerosion patterns. Indicator microborings in the corals for the shallow-euphotic zone II to deep-euphotic zone (in particular Fascichnus dactylus) are scarce and only present at the base of the succession. The deglacial sea-level rise seems to have reduced the light levels, leading to microendolithic trace patterns in the coral skeletons that indicate dysphotic conditions for the middle to upper part of the deglacial succession. These photic conditions were only sufficient for low-light specialists such as Ostreobium quekettii (ichnotaxon I. elegans) and Plectonema terebrans (ichnotaxon S. filosa).

Ichnospecies composition in corals, encrusting coralline algae and microbialites from the middle to upper part of the Tahitian post-LGM succession are largely identical and thus indicate that encrustation took place soon after coral demise. This interpretation is corroborated by radiocarbon dates. For the base of the succession, in contrast, the relative palaeobathymetry between corals (shallow euphotic II to deep euphotic conditions) and microbial crusts (dysphotic conditions) as indicated by microbioerosion shows a time lag during which the photic regime has changed. This again is confirmed by radiocarbon dates.

Microbialites have grown under photic conditions as is indicated by the microbioerosion traces produced by phototrophic organisms (specifically Ostreobium quekettii and Plectonema terebrans). For some samples they likely have developed in ‘cryptophotic’ niches and are thus most appropriately addressed as ‘cryptophotic microbialites’.

The higher porosity of coralline algal crusts and clotted microfabric of the microbial crusts compared to the coral skeleton renders these substrates less favourable for penetration by microbioeroders. This is reflected in the lower degree and the lower diversity of microbioerosion in coralline algae and microbialites. The penetration depth of microendoliths is highest at the base of the post-glacial succession where Ostreobium quekettii reaches up to 10 mm in depth. It is decreasing towards the top of the succession, thereby underlining the palaeobathymetric deepening-upwards trend seen in the ichnocoenosis composition.

An alternate and/or additional factor to taken into account for explaining the Tahitian situation is an increased turbidity due to an increase in nutrient and sediment influx during deglaciation. Such an increased turbidity could result in condensed photic zones, which seem to support the shift towards dysphotic conditions at the base of the succession in addition to the sea-level rise. Alternative sources of nutrients are basalt–seawater interactions that are yet to be understood. Enhanced nutrient levels would have strongly promoted encrustation by coralline algae and microbial growth. At the same time they would have reduced coral growth by lowering light availability, and by adding overfeeding stress and enhanced bioerosion rates. These factors would have impeded the reef from keeping pace with the sea-level rise and could have added to the drowning of the deglacial reefs. This model of increased nutrient levels solves the absence of the shallowest
ichnoecoenoses and the paradox of the co-occurrence of oligotrophic zooxanthellate corals with microbial mats that tend to develop under eutrophic conditions.

In summary, three factors appear to have contributed to the coral/microbialite association of the Tahitian reef complex through time. Namely the proposed possible but locally restricted microbialite formation in ‘cryptophotic’ niches, the deglacial sea-level rise, and a condensed photic zonation as a result of elevated nutrient levels. Further research will be required to gain a better understanding of the relative contribution of these factors – an important prerequisite to fully interpret the reef succession in terms of accurately reconstructing the ecological conditions during the deglacial sea-level development.

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4.2 Data report: Bioerosion in the reef framework, IODP Expedition 310 off Tahiti (Tiarei, Mara’a, and Faa’a sites)

Katrin Heindel¹, Hildegard Westphal¹, Max Wisshak²

1) MARUM – Centre of Marine Environmental Sciences, University of Bremen, Leobener Straße, 28359 Bremen, Germany, kheindel@uni-bremen.de
2) GeoZentrum Nordbayern, Erlangen University, Loewenichstr. 28, 91054 Erlangen, Germany


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Abstract. – The coral reef framework off Tahiti was drilled during Integrated Ocean Drilling Program (IODP) Expedition 310 in order to study environmental change (including sea-level rise) following the Last Glacial Maximum (LGM). Cores from sites located in the three drilling areas (Tiarei to the north, Faa’a to the west, and Mara’a to the southwest) of the island of Tahiti were studied in order to characterise the microbioerosion patterns in the post-LGM deglacial reef framework. A total of 19 samples were examined for information on the environmental conditions directly after demise of the shallow-water corals, and during subsequent encrustation by coralline algae and microbialites. Microbioerosion patterns imply that conditions during reef growth were deeper euphotic to dysphotic. The reasons for the largely absent shallow euphotic indications lay either in the proposed rapid sea-level rise leaving a drowned reef, in a “cryptophotic” position of most samples, in enhanced turbidity condensing the photic zonation, or in a combination of these factors. The sea-level rise scenario combined with increased nutrient levels are considered as the primary factors since entirely cryptophotic conditions of the sediment cores are less probable.

Keywords: Bioerosion, microbialites, coral reef, photic conditions, ichnotaxa, ichnocoenoses, DP Hunter, IODP Expedition 310, Tahiti Sea-level
4.2.1 Introduction

During Integrated Ocean Drilling Program (IODP) Expedition 310, drowned Pleistocene to Holocene barrier reef terraces seaward of the modern fringing reefs of Tahiti were drilled in order to recover the deglacial reef sequence. The drilling strategy aimed at recovering cores along transects perpendicular to the strike direction of the reefs (Camoin et al., 2007). More than 600 m of core material was recovered (Camoin et al., 2007).

Tahiti is located at 17°50'S, 149°20'W in the central Pacific Ocean (French Polynesia, Society archipelago). A total of 19 samples from 14 holes from the three sites Tiarei, Mara’a, and Faa’a were studied (for exact positions of the sites and samples studied see Tables 5, 6). Terrestrial input of material eroded from the volcanic island is strongest in the Tiarei area, which is located close to the discharge of the largest drainage system of Tahiti, the mouth of the Papenoo River. The samples studied here are from sites in water depths up to 117 m, whereby samples from sites located on ridges are in water depths of 56-81 m (Table 6; Fig. 19, Fig. 20). Eleven samples were studied from the Tiarei area in the north, seven samples from Mara’a in the south, and one sample from Faa’a west of the island of Tahiti (Fig. 20). This study focuses on the post-Last Glacial Maximum (LGM) interval of the IODP Expedition 310 cores. The typical repetitive pattern of the Tahitian post-LGM reef sequence consists of corals encrusted by coralline algae and subsequently by microbial crusts (Camoin et al., 2007). According to U/Th age dates, the post-LGM interval is from 16,000 to 8,000 yr before present (BP) (Camoin et al., 2007).

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<tr>
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<th>Longitude</th>
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Table 5: Positions (latitude, longitude), water depths (mbsl) of the top of the holes, and total water depths (mbsl) of the drilled bore holes.
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</table>

**Table 6**: IODP Expedition 310 Sample Codes of analysed samples (Expedition, Hole, Core, Section, Top Depths [cm], and Bottom Depths [cm]). Additionally given, approximate water depths (mbsl) of the samples and sample-positions in the deglacial Tahitian reef-succession: base (oldest sequences), middle ranges, and top (youngest sequences).

**Fig. 19**: Seismic line of the Tiarei area. Note series of drowned reefs forming submarine ridges (relative age of the drowned reefs is given by numbers 1 to 3) and volcaniclastic sediment bodies shed from the island of Tahiti. (Seismic data is from the site survey [Camoin, et al., 2003] as provided on the IODP Site Survey Data Base Web site: http://ssdb.iop.org). TWT = two-way traveltime.
Approach: Bioerosion in marine carbonate substrates

Bioerosion describes the erosion of marine hard substrates by living organisms via a number of mechanisms. Bioeroders are grazing organisms like gastropods, chitons, echinoids, etc.; sponges, bryozoans, worms, etc. (macroborers, trace diameter > 100 μm); and bacteria, algae, and fungi (microborers, trace diameter < 100 μm) (e.g., Golubic et al., 1975; Warme, 1975). Mechanisms of bioerosion include biotic boring, rasping, and scraping. The traces left by those bioerasive activities are classified as ichnotaxa and are highly sensitive paleoenvironmental indicators (Bromley, 2004; Glaub and Vogel, 2004). Microbioeroders are considered reliable paleoenvironmental indicators (temperature, light availability, and trophic conditions) because they are evolutionary conservative organisms (Vogel and Glaub, 2004).

For standardized interpretation of photic conditions, typical communities of microbioerosion traces have been defined (index ichnocoenoses) (Glaub, 1994, 1999; Vogel et al., 1995, 1999; Glaub et al., 2002; Vogel and Marincovich, 2004). Borings of the different
photic zones show typical preferred orientations. In the shallower euphotic zones the penetration activities tend to be vertically oriented (e.g., Fascichnus isp. produced by the cyanobacterium *Hyella* spp.), whereas the traces found in deeper euphotic and dysphotic zones tend to be horizontally oriented (e.g. *Ichnoreticulina elegans* produced by the chlorophyte *Ostreobium quekettii*).

Three photic zones have been defined, the euphotic zone (>1% surface illumination), the dysphotic zone (0.01%-1% surface illumination), and the aphotic zone (<0.01% surface illumination) (Liebau, 1984; Glaub, 1994). The euphotic zone is divided into the shallow euphotic zones I, II, and III and the deep euphotic zone (Liebau, 1984; Glaub, 1994). Index ichnocoenoses describe most of the different photic zones. No index ichnocoenosis has been defined yet for the shallow euphotic zone I, but it is well known that this zone is typically dominated by cyanobacteria with sheath pigmentation. The *Fascichnus acinosus/Fascichnus dactylus* ichnocoenosis is the typical vertically orientated trace community of the shallow euphotic zone II and is produced by cyanobacteria. The change from vertical to horizontal orientation of the borings starts with the index ichnocoenosis of the shallow euphotic zone III: *Fascichnus dactylus/ "Palaeoconchocelis starmachi"*. In the shallow euphotic zone III, microbioerosion is still dominated by traces of cyanobacteria but the traces now are horizontally orientated. Additionally, borings of eukaryotes are frequently encountered. The index ichnocoenoses of the deep euphotic zone is "*Palaeoconchocelis starmachi"/Ichnoreticulina elegans*. Entirely, that zone shows the maximal trace diversity and is dominated by horizontally orientated bioerosion patterns of eukaryotes, mainly produced by rhodophytes and chlorophytes. The abundance of heterotrophs increases. The dysphotic zone is controlled by heterotrophs and the traces *Ichnoreticulina elegans* (chlorophytes) and/or *Scolecia filosa* (cyanobacterium) whose producers can cope with very low illumination rates. The index ichnocoenosis of the dysphotic zone is not yet defined. Under aphotic conditions, bioerosion is limited to heterotrophic organisms. The index ichnocoenosis is composed of *Saccomorpha clava/Orthogonum lineare* (Glaub, 1994, 1999; Vogel and Marincovich, 2004; Wisshak, 2006).

### 4.2.2 Methods and Materials

Nineteen samples were selected for the study of microbioerosion in order to allow for detecting trends along the deglacial succession from the LGM to the final drowning of the drilled coral reefs (16,000-8,000 yr BP) (Camoin et al., 2007). Seven samples were taken close to the base of the deglacial (post-LGM) reef succession from Faa’a, Mara’a, and Tiarei; eight samples represent the middle part of the post-LGM reef from Mara’a and Tiarei; and four samples represent the upper deglacial succession from Mara’a and Tiarei (Table 6).

For taxonomic description of the bioerosion traces, the samples were impregnated with epoxy resin and subsequently dissolved, producing so-called casts of the bioerosion patterns inside the carbonate. For a detailed description of the vacuum-embedding
technique after Golubic et al. (1970, 1983) see Beuck and Freiwald (2005) and Wisshak (2006). Determination of the bioerosion traces down to ichnospecies level was attempted where possible.

Two different methods of cast preparation were used: (1) Selected samples were cut vertical to growth direction to cover the complete growth succession from corals to coralline algal crusts to microbialite crusts. Organic matter was eliminated with hydrogen peroxide followed by cleaning of the carbonate in the ultrasonic bath. After impregnating and curing the resin, the impregnated samples were etched shortly in hydrochloric acid (5%) in order to remove only the uppermost ~100 μm of the carbonate substrate (coral, coralline red algae, and microbialite). These casts were analysed with respect to the vertical extension of microboring in the substrate, potential changes in the composition of the microbioeroder communities with progressive penetration depths, and substrate dependence of the microborer communities. (2) Other samples were taken from upper, not further encrusted surfaces of the substrate (coral and microbialite). The impregnated sample was completely dissolved in order to study superficial microbioerosion patterns and the horizontal extension of microbioerosion patterns. The casts of all samples were sputter-coated with gold for scanning electron microscopy (SEM) analysis. The SEM images (Fig. 21-33) show resin-casts of boreholes – “negatives” of the actual traces, which are boreholes inside the carbonate.

4.2.3 Results

In the following, a detailed inventory of the ichnotaxa is given. Traces, which require further investigation are left in open nomenclature (e.g., “Dendrinid-form”).

Spectrum of macrobioerosion

Three ichnotaxa of macrobioeroders are present in corals, encrusting coralline algae, and in microbialites in the entire post-LGM reef. The sponge borings of the ichnogenus Entobia Bronn, 1837 (Fig. 21) are common to abundant in all samples. The producer of Entobia is the boring sponge Cliona and other Hadromerida. Additionally, domiciles of polychaetes have been identified. Caulostrepsis isp. was produced by the spionid worm Polydora, and the ichnospecies Maeandropolydora isp. was produced by the same or other polychaete worms.

Spectrum of microbioerosion

In the typical Tahitian reef-substrates of IODP Expedition 310 (corals, encrusting coralline algae, and microbial crusts), a total of nine different traces of microborers were identified. Two main groups can be distinguished: traces of phototrophic euendoliths (cyanobacteria and chlorophytes) and traces of heterotrophic euendoliths (bacteria and fungi). The microbioerosion patterns produced by phototrophic organisms are dominated by cyanobacteria. These include Fascichnus dactylus (trace maker, e.g., Hyella caespitosa),
Eurygonum nodosum (trace maker Mastigocoleus testarum), and Scolecia filosa (trace maker Plectonema terebrans). Additionally, ichnotaxa of chlorophytes were identified including Rhopalia catenata (trace maker Phaeophila sp.) and Ichnoreticulina elegans (trace maker Ostreobium queketti). The microborings produced by fungi are Saccomorpha clava and Saccomorpha cf. clava (both trace maker Dodgella priscus), and Orthogonum fusiferum (trace maker Ostracobable implexa). Ichnotaxa produced by unknown heterotrophic organisms identified during this study are Scolecia serrata, Scolecia cf. serrata, and Orthogonum lineare. Previously unknown traces produced by unknown organisms are the “Dendrinid-form” and the “Worm-form”.

Fig. 21 Entobia isp. (SEM images of resin-casts, ‘negatives’ of the boreholes inside the carbonate) produced by the sponge Cliona. Fine filamentous casts/traces likely represent borings of the endolithic green alga Ostreobium. A. Large Entobia chambers show a verrucose surface sculpture, the imprints of the carbonate-carving cells. B. Exploratory extensions emanating from a large Entobia chamber. C. An exploratory Entobia tunnel. D. Detailed view of an exploratory extension. E. Detail view of scars left by carbonate carving Cliona cells. Note the concentric surface feature marking the progression of cell margins carving carbonate chips. F. Tip of Entobia exploratory tunnel protruding from the coral skeleton.
Three samples are from aphotic habitats or more accurately related to as “cryptophotic” habitats (cryptic and/or shaded habitats characterised by low light conditions within the otherwise euphotic reef; e.g., dead underside of corals, shaded crevices, etc.) (Heindel et al., in press), as is reflected by the identified heterotrophic microendoliths: Sample 310-M0025A-9R-1W 22-29 is from a downward surface of a coral, and the Samples 310-M0025B-10R-1W 62-69 and 310-M007B-11R-1W 54-60 are from small cavities in the coral framework encrusted by microbialite.

**Traces of phototrophic euendoliths**

**Traces produced by cyanobacteria**

Ichnotaxon *Fascichnus dactylus* (Radtké, 1991), Fig. 22 A-B

*Description:* The trace was found in radiating bundles or larger carpets of up to 100 μm long galleries, 2-4 μm in diameter. The relief of the galleries is smooth to slightly rough. Their distal ends are slightly thickened. Bifurcations were only rarely observed.

*Distribution:* In coral skeletons from the base of the deglacial succession: Samples 310-M0019A-9R-1W 65-70 (Faa’a), 310-M0007B-26R-1W 77-92, and 310-M0016A-35R-1W 23-27 (Mara’a).

*Remarks:* *F. dactylus* was exclusively found inside coral skeletons close to the substrate surface (upper tens of micrometers) and below the encrusting coralline algal crusts. For *F. dactylus* several extant trace makers are known, the most abundant of which is *Hyella caespitosa*. The former name *Fasciculus* (nomen nudum) was replaced only recently by the new ichnogenus name *Fascichnus* by Radtké and Golubic (2005).

![Fascichnus dactylus](image1.jpg)

*Fig. 22* *Fascichnus dactylus* (SEM images of resin-casts of the boreholes) colonies produced by the cyanobacterium *Hyella caespitosa* and related species. A-B. Typical thick and short galleries of *F. dactylus* with indicated cell walls. *F. dactylus* is recorded solely in coral skeletons from Tahiti deglacial coral reefs (SEM).

Ichnotaxon *Eurygonum nodosum* Schmidt, 1992, Fig. 23 A-D

*Description:* The gallery diameter of this ichnospecies varies from 6 to 10 μm and the traces are characterised by lateral swellings developed along the individual galleries in irregular intervals (heterocysts). These swellings are globular (7-15 μm in diameter). The repetitive bifurcations alternate from unilateral to bilateral mode with angles between 45° and 90°.
**Distribution:** In coral skeletons from the base of the deglacial succession: Samples 310-M0019A-9R-1W 65-70 (Faa’a), 310-M0016A-3SR-1W 23-27 (Mara’a), 310-M0024A-11R-2W 73-89, and 310-M0009D-9R-1W 108-114 (Tiarei).

**Remarks:** These microborings were exclusively observed inside the corals up to 5 mm below the surface. The producer of *E. nodosum* is *Mastigocoleus testarum*.

![Image](image-url)

**Fig. 23** *Eurygonum nodosum* (SEM images of resin-casts of the boreholes), a trace produced by the cyanobacterium *Mastigocoleus testarum*. A-D. The frequently bifurcated trace produces filamentous casts of variable diameter and develops characteristic lateral swellings, which harbour heterocysts, the nitrogen fixing cells (arrows). B. Short lateral branch probably containing heterocysts (arrow). C-D. Variations in *E. nodosum* borings. *E. nodosum* is exclusively recorded in coral skeletons from Tahiti deglacial coral reefs.

Ichnotaxon *Scolecia filosa* Radkte, 1991, Fig. 24 A-D

**Description:** *S. filosa* is characterised by “spaghetti-like” curved, thin (almost constantly 2 μm in diameter), and long individual galleries forming large networks that are commonly found collapsed to the cast surface. They only rarely bifurcate.

**Distribution:** In corals, coralline algae, and microbialites from the base of the deglacial succession: Samples 310-M0019A-9R-1W 65-70 (Faa’a), 310-M0007B-26R-1W 77-92 (Mara’a), 310-M0024A-11R-2W 73-89 and 310-M0009D-9R-1W 108-114 (Tiarei); in corals, coralline algae, and microbialites from the middle ranges of the deglacial succession: Samples 310-M0018A-1R-1W 41-47 (Mara’a), 310-M0024A-1R-1W 3-6, 310-M0021B-2R-1W 96-103, 310-M0009B-1R-1W 33-46, and 310-M0009E-3R-1W 99-110 (Tiarei); and in corals, coralline algae, and microbialites from the top of the deglacial succession: Samples 310-M0023A-2R-1W 40-47 and 310-M0023A-8R-1W 5-41 (Tiarei).
Remarks: *S. filosa* was identified in all three reef-framework elements but is mostly present inside the coral skeletons and less in coralline algae. The boring organism producing this trace is the cyanobacteria *Plectonema terebrans*.

![Images of Scolecia filosa and Plectonema terebrans](image)

**Fig. 24** *Scolecia filosa* (SEM images of resin-casts of the boreholes) produced by the cyanobacterium *Plectonema terebrans*. **A-D.** *S. filosa* forms dense meshworks of “spaghetti-like” curved, thin and long galleries, which rarely bifurcate. The trace is recorded in coral skeletons (A-B) and in microbial crusts (C-D) of the deglacial sequence of Tahitian coral reefs.

**Traces produced by chlorophytes**

Ichnotaxon *Rhopalia catenata* Radtke, 1991, Fig. 25 A-D

**Description:** The type of *R. catenata* in the present substrates is characterised by 5-7 μm thick galleries. Different pronounced swellings (5-20 μm in diameter) occur in irregular intervals along the galleries and are connected to the substrate surface by short rhizoidal appendices (2 μm). The swellings appear from oval (egg-shaped) to nodular/spheroidal, whereas the latter morphology is mostly more pronounced than the oval form. The bifurcations of *R. catenata* are dichotomous (angles between 45° and 60°).

**Distribution:** In coral skeletons from the base of the deglacial succession: Samples 310-M0007B-26R-1W 77-92 (Mara’a) and 310-M0009D-9R-1W 108-114 (Tiarei).

**Remarks:** *R. catenata* is produced by *Phaeophila* sp. and occurs in the investigated Tahitian reef samples exclusively in corals in a maximum depth similar to *E. nodosum* (as deep as 5 mm).
**Fig. 25** *Rhopalia catenata* (SEM images of resin-casts of the boreholes) produced by the chlorophyte *Phaeophila dendroides*. **A-D.** The trace shows the typical swellings. **D.** The typical appendices connect the trace with the coral skeleton surface. *R. catenata* is exclusively reported from coral skeletons.

**Ichnotaxon Ichnotreticulina elegans** (Radtke, 1991), Fig. 26 A-F

**Description:** The morphology of *I. elegans* is highly complex (Radtke and Golubic, 2005). The typical zigzag pattern is the most obvious feature of *I. elegans*. From a parallel and close to the substrate surface extending straight or winding main first order gallery (4-5 μm in diameter), second and third order galleries develop mainly at right angles and form large and dense zigzag-shaped networks (2-5 μm). Thin and straight “exploratory” filaments (1-2 μm) extend from the same colony. In some cases little appendices (≤ 1 μm) emerge from individual first order galleries (e.g., in Sample 310-M0007B-26R-1W 77-92 from Mara’a and 310-M0023A-2R-1W 40-47 from Tiarei). Some thick galleries (up to 5 μm) show arch-like branches, which connect *I. elegans* with the substrate surface (cf., Radtke and Golubic, 2005). The individual arches span a distance of 10-20 μm.

**Distribution:** In corals, coralline algae, and microbialites from the base of the deglacial succession: Samples 310-M0007B-26R-1W 77-92 and 310-M0016A-35R-1W 23-27 (Mara’a), 310-M0024A-11R-2W 73-89 and 310-M0009D-9R-1W 108-114 (Tiarei); in corals, coralline algae, and microbialites from the middle ranges of the deglacial succession: Samples 310-M0015A-9R-1W 6-10, 310-M0018A-1R-1W 41-47, and 310-M0018A-6R-1W 6-10 (Mara’a), 310-M0024A-1R-1W 3-6, 310-M0021B-2R-1W 96-103, 310-M0009B-1R-1W 33-46, and 310-M0009E-3R-1W 99-110 (Tiarei); and in corals, coralline algae, and microbialites from the top of the deglacial succession: Samples 310-M0017A-5R-1W 28-32...
(Mara’a), 310-M0023A-2R-1W 40-47, 310-M0023A-3R-1W 10-12, and 310-M0023A-8R-1W 5-41 (Tiarei).

Remarks: I. elegans is produced by Ostreobium quekettii. The former ichnogenus name Reticulina (nomen nudum) was substituted by Ichnoreticulina only recently by Radtke and Golubic (2005).

Fig. 26 Ichnoreticulina elegans (SEM images of resin-casts of the boreholes) produced by the chlorophyte Ostreobium quekettii. A-F. The main characteristic of I. elegans is the dense zigzag pattern-meshwork. A-B. The common diameter of the zigzag-shaped galleries is ~2 μm. C-D. I. elegans develops also thicker galleries up to 5 μm in diameter. E. Unusual little appendices (~1 μm) emerge from individual, thick galleries (3-4 μm, triangle). Thin and straight exploratory filaments (1-2 μm, arrows) extend close and parallel to the substrate surface. F. Arch-like branches (5 μm), which connect I. elegans to the substrate surface with an arch-span of 10-20 μm. I. elegans was found in all three substrates (coral, coralline algae, and microbialite).
Traces of heterotrophic euendoliths

**Traces produced by fungi**

Ichnotaxon *Saccomorpha clava* Radtke, 1991, Fig. 27 A-D

*Description:* Sphere-, pear- and club-shaped sacks (up to 30 μm long) connected to the surface by a narrow neck, usually lacking a collar, were identified as *S. clava*. The individual sacks are interlinked by one or several thin filaments originating from the main sack or at the base of the necks. Four morphotypes exist in the analysed reef substrates: (1) scattered straight or (2) curved sacks (both 10-15 μm in diameter), (3) clusters of mainly sphere- and club-shaped sacks (10-15 μm in diameter), and (4) large individual branched sacks (20-30 μm in diameter).

*Distribution:* In corals and microbialites from the base of the deglacial succession: Samples 310-M0025A-9R-1W 22-29 and 310-M0025B-10R-1W 62-69 (Tierei); in corals and microbialites from the middle ranges of the deglacial succession: Samples 310-M0015A-9R-1W 6-10 and 310-M0018A-6R-1W 6-10 (Mara’a), 310-M0009B-1R-1W 33-46 and 310-M0009E-3R-1W 99-110 (Tierei); and in corals and microbialites from the top of the deglacial succession: Samples 310-M0007B-11R-1W 54-60 and 310-M0017A-5R-1W 28-32 (Mara’a), 310-M0023A-2R-1W 40-47, 310-M0023A-3R-1W 10-12, and 310-M0023A-8R-1W 5-41 (Tierei).

*Remarks:* *S. clava* was found independent of photic conditions in all photic zones in the entire deglacial reef sequence. The presumed trace maker of this ichnospecies is *Dodgella priscus*, whereby in the present case this may not apply to all morphological variants.

Ichnotaxon *Saccomorpha cf. Clava*, Fig. 27 E-F

*Description:* Generally, the morphology is comparable to morphotypes (2) and (3) of *S. clava* (s. above), whereas *Saccomorpha cf. clava* is longer and slightly thicker (30-60 μm long and 10-20 μm in diameter). Figure Fig. 27E shows one specimen with several noticeably long and thin filaments originating mainly from the base of the neck.

*Distribution:* In microbial crust of the Sample 310-M0018A-1R-1W 41-47 (Mara’a) from the middle ranges of deglacial succession; in the coral of the Sample 310-M0009D-9R-1W 108-114 (Tierei) from the base of deglacial succession, and in the coral skeleton of 310-M0023A-8R-1W 5-41 (Tierei) from the top of the succession.

*Remarks:* Same as for *S. clava, Dodgella priscus*, may be the producer of this morphological variant.
Fig. 27 Saccomorpha clava (SEM images of resin-casts of the boreholes) produced by the fungus Dodgella priscus. A-F. Thin filaments interlinking the individual S. clava specimens contain hyphae. They emerge from the sacks and/or from the base of the necks, attached to the substrate surface. A-B. S. clava occurs in clusters of mainly club-shaped sacks (morphotype 3). C. S. clava occurs as scattered straight sacks (morphotype 1), or (D) as large individual branched sacks (morphotype 4). E-F. Saccomorpha cf. clava, a trace produced also by the fungus Dodgella priscus is longer and slightly thicker than S. clava. E. The trace is developed as clusters of curved sacks (morphotype 2 and 3). F. S. cf. clava is developed as a large individual branched sack (morphotype 4). S. clava was found in all three substrates (coral, coralline algae, and microbialite), while S. cf. clava was found in corals and microbialites.

Ichnotaxon Orthogonum fusiferum Radtke, 1991, Fig. 28 A-B

Description: Thin, straight to slightly winding galleries (~2 μm in diameter) with typical swellings (3-5 μm in diameter) along the galleries or at the mostly perpendicular bifurcations.

Distribution: In the coral of Sample 310-M0009B-1R-1W 33-46 from the middle ranges of the deglacial succession and in the coral of Sample 310-M0023A-8R-1W 5-41 from the top
of the deglacial succession (both Tiarei).

Remarks: The trace is produced by Ostracoblabe implexa and was exclusively found in corals.[Editor: This is part of the chapter “paleobathymetric significance”, therefore we deleted it here].

\[image\]

**Fig. 28** Orthogonum fusiferum (SEM images of resin-casts of the boreholes) produced by the fungus Ostracoblabe implexa. A-B. The typical swellings develop at bifurcations with commonly right angles (arrows in A) or along thin and mostly straight galleries (arrow upper right-handside in A and arrow in B). *O. fusiferum* was solely found in coral skeletons.

**Traces produced by unknown heterotrophs**

Ichnotaxon Scolecia serrata Radtke, 1991, Fig. 29 A-F

**Description:** This trace is the thinnest among all observed ichnotaxa (~1 \(\mu\)m in diameter) and shows a characteristic serrate microsculpture. *S. serrata* forms dense, often interconnected networks in very narrow windings parallel to the substrate surface.

**Distribution:** In corals, coralline algae, and microbialites from the base of the deglacial succession: Samples 310-M0007B-26R-1W 77-92 (Mara’a), 310-M0025B-10R-1W 62-69 and 310-M0024A-11R-2W 73-89 (Tiarei); in corals, coralline algae, and microbialites from the middle ranges of the deglacial succession: Samples 310-M0015A-9R-1W 6-10, 310-M0018A-1R-1W 41-47, and 310-M0018A-6R-1W 6-10 (Mara’a), 310-M0024A-1R-1W 3-6, 310-M0021B-2R-1W 96-103, and 310-M0009E-3R-1W 99-110 (Tiarei); and in corals, coralline algae, and microbialites from the top of the deglacial succession: Samples 310-M0017A-5R-1W 28-32 (Mara’a), 310-M0023A-2R-1W 40-47, 310-M0023A-3R-1W 10-12, and 310-M0023A-8R-1W 5-41 (Tiarei).

Remarks: As in recent settings, *S. serrata* is frequently associated with *I. elegans*, where its galleries run at the surface and in between the thicker tubes of *I. elegans* (Fig. 29E). The producer is an unknown heterotrophic organism, probably belonging to filamentous bacteria (Budd and Perkins, 1980).
Ichnotaxon *Scolecia cf. Serrata*, Fig. 30 A-F

*Description:* This unusual appearance of *Scolecia serrata* shows the typical serrate microsculpture with rare bifurcations, but the galleries of *S. cf. serrata* are slightly thicker (~2 µm in diameter) and they often form spherical aggregates resembling “bags of wool”. In the latter, narrow windings of galleries seem to twine around sphere-like traces such as *Saccomorpha sphaerula*, the emerging hyphae of which are clearly visible. Nevertheless, the association of spherical buildings of larger diameter filaments with radiating very thin filaments is unique and quite distinct from the usual prostrate and space filling habit of *S. serrata*. Hence, this trace might refer to a new ichnotaxon. However, this type of trace
(association of two traces?) was only found in one current sample. There is no “fossil affirmation” (older than Last Deglacial). Future studies are required to introduce a new ichnotaxon.

**Distribution:** Exclusively in the coral-part of the Sample 310-M0017A-5R-1W 28-32 (Mara’a) from the top of the deglacial succession.

**Remarks:** Since this trace is regarded as (previously unknown) morphological variant of *S. serrata*, the same unknown (bacterial?) heterotrophic producer can be assumed.

![Images of SEM images of resin-casts of the boreholes](image)

**Fig. 30** *Scolecia cf. serrata* (SEM images of resin-casts of the boreholes) is regarded as morphological variant of *S. serrata*. **A-F.** *S. cf. serrata* shows the same characteristics as *S. serrata* (Fig. 29) but the galleries are slightly thicker (clearly visible in D and E). Eye-catching is the supposed association with a sphere-like trace such as *Saccomorpha sphaerula*. The spherical aggregates (“bags of wool”; arrows in A-B) are produced by *S. cf. serrata* twining around the assumed spherical fungal traces. The fungal traces are might be indicated by the thin hyphae emerging from the “bags of wool” (arrows in C-F). *Scolecia cf. serrata* was exclusively recorded inside the coral skeleton.
Ichnotaxon *Orthogonum lineare* Glaub, 1994, Fig. 31 A-D

**Description:** *O. lineare* has a perpendicular bifurcation pattern with 8-10 μm thick galleries without swellings. Casually, short spiny protrusions (apophysis; Fig. 31C-D) protrude from the main galleries.

**Distribution:** In corals, coralline algae, and microbialites from the base of the deglacial succession: Samples 310-M0025A-9R-1W 22-29 and 310-M0025B-10R-1W 62-69 (Tiarei); in corals, coralline algae, and microbialites from the middle ranges of the deglacial succession: Samples 310-M0015A-9R-1W 6-10 (Mara’a), 310-M0009B-1R-1W 33-46 and 310-M0009E-3R-1W 99-110 (Tiarei); and in corals, coralline algae, and microbialites from the top of the deglacial succession: Samples 310-M0017A-5R-1W 28-32 (Mara’a) and 310-M0023A-2R-1W 40-47 (Tiarei).

**Remarks:** In contrast to most recent occurrences of this trace, the present traces are abundantly not smooth but rather verrucous (tiny knots arranged closely along the galleries). The uncommon zigzag-like course of individual galleries of *O. lineare* is probably caused by the parallel run to *Entobia* boring cells and/or coralline algae cells (Fig. 31 A-B). The producer of *O. lineare* is an unknown heterotrophic organism.

![Fig. 31 Orthogonum lineare (SEM images of resin-casts of the boreholes) produced by an unknown heterotrophic organism. A-B. The parallel run of the galleries to Entobia boring cells and/or coralline algae cells produces the uncommon zigzag-like course of O. lineare. Apophyses emerge from the main galleries (arrows in B and D). C-D. Within this study, O. lineare is abundantly not smooth but rather verrucose. The diagnostic perpendicular bifurcation pattern is not illustrated. O. lineare was found in all three substrates (coral, coralline algae, and microbialite).](image-url)
Traces of unknown affinity

Ichnotaxon “Dendrinid-form”, Fig. 32 A-D

Description: A central gallery bifurcates in a dendriniform pattern often at right angles and forms a dense network parallel to the substrate surface. The microborings have developed a zigzag pattern otherwise typical for *I. elegans* but are of much larger diameter (10-15 μm). The surface of the individual galleries appears rough.

Distribution: Identified exclusively in *Entobia* cavities of the coral part in Sample 310-M0023A-2R-1W 40-47 (Tiarei) from the top of the deglacial succession.

Remarks: This trace shows some affinity to dendrinid ichnospecies subsumed under the ichnofamily Dendrinidae (Bromley et al., 2007). The producer is unknown.

![Fig. 32](image)

Ichnotaxon “Worm-form”, Fig. 33 A-D

Description: This previously unknown microboring shows a complex morphology with widening galleries, from which close to their rounded ends a lateral prolongation of the main gallery emerges, which repeats this pattern in reduced dimension. The basal galleries reach diameters of up to 40 μm, whereas the more distal galleries are only few micrometers in diameter.
**Distribution:** In microbial crust of the sample 310-M0015A-9R-1W 6-10 (Mara’a) from the middle ranges of deglacial succession; in microbialite of the sample 310-M0025B-10R-1W 62-69 (Tiarei) from the base of deglacial succession.

**Remarks:** The producer is unknown and it is not entirely conclusive whether these casts actually represent a previously unknown microboring or rather a cast of a calcareous epizoan, such as a polychaete worm, or a linear bryozoan colony.

![Images of ichnofossils](image_url)

**Fig. 33** The "Worm-form" (SEM images of resin-casts of the boreholes) is a potential microboring with unknown producer. A-D. The complex morphology is formed by repetitive and to the distal end widening galleries that decrease in size from the basal to the distal galleries. The "Worm-form" was found only in microbial crusts.

**Relative abundances and paleobathymetric significance**

The mean abundances of all traces in the coral skeletons are higher than those in microbialites and coralline algal crusts. Averaged, Scolecia filosa, Ichnoreticulina elegans, and Saccomorpha clava are common, whereas Fascichnus dactylus, Eurygonum nodosum, Rhopalia catenata, Saccomorpha cf. clava, Orthogonum fusiferum, Scolecia serrata, Scolecia cf. serrata, Orthogonum lineare, and the "Dendrinid-form" are rare. In coralline algal crusts, S. filosa, I. elegans, S. serrata, and O. lineare were rarely encountered, whereas all other traces are absent. In microbialites, S. filosa, I. elegans, S. clava, S. cf. clava, S. serrata, O. lineare, and the “Worm-form” were found in low mean abundance, while F. dactylus, E. nodosum, R. catenata, O. fusiferum, S. cf. serrata, and the “Dendrinid-form” are absent.

In total, I. elegans is the most frequent ichnotaxon with a presence in 79% of the analysed samples, followed by S. serrata (68%), S. filosa and S. clava (58% each), O. lineare (42%), E.
nodosum (21%), and *F. dactylus* and *S. cf. clava* (16% each). *R. catenata, O. fusiferum*, and the “Worm-form” show presences of 11% each. The least frequent traces are *S. cf. serrata* and the “Dendrinid-form” (5% each).

**Microbioerosion at the base of deglacial succession**

Microbioerosion patterns in corals at the base of the deglacial succession are dominated by light-dependent cyanobacterial traces. *Fascichnus dactylus, Eurygonum nodosum*, and *Scolecia filosa* are common at Faa’a, whereas the sole heterotrophic trace *Orthogonum lineare* are rare. In the Mara’a area, the cyanobacterial traces occur in varying abundances: *F. dactylus* from rare to common, *E. nodosum* and *S. filosa* from common to abundant. The chlorophythal traces *Rhopalia catenata* and *Ichnoreticulina elegans* are abundant. At Mara’a, the only heterotrophic trace observed in corals is *Scolecia serrata* with common abundance. In the Tiarei area, *E. nodosum* and *S. filosa* are common, while the sole chlorophythal trace, *I. elegans*, is rare. The fungal *Saccomorpha clava* is common, whereas *Saccomorpha cf. clava* and the traces of unknown heterotrophic producers, *S. serrata* and *O. lineare*, are rare (Table 7).

The trace associations in coralline algal crusts in the Mara’a sites are dominated by the common *I. elegans* and *S. serrata*, while *S. filosa* is very rare. In Tiarei sites, *S. filosa, I. elegans, S. serrata*, and *O. lineare* are all rare. At the Faa’a site, only the bioerosion patterns that were found inside coral skeletons could be identified with confidence (Table 7).

The trace associations in microbialites at the base of the deglacial succession in the Mara’a sites are dominated by the common ichnotaxon *I. elegans*, while *S. filosa* and *S. serrata* are rare. At Tiarei the microbioerosion inventory is dominated by the common fungal trace *S. clava*, whereas *S. filosa, I. elegans, S. serrata, O. lineare*, and the “Worm-form” are rare (Table 7).

The key ichnotaxon of the shallow euphotic zones II and III, *Fascichnus dactylus*, was found exclusively in the sample from Faa’a and in two samples from Mara’a. The horizontally oriented traces *E. nodosum* and *Rhopalia catenata* are known to be common in the shallow euphotic zone III and in the deeper euphotic zone (Vogel and Marincovich 2004) and are considered indicative for these zones. In analysed samples, *F. dactylus, E. nodosum* and *R. catenata* are the ichnotaxa with the shallowest photic indication and were found exclusively inside coral skeletons and at the base of the deglacial reef succession. Traces produced by microborers that cope with very low illumination rates (dysphotic conditions), *S. filosa* and *I. elegans*, were found in all three substrates alongside traces of heterotrophic bioerosion agents such as *S. serrata* and *O. lineare* (cryptophotic conditions). The fungal trace *S. clava* was not identified in coralline algae, while the other fungal trace *Orthogonum fusiferum* was not found at all at the base of the succession.
Microbioerosion in the middle ranges of deglacial succession

Microbioerosion patterns in corals in the middle ranges of the deglacial succession are composed of traces produced by low-light specialists and by traces of microbioeroders penetrating in the dark. At Mara’a, all identified ichnotaxa are common on average: S. filosa, I. elegans, S. clava, S. serrata, and O. lineare. In Tiarei sites the most frequent traces are I.
elegans (abundant), S. filosa (common), and S. clava (common), while S. serrata and O. lineare are rare to common. O. fusiferum is rare (Table 7).

<table>
<thead>
<tr>
<th>MIDDLE RANGES OF DEGLACIAL REEF SUCCESSION</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sites</td>
</tr>
<tr>
<td>Samples IODP 310</td>
</tr>
<tr>
<td>Fascichnus dactylus</td>
</tr>
<tr>
<td>Eurygonum nodosum</td>
</tr>
<tr>
<td>Scolecia filosa</td>
</tr>
<tr>
<td>Rhopalia catenata</td>
</tr>
<tr>
<td>Ichnoreticulina elegans</td>
</tr>
<tr>
<td>Saccomorpha clava</td>
</tr>
<tr>
<td>Saccomorpha cf. clava</td>
</tr>
<tr>
<td>Orthogonum fusiferum</td>
</tr>
<tr>
<td>Scolecia serrata</td>
</tr>
<tr>
<td>Scolecia cf. serrata</td>
</tr>
<tr>
<td>Orthogonum lineare</td>
</tr>
<tr>
<td>&quot;Dendrinid-form&quot;</td>
</tr>
<tr>
<td>&quot;Worm-form&quot;</td>
</tr>
<tr>
<td>Photic indication in corals</td>
</tr>
<tr>
<td>Photic indication in corallal crusts</td>
</tr>
<tr>
<td>Photic indication in microbialites</td>
</tr>
</tbody>
</table>

X = abundant, X = common, x = rare, — no microbioerosion

Table 8: Semi-quantitative analysis of the microborer traces from the middle ranges of the Tahitian deglacial reef-succession observed by scanning electron microscopy in corals, corallal crusts and microbialites. The Table includes the palaeobathymetric interpretation (photic indication) derived from the ichnocoenosis in each sample (dys = dysphotic conditions).

In coralline algal crusts the trace associations in Mara’a and Tiarei sites are composed of S. filosa, I. elegans, S. serrata, and O. lineare. All observed traces are rare (Table 8).

The trace associations in microbial crusts at Mara’a and Tiarei consist of S. filosa, I. elegans, S. clava, S. cf. clava, S. serrata, O. lineare, and the “Worm-form”. At Mara’a, I. elegans, S. serrata, and O. lineare show common abundances, whereas all other ichnotaxa are rare. In Tiarei sites, I. elegans and S. clava are represented also commonly in microbialites, while other ichnotaxa are rare (Table 8).

Microbioerosion at the top of deglacial succession

The top of the deglacial succession is mainly characterised by microborings with dysphotic indication (cf., the middle ranges; Table 9; Fig. 34). In the youngest part of the deglacial reef sequence the mean diversity of traces is strongly reduced if compared to the base and slightly reduced when compared to the middle ranges.
### TOP OF DEGLACIAL REEF SUCCESSION

<table>
<thead>
<tr>
<th>Sites</th>
<th>Mara’a</th>
<th>Tiarei</th>
</tr>
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<tbody>
<tr>
<td>Samples IODP 310</td>
<td>M0007B 11R 1W 54-60</td>
<td>M0017A 5R 1W 28-32</td>
</tr>
<tr>
<td>Fascichnus dactylus</td>
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</tr>
<tr>
<td>Eurygonum nodosum</td>
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<td></td>
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<tr>
<td>Scolecia filosa</td>
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<td></td>
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<tr>
<td>Rhopalia catenata</td>
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<tr>
<td>Ichnoreticulina elegans</td>
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<td>Saccomorpha clava</td>
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<tr>
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<td>Scolecia serrata</td>
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<td>Scolecia cf. serrata</td>
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<tr>
<td>Orthogonum lineare</td>
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<tr>
<td>&quot;Dendrind-form&quot;</td>
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<td></td>
</tr>
<tr>
<td>&quot;Worm-form&quot;</td>
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</tbody>
</table>

| Photic indication in corals | — | dys | dys | dys |
| Photic indication in coralline algal crusts | — | — | dys | dys |
| Photic indication in microbialites | cry | dys | dys | dys |

X = abundant, X = common, x = rare, — no microbioerosion

**Table 9:** Semi-quantitative analysis of the microborer traces from the top of the Tahitian deglacial reef-sucception observed by scanning electron microscopy in corals, coralline algal crusts and microbialites. The Table includes the palaeobathymetric interpretation (photic indication) derived from the ichnocoenosis in each sample (dys = dysphotic conditions, cry = cryptophotic conditions).

The trace associations in **corals** are dominated in the Mara’a sites by the abundant *I. elegans* and *S. serrata*, whereas *O. lineare* and *Scolecia cf. serrata* are common, and *S. clava* is rare. At Tiarei, *I. elegans* and *S. clava* are abundant, while *S. filosa* is common and *O. fusiferum, S. serrata*, and the “Dendrind-form” are rare (Table 5).

**Coralline algal crusts** at Mara’a show no signs of microbioerosion. At Tiarei sites, all identified ichnotaxa (*S. filosa, I. elegans, S. serrata, and O. lineare*) are rare (Table 9).

In **microbial crusts** at the top of the succession of Mara’a, *I. elegans* is common, whereas *S. serrata, S. clava,* and *O. lineare* are rare. Microbialites in the Tiarei sites from the top of the succession are composed of the common *I. elegans* and *S. clava* as well as the rare *S. filosa, S. serrata,* and *O. lineare* (Table 9).

The traces *S. filosa* and *I. elegans* produced by low light specialists (*cyanobacterium Plectonema terebrans,* chlorophyte *Ostreobium quekettii*) are known to thrive down to the dysphotic zone (Vogel and Marinovich, 2004). Both ichnotaxa were found along with traces of heterotrophic origin (see below) throughout the entire Tahitian deglacial reef-sequence and in all three framework elements. This indicates dysphotic conditions for the deposition of the middle and upper part of the deglacial reef sequence (Table 8, 9). The producer of *Scolecia serrata* is a heterotrophic organism and was observed in all
substrates, apparently independent of photic conditions. *Orthogonum lineare* was also identified in the entire Tahitian reef succession and occurs mainly inside *Entobia* cavities (Fig. 21). *Saccomorpha clava* and *Orthogonum fusiferum* produced by fungi are present in coral and microbialite samples independent of sampling positions. However, the abundances of all heterotrophic traces are most pronounced in cryptophotic microhabitats: dead underside of corals, deep inside the coral porosity, and in *Entobia* cavities (Sample 310-M0007B-11R-1W 54-60 from the upper part of the reef; 310-M0025A-9R-1W 22-29 and 310-M0025B-10R-1W 62-69 from the base of the deglacial reef; Fig. 34).

![Fig. 34 Deepening-up with final drowning of the deglacial reef sequence indicated by microbioerosion. Faa’a: Hole M0019A; Mara’a: Holes M0007B, M0017A, M0015A, M0016A, M0018A; Tiarei inner ridge: Hole M0023A; Tiarei outer ridge: Holes M0009D, M0009E, M0024A, M0025A, M0025B, M0021B, M0009B. The base of the deglacial reef represents euphotic conditions indicated by typical microbioeroders in corals. Cryptophotic conditions indicated by typical microborers are locally developed in shaded niches within the photic zone (Cores M0025A-9R-1W, M0025B-10R-1W, and M0007B-11R-1W). Toward the top of the deglacial reef the euphotic indications change to dysphotic indications, which traces the post-LGM sea-level rise. Yellow = deglacial reef (Unit 1), gray = Older Pleistocene (Unit 2), cryptoph = cryptophotic.](image)

### 4.2.4 Summary

The present results and specifically the lack of shallow euphotic indications in the bioerosion ichnocoenoses through the middle and upper deglacial reef succession can be attributed to three possible causes or their combination:

1. The microbioerosion patterns are in good agreement with the notion of a rapid deglacial sea-level rise when considering that only the ichnocoenoses developed in corals at the base of the succession indicate shallow euphotic zone II to deep euphotic conditions present during relative sea-level lowstand. The deepening-up effect is demonstrated by the ichnocoenoses found in corals, coralline algae, and microbial crusts from the middle and top ranges of the deglacial succession, which reflect dysphotic conditions due to reef growth progressively lagging behind sea-level rise (Fig. 34). Furthermore, encrustation of the coral framework by microbialites soon after the demise of the corals is indicated by the similar photic conditions in corals.
and microbialites as indicated by ichnocoenoses.

(2) Most of the recorded ichnocoenoses were not established in deeper waters but partly in cryptic and shaded areas of the otherwise photic reef (dead underside of corals, small cavities, shaded crevices, etc.) and are thus better labeled cryptophotic. This applies particularly for the cases of algal crusts and microbialites that – at least at the base of the reef succession – show ichnotaxa indicating a lower illumination state if compared to the encrusted coral skeletons. However, the implications on the timing of microbialite versus coral growth is not entirely conclusive since the contemporaneous development in the cryptic scenario can not be distinguished from the delayed microbialite growth after sea-level rise, based solely on the ichnocoenosis composition.

(3) Another potential factor capable of causing low illumination states in relatively shallow water is a decrease in water transparency due to an increase in nutrient level and sediment input by local river runoff. This model would explain the co-occurrence of mesotrophic/ eutrophic microbialites on the one hand and zooxanthellate corals (weakened by rapid sea-level rise?) on the other.

The relative importance of these possible causes will be evaluated when integrating other data such as reliable radiocarbon dating and sedimentological proxies in further studies (cf., Heindel et al., in press). Nevertheless, the sea-level rise scenario combined with elevated nutrient levels are tentatively considered as the primary factors since entirely cryptophotic conditions of the sediment cores are less probable.

Acknowledgments. – This research used samples and/or data provided by the Integrated Ocean Drilling Program (IODP). The authors would like to thank the Expedition 310 Scientific Party, the co-chiefs G. Camoin and Y. Iryu, and the staff of the Bremen Core Repository. The MARUM (DFG-Research Center / Excellence Cluster "The Ocean in the Earth System") is acknowledged for providing infrastructure and support for this research. Many thanks to the Stjepko Golubic for his very helpful and constructive comments and to Gilles Lericolais (Ifremer, Brest) for help with the seismic data. The SEM analyses were undertaken in the laboratory of André Freiwald, GeoZentrum Nordbayern (Erlangen University). Funding for this research was provided by German Science Foundation (DFG) project We 2492/5 to HW. HW is a member of the Expedition 310 Scientific Party.
4.3 Formation of deglacial Tahitian coral reef-microbialites (IODP 310) involving sulphate-reducing bacteria

Katrin Heindel, Daniel Birgel, Jörn Peckmann, Henning Kuhnert, Hildegard Westphal

MARUM – Centre of Marine Environmental Sciences, University of Bremen, Leobener Straße, 28359 Bremen, Germany, kheindel@uni-bremen.de

In preparation for Palaios

Abstract. – During IODP Expedition 310 “Tahiti Sea-Level”, drowned Pleistocene to Holocene barrier reef terraces have been drilled on the slope of the volcanic island of Tahiti. The Tahitian deglacial reef-succession typically consists of coral framework encrusted by coralline algae and subsequently by microbialites. The high abundance of microbialites (up to 80 vol. % of the cores) is uncommon, when compared to modern shallow-water coral reefs. The genesis of these deglacial microbialites and the conditions favoring their formation are still poorly understood. In the present study, for the first time lipid biomarkers were successfully used to narrow down, which organisms have been involved in the microbialite formation. Marine primary production-derived fatty acids comprise 47% (short-chain fatty acids), whereas terrestrial-derived fatty acids represent only 10% (long-chain fatty acids) of all of them. Bacterially-derived terminally-branched fatty acids (iso- and anteiso C_{15/17}) are very abundant with an average contribution of 20% of all fatty acids. Iso- and anteiso C_{15/17} fatty acids are typically biomarkers derived from sulphate-reducing bacteria. Because enzymatic carbon isotope fractionation of heterotrophic sulphate reducers is insignificant, the minor shift between the average δ^{13}C values from the bulk organic matter (−19.4‰) to the mean compound-specific δ^{13}C values of the iso- and anteiso C_{15/17} fatty acids (−19.2‰) agrees with sulphate reducers as source of the bacterial fatty acids. No lipid biomarkers were found indicating the involvement of oxygenic phototrophs (cyanobacteria) in the microbialite formation. The element composition (Al, Si, Fe, and Ba) of the microbialites reveals a strong terrigeneous influx of basalt-derived minerals (pyroxene, plagioclase, and magnetite) from Tahiti, which has elevated the nutrient levels. Consequently, these nutrients assumingly intensified the primary productivity, which provided the organic matter for the sulphate reducers. During the last deglaciation, sulphate-reducing bacteria apparently were involved in mediating the formation of the microbialites in the coral reefs off Tahiti.

Keywords microbialites, coral reefs, lipid biomarker, heterotrophy, sulphate-reducing bacteria, EPS, coral mucus, Laser-ablation ICP-MS, DP Hunter, IODP Expedition 310, Tahiti
4.3.1 Introduction

Pleistocene coral reefs from the Pacific are well known to contain abundant microbialites (Camoin and Montaggioni, 1994; Cabioch et al, 1999; 2006; Camoin et al., 1999; 2006). Similar occurrences of microbialites are unknown from modern coral reefs. An association of Quaternary microbialites and coralgal communities was described first from high-energy reefs of Tahiti by Montaggioni and Camoin (1993). The pattern of the Tahitian deglacial reef-succession typically consists of corals that are encrusted by coralline algae and subsequently by microbialites (microbial carbonate crusts). The predominance of microbialites, which occlude much of the primary porosity of the coral reefs and their thickness of up to 15 cm, is very rarely observed in modern and ancient shallow-water coral reefs (Camoin and Montaggioni, 1994). One similar example of post-Last Glacial Maximum (LGM) reef-microbialites is known from Vanuatu in the North of New Caledonia (South-West Pacific; Cabioch et al., 1999; 2006). In the modern reefs off Tahiti, similar microbialites have not been observed to form.

The occurrence of the thick microbial crusts in the post-LGM reefs of Tahiti has been interpreted by previous authors as a result of environmental change accompanying the rapid last deglacial sea-level rise, and was suggested to be linked to volcanic hinterlands (Cabioch et al, 1999; 2006; Camoin et al., 1999, 2006). Although numerous studies have dealt with the Tahitian microbialites, their genesis and environmental requirements are still poorly understood. A better understanding of these microbialites and their genesis is needed to use them for a more precise reconstruction of the last deglacial sea level curve and the environmental conditions.

The definition of the term microbialite is still under debate in the geological and biological community. The traditional definition of Burne and Moore (1987) states that “microbial carbonates are organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation”. Kalkowsky (1908), Krumbein (1983) and Van Gemerden (1993) have described microbialites as laminated organosedimentary structures. Here, we use the term microbialite strictly descriptive for laminated and dendritic grey calcareous crusts.

Lithification in microbial mats takes place when precipitation of minerals outweighs dissolution (Dupraz and Visscher, 2005). One crucial factor is the induction of carbonate precipitation by production and consumption of extracellular polymeric substances (EPS) through different processes (e.g. Trichet and Défarge, 1995; Défarge et al., 1996; Reitner et al., 2000; Reid et al., 2000, 2003; Dupraz et al., 2004; Dupraz and Visscher, 2005; Hendry et al., 2006). These processes were suggested to be more important for the calcification process than the microbial activity itself (Riding, 2000; Arp et al., 2001; Dupraz et al., 2004; Gautret et al., 2004). EPS is highly hydrated mucilage, which is composed of a variety of molecules such as polysaccharides and amino acids (Costerton et al., 1995; Decho, 2000) in that the microbial cells are embedded (Decho, 1990a; b). EPS has a high binding capacity
for cations (mainly Ca²⁺, Mg²⁺) because of negatively charged carboxyl-groups, which initially impede carbonate precipitation (Hartley et al., 1996; Dupraz and Visscher 2005). The carbonate precipitation is activated by different microbial and/or chemical alterations of EPS. The three most appropriated processes are introduced here:

1. Heterotrophic bacterial degradation of EPS leads to the release of cations, which increase the saturation index and carbonate is precipitated by replacing the decaying EPS polymers by (high-Mg-) calcite (Dupraz et al., 2004, Decho et al., 2005; Visscher and Stolz, 2005).

2. The carboxyl-groups in the EPS matrix create a molecular template and therefore carbonate precipitation is activated via organomineralization (Trichet and Défarge, 1995).

3. The saturation of the carboxyl-groups with cations annuls the inhibition of precipitation; hence, the mineral nucleation inside the EPS matrix can start (Arp et al., 2003).

Moreover, laboratory experiments have shown that carbonates precipitated because of an increased availability of Mg²⁺ ions due to sulphate removal by sulphate-reducing bacteria (Vasconcelos et al., 1995; Castanier et al., 1999; 2000; Sagemann et al., 1999, van Lith et al., 2003a; b).

The present study deals with the microbial crusts from the post-LGM coral reef interval of Tahiti, which was recovered during IODP Expedition 310. The purpose of this study is to unravel the genesis of the Tahitian reef-microbialites and give answer to two main questions.

1. Which microbes and microbial processes induced the carbonate precipitation?

2. Which environmental conditions led to the genesis of these thick and voluminous microbialites during the post-LGM?

The microbes were identified by lipid biomarker analysis. Lipid biomarkers are molecular fossils, which are degradation products of intact membrane lipids, for example. Some of these lipids have a fossilization potential that is far superior to that of their producers. Lipid biomarkers have been reported from rocks as far back as the Proterozoic (e.g., Summons et al., 1990; Logan et al., 1997; 1999; Brocks et al., 2005) and the Archean, but that is controversially debated (e.g., Brocks et al. 2003 and references therein). Since these molecular fossils are preserved in a precipitation product of their own metabolic activity, they can be used as evidence for the syngenicity of molecular fossils and the enclosing deposit (carbonate). For instance, biomarkers of sulphate-reducing bacteria are potentially well preserved in authigenic carbonates as old as the Late Pennsylvanian (Late Carboniferous; Birgel et al., 2008b). Complementary to the lipid biomarker analysis, other geochemical parameters are used to evaluate the environmental conditions during the genesis of Tahitian microbialites. These were the lipid biomarker-specific carbon isotopes, the element composition, calcium carbonate and organic carbon contents, and the stable
isotopic composition of oxygen and carbon in the calcium carbonate and the organic carbon of the microbialites.

4.3.2 Study area and materials

Tahiti is located at 17°50’S and 149°20’W in the central Pacific Ocean (French Polynesia, Society archipelago) on top of a hot spot that was volcanically active during the last million years (e.g., Duncan and McDougall, 1976; Searle et al. 1995). The subsidence rates are uniform in the range of 0.15 mm/yr (Pirazzoli and Montaggioni 1988; Le Roy 1994) to 0.25 mm/yr (Bard et al. 1996). During IODP Expedition 310, more than 600 m of core material were recovered. U-series dating of selected corals demonstrate that the drilled cores cover the major part of the Tahitian post-LGM reef sequence (16,000 to 8,000 yr BP; Camoin et al., 2007).

A set of samples were analyzed from the site Tiarei in the North and from the site Mara’a in the South of the island (Fig. 35). Out of these samples, 13 selected microbialites analyzed with specific methods are given in Table 10. Today, fluvial input of material eroded from the volcanic island is most voluminous near the site Tiarei in the North of Tahiti, where the largest drainage system of Tahiti, the Papenoo River, discharges (Fig. 35). It is assumed that this pattern was already active during the late Pleistocene (Hildenbrand et al., 2004; 2006).

The deglacial reef framework is constructed by zooxanthellate corals (mainly massive Porites sp., Pocillopora sp. and Acropora sp.) that show partial encrustation by coralline red algae. The corals or coralline algae, respectively, are subsequently encrusted by microbialites. The primary macroporosity of the deglacial coral reef framework is almost entirely encrusted by microbialites (up to 80 vol. % of the cores). The main growth direction of the microbialites is upwards, but microbial encrustation also occurs at the down-facing sides of the corals (Westphal et al., in prep.). The typical thickness of the Tahitian microbialite

![Fig. 35 Map of Tahiti including Tiarei, Faa’a, and Mara’a areas with indicated drilling sites (modified after Camoin et al., 2003; Heindel et al., in press).](image-url)
crusts ranges between 2 and 8 cm, but thicknesses of up to 15 cm are also common. The
correlated clouds on peloidal microfabrics of the microbial crusts imply a microbial origin (e.g.,
Chafetz, 1986; Gerdes et al., 1994; Kazmierczak et al., 1996; Westphal et al., in prep). The
Tahitian microbialites occur in two growth habits: a laminated microbialite and a later
dendritic microbialite (cf., Camoin et al., 2007; Westphal et al., in prep); (Fig. 36) In this
study, laminated microbialites were subdivided into (1) strongly laminated microbialite
(distinct and dark laminae) and (2) faintly laminated microbialite (lighter laminae). Both
laminated growth patterns are more homogeneous than the dendritic microbialite and
exhibit less visible microporosity. The dendritic microbial crusts are microporous and
include more detrital components (Camoin et al., 2007; Westphal et al., in prep.). The
faintly laminated microbialites are more common at the site Mara’a, consisting of relatively
light-colored carbonate, which is intermediate with respect to homogeneity and visible
microporosity. The microbialites of the Tiarei site are dark colored and have a highly
variable porosity (Westphal et al., in prep.; Fig. 36). Generally, the lamination is parallel to
the encrusted surface. Single laminae reach up to 2 mm in thickness but usually are less
than 1 mm thick.

<table>
<thead>
<tr>
<th>Site</th>
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<td>M0016A</td>
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<td>1W</td>
<td>66-73</td>
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</table>

**Table 10:** IODP sample code, study sample code, water depth, growth pattern of the microbialites, and undertaken analyses. s lam – laminated microbialite, f lam – faintly laminated microbialite, dend – dendritic microbialite, sed – sediment, LBM – lipid biomarkers, XRD – X-ray diffraction, LA-ICP-MS – laser ablation inductively coupled plasma mass spectrometry, δ¹³C – compound-specific carbon isotopic ratios, δ¹³C_{org} – carbon isotopic ratios of the total organic carbon.
**Fig. 36** The different growth patterns of the Tahitian microbialites from the sites Tiarei and Mara’a. 

**A.** Laminated microbialite from Tiarei (TAH 15), which encrusts coralline algae growing on a coral. 

**B.** Dendritic microbialite from Tiarei (TAH 10). 

**C.** Strongly laminated microbialite from Mara’a with *Halimeda* filled pockets (TAH 19). The *Halimeda* plates were removed for biomarker analysis. 

**D.** Dendritic microbialite from Mara’a. Coral encrusted by coralline algae (white layer) at the base. 

**E.** Strongly laminated microbialite from Mara’a (TAH 4), which encrusts coralline algae on top of a coral. 

**F.** Faintly laminated microbialite from Mara’a (TAH 13), which encrusts a coral.
4.3.3 Methods

**Powder X-ray diffraction**

Two strongly laminated and two faintly laminated microbialites from the sites Mara’a and Tiarei, respectively, were decalcified and ground. The samples were measured with a Philips/Panalytical X’Pert Pro multipurpose diffractometer equipped with a Cu-tube (kα 1.541, 45 kV, 40 mA), a fixed divergence slit of 1/4°, a secondary monochromator, and the X'Celerator detector system. The measurements were done as a continuous scan from 3° to 85° 2 θ with a calculated step size of 0.016° 2 θ (calculated time per step was 100 seconds). X-ray diffraction (XRD) analysis and quantification of the mineral phases were based on the full-pattern method QUAX (Emmermann and Lauterjung, 1990; Vogt et al., 2002). Abundant amorphous silicate (SiO₂), Fe/Mn-oxides, and Fe/Mn-hydroxides might cause interferences during XRD, introducing a larger error in the quantification. The standard deviation for clay minerals (phylllosilicates) is ± 5-10%, for plagioclase, pyroxene, magnetite, and pyrite ± 2-5%.

**Elemental composition**

For the elemental analysis with laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) one strongly laminated microbialite from the site Mara’a was selected (Fig. 36, Table 10). A thick section (80 µm) was prepared, on which a 3 cm transect perpendicular to lamination was measured (Fig. 37). The sample was ablated by a laser beam (irradiance: ~ 0.36 GW/cm²) with a pulse rate of 5 Hz. Ablation spot diameter was 100 µm and the spacing between the spot centers was approximately 300 µm. A helium flow of 0.39 l/min transported the ablated material out of the sample chamber and was admixed with argon before entering the plasma. Each spot was cleaned with a short laser pulse before starting the ablation for the measurement. The measurements of the elements were performed with a NewWave UP193 Solid State Laser Ablation System (l = 193 nm) connected to a Thermo-Finnigan Element 2 sector field ICP-MS. This technique enables the simultaneous analyses of several elements. Elemental concentrations were derived from measuring the following isotopes: ²⁹Si, ²⁷Al, ⁵⁷Fe, ¹³⁸Ba. The data were calibrated against the NIST610 glass standard assuming the composition after Pearce et al. (1997). The NIST-610 standard was measured after every 10th sample. Calcium (⁴⁴Ca) was used as internal standard, assuming a concentration of 40.04 wt. % in the sample (equivalent to pure calcium carbonate). The error in this assumption affects the absolute element concentrations, but not the element:Calcium (Ca) ratios used in this study. The proportion of the elements with respect to the bulk calcium carbonate (wt. %) was calculated with the equation: element oxide (wt. %) = element (mol) / Ca (mol) : [element (mol) / Ca (mol) + 1] * 100, and given as element oxides. The raw data were evaluated with the GeoPro2 (CETAC) software package that facilitates the blank subtraction and the subsequent conversion of intensities (counts per second) to concentrations (ppm). The relative
standard deviation for element:Ca ratios based on repeated analyses of the NIST610 and NIST612 standards was 3–5%.

**Stable isotopes of calcium carbonate and TOC**

For stable oxygen and carbon isotopic measurements of the calcium carbonate, the laminated and dendritic microbialites were sub-sampled by drilling with a hand-held dental drill. Isotopic analyses were performed on a Carbo-Kiel automated preparation system, connected to a Finnigan MAT 251 mass spectrometer. Standard deviations are < 0.07‰ for δ¹⁸O and < 0.05‰ for δ¹³C. The isotopic composition of the total organic carbon (TOC) of decalcified microbialite samples was measured with a Finnigan MAT Delta E mass spectrometer with a standard deviation of < 0.1‰.

**Calcium carbonate and TOC contents**

The calcium carbonate contents of microbialites and loose inter-reef sediment samples from both sites were measured with the Carbometer method (Müller and Gastner, 1971). The carbonate contents reported here are from averaged triple measurements. The internal error is < 1%. The TOC contents of microbialites from the sites Mara’a and Tiarei were measured on a LECO CS-200 elemental analyzer; in addition sediment samples were measured for comparison. The standard deviation is 0.016%.

**Lipid extraction and analysis and compound-specific carbon isotopes**

Initially, 20 microbialites from the sites Mara’a and Tiarei were chosen to represent the different growth patterns (strongly laminated, faintly laminated, and dendritic) and were analyzed for lipid biomarkers. The dendritic parts of some laminated samples (e.g., TAH 15, Fig. 36) were cut off and not used for lipid biomarker analysis. A minimum weight of 50 g for strongly laminated and faintly laminated microbialites and 80 g for dendritic samples was found to be required to obtain a reliable lipid biomarker signal. The strongly laminated and faintly laminated microbialites turned out to be most suitable for lipid biomarker analysis because of the tighter texture, which reduces contamination and microbial degradation after lithification. Only one dendritic sample yielded reproducible results. Overall, out of the 20 samples analyzed, seven samples (three strongly laminated, three faintly laminated, and one dendritic microbialite) proved to be suitable for biomarker analysis. In order to subtract background marine and terrigenous signals, we analyzed one loose inter-reef sediment sample. The decalcification of the microbialite samples, the extraction and column chromatography followed the protocol of Birgel et al. (2006, 2008a). Here, only the fatty acid fraction will be discussed. Methylesters (MEs) were prepared from free fatty acids by adding 1 ml bortriflourid (BF₃) in a screwcap vial (1 h, 70°C) to the fatty acid fraction. All fractions were measured with a gas chromatography (GC)-mass spectrometer (MS) using a Thermo Electron Trace MS equipped with a 30 m RTX-5MS fused silica column (0.32 mm i.d., 0.25 μm film thickness). The carrier gas was He. The GC temperature program was 60 °C (1 min) to 150 °C at 15 °C min⁻¹, to 330 °C at 4 °C min⁻¹ (hold 60 min).
Identification of individual compounds was based on GC retention times and published mass spectral data.

Compound-specific carbon isotope analyses were carried out with a Thermo Electron Trace GC chromatograph connected via a Thermo Electron combustion interface-III to a Thermo Electron Delta-Plus XP spectrometer. GC conditions were as above. Carbon isotope ratios are given as δ values (δ¹³C ‰) relative to the Vienna Pee Dee Belemnite (V-PDB) standard and are corrected for addition of carbon during preparation of ME derivates. Several CO₂-pulses of known δ¹³C values at the beginning and end of each run were used for calibration. Instrument precision was determined with a mixture of n-alkanes (n-C₁₅ to n-C₂₉) with known isotopic composition. Standard deviations are < 0.4‰. Each compound-specific isotopic value reported here is an average value derived from triplicate measurements.

4.3.4 Results

Element composition (LA-ICPMS and XRD)

Elemental concentrations were measured in the strongly laminated microbialite TAH 4 from the site Mara’a (Fig. 36, Fig. 37) and are expressed as ratios versus calcium. Al/Ca varies between 1 and 37 mmol/mol (mean: 8 mmol/mol) and the equivalent Al₂O₃ content ranges from 0.1 to 4 wt. % (mean: 1 wt. %). Si/Ca varies between 2 to 106 mmol/mol (mean: 22 mmol/mol; SiO₂: 0.2 to 10 wt. %, mean: 2 wt. %). Fe/Ca is between 1 to 60 mmol/mol (mean: 10 mmol/mol; FeO: 0.1 to 6 wt. %, mean: 1 wt. %). Ba/Ca ranges from 4 to 45 μmol/mol (mean: 10 μmol/mol; BaO: 0.0004 to 0.004 wt. %, mean: 0.001 wt. %). The microbialite sample shows eight major dark laminae (lamina 1 close to the base, lamina 8 close to the top of the microbialite; Fig. 37). The concentrations of Al, Si, Fe, and Ba are usually highest within these laminae. The highest concentrations of Al were measured in the laminae 2, 3, 4; of Si in laminae 9; of Fe in laminae 2, 4, 9; and the maximal value of Ba was found in laminae 6 and 9 (Fig. 37).

With Powder X-ray diffraction analysis, clay minerals (phyllosilicates), pyroxene, and plagioclase were found in significant concentrations at both sites, but more abundant in the microbialites from Tiarei (n=2). Magnetite is slightly more abundant in the microbialites from Mara’a (n=2; Table 11), whereas pyrite was detected in significant amounts in the Mara’a samples (Table 11). Other minerals were only detected in trace amounts.

<table>
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<th>Site</th>
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<th>Plagioclase</th>
<th>Magnetite</th>
<th>Pyrite</th>
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<tr>
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<td>6.0</td>
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</table>

Table 11: Powder X-ray diffraction analysis done on two samples from Tiarei and two samples from Mara’a. Values given in wt. %, tr – trace amounts.
Fig. 37 Element/calcium (mmol/mol; μmol/mol) and oxide (wt.%) concentrations of Al, Si, Fe, and Ba of sample TAH 4 from Mara’a. The white line indicates the laser beam track perpendicular to the lamination (3 cm length). The black arrow indicates the growth direction of the microbialite.

**Stable isotopic composition of the calcium carbonate**

The isotopic composition of all microbialites from Mara’a and Tiarei range for δ¹⁸O values from −1.06 to 0.74‰ and for δ¹³C values between 0.34 and 3.87‰. At the site Mara’a, the strongly laminated microbialites (n=353) show δ¹⁸O values from −0.40 to 0.35‰ and δ¹³C from 2.73 to 3.63‰. The δ¹⁸O values of faintly laminated microbialites (n=62) range from −0.86 to 0.43‰ and the δ¹³C values from 2.80 to 3.58‰. The stable isotopes from dendritic samples have lower values (n=18): δ¹⁸O from −0.48 to 0.26‰ and δ¹³C from 3.06 to 3.74‰. At the site Tiarei, the laminated samples (n=166) show δ¹⁸O values from −0.31 to 0.74‰ and δ¹³C values from 2.99 to 3.87‰. The isotopic range of the dendritic samples (n=32) is wider than that of the laminated ones: δ¹⁸O values from −1.06 to 0.61‰ and δ¹³C values from 0.34 to 3.72‰. Compared to the samples from the site Tiarei, the strongly and
faintly laminated microbialites from Mara’a have a smaller range and a slight shift towards lower δ¹⁸O (average difference: −0.26‰) and δ¹³C values (average difference: −0.34‰) (Fig. 38).

![Graph showing δ¹⁸O vs. δ¹³C for different types of microbialites](image)

**Fig. 38** The stable isotopic composition of microbialites from Mara’a (strongly laminated, faintly laminated, and dendritic) and Tiarei (laminated and dendritic). The isotopic compositions plot in a smaller range within the field of previously published values from the Tahitian microbialites (Camoin et al. 1999, 2006).

**Calcium carbonate and TOC contents**

In microbialites the calcium carbonate contents vary from 63% in a dendritic microbialite from Tiarei to up to 98% in a laminated microbialite from Mara’a (Fig. 39). On average, samples from the Mara’a site have significantly higher carbonate contents (94%) than those from the Tiarei site (74%). Laminated samples at both sites have higher carbonate contents than dendritic samples. At the Mara’a site, the strongly laminated microbialites (n=9) contain 93 to 98% carbonate, the faintly laminated microbialites (n=3) 93 to 94%, and the dendritic microbialites (n=9) 89 to 96%. The strongly laminated microbialites (n=7) from the Tiarei site contain 69% and 90% carbonate and the dendritic ones (n=10) between 63% and 96% (Fig. 39). The control samples of lose sediment have carbonate contents from 63% (Tiarei; n=4) to 93% (Mara’a; n=3).

Generally, the TOC contents of the microbialite samples are low (range: 0.05 - 0.22%, average 0.1%). The faintly laminated microbialites at Mara’a show the overall highest TOC contents (n=3, range 0.06 to 0.22%). The strongly laminated microbialites (n=9) from site Mara’a range from 0.07 to 0.11%, whereas TOC contents of the dendritic microbialites (n=9) range from 0.06 to 0.16% (average of all samples from Mara’a: 0.11%; Fig. 39). The samples from the site Tiarei generally show lower TOC values: laminated microbialites
(n=7) here show TOC contents from 0.07 to 0.12% and dendritic microbialites (n=10) from 0.05 to 0.15% (average of all samples from Tiarei: 0.10%); (Fig. 39). The TOC contents of the control samples of lose inter-reef sediment show similar values to those of the microbialites and range from average values of 0.1% (Mara’a; n=2) to 0.2% (Tiarei; n=3).

**Carbon isotopes of TOC**

The TOC was extracted from laminated microbialites, one from Mara’a and two from Tiarei. The triplicate measurements of the isotopic compositions of the TOC show a narrow range from −19.8 to −19.2‰ (Mara’a: −19.4 to −19.2‰; Tiarei: −19.8 to −19.3‰). The δ13C values are slightly less depleted in 13C at the Mara’a site (average difference: 0.23‰); (Fig. 42, in discussion).

**Lipid biomarkers (fatty acids)**

Short chain n-fatty acids from C14 to C23 (Fig. 41) comprise 41 to 65% of the fatty acids detected in microbialites from the site Mara’a (average: 49%) and Tiarei (average: 46%). The inter-reef loose sediment sample contains 76% (Fig. 40; Table 12a, b; 13). In all samples, short-chain fatty acids are maximizing at C16:0 and C18:0. Monounsaturated acids were detected in trace amounts with the exceptions of C18:1ω7 and C18:1ω9.

Long-chained n-fatty acids range from C24 to C30 (Fig. 41) and comprise 7 to 21% of the
fatty acids in microbialites (average at Mara’a: 12%; average at Tiarei: 9%). The sediment sample shows 4% (Fig. 40; Table 12a, b; 13). The long-chain fatty acids are maximizing at C\textsubscript{24:0} and C\textsubscript{26:0}.

Terminally-branched (iso- and anteiso) fatty acids from C\textsubscript{15} to C\textsubscript{19} (Fig. 41) enclose 9 to 29% of the fatty acids in microbialites from the site Mara’a (average: 19%) and from the site Tiarei (average: 21%). The iso- and nteiso fatty acids in the sediment comprise 6% of all fatty acids (Fig. 40; Table 13). The most abundant terminally-branched fatty acids are iso- and anteiso C\textsubscript{15} and iso- and anteiso C\textsubscript{17} (Fig. 40; Table 12a, b; 13). Iso-branched fatty acids are predominating over anteiso-fatty acids and range between 4 and 25% of all fatty acids (Mara’a: 17%; Tiarei: 15%; sediment sample: 4%; given as average values), whereas anteiso-branched fatty acids vary from 0 to 6% (Mara’a: 4%; Tiarei: 5%; sediment sample: 2%; given as average values).

**Fatty acid-specific carbon isotopes**

The compound-specific δ\textsuperscript{13}C values of short-chain n-fatty acids from microbialites vary from −20.8 to −19.0‰ (average Mara’a: −19.7‰; Tiarei: −20.3‰). The sediment δ\textsuperscript{13}C value averages at −21.5‰ (Fig. 42, in discussion). Long-chain n- fatty acids show compound-specific δ\textsuperscript{13}C values between −23.5 and −19.2‰ (average Mara’a: −20.2‰; Tiarei: −23.3‰). The sediment δ\textsuperscript{13}C value averages at −21.0‰. The iso-fatty acids in microbialites show values from −18.8 to −17.2‰ (average Mara’a: −17.5‰; Tiarei: −18.7 ‰), whereas the anteiso-fatty acids range between −21.3 and −19.5‰ (average Mara’a: −20.6‰; Tiarei: −20.0‰). The sediment shows δ\textsuperscript{13}C values for iso-fatty acids of −19.7‰ and for anteiso-fatty acids of −23.3‰. Generally, the iso-branched fatty acids have higher δ\textsuperscript{13}C values than the anteiso-branched fatty acids. The δ\textsuperscript{13}C values of the iso-/anteiso fatty acids detected in the loose inter-reef sediment are depleted in \textsuperscript{13}C compared to the microbialites (average difference δ\textsuperscript{13}C (microbialite-sediment): 2.3‰). Comparing the two sites Mara’a and Tiarei, the δ\textsuperscript{13}C values of the iso-/anteiso fatty acids are slightly higher at the Mara’a site (average Mara’a: −19.1‰; average Tiarei: −19.3‰); (Fig. 42, in discussion).
Fig. 40 Contents of fatty acids (wt. %) measured on two microbialites from Tiarei (dendritic and laminated), five microbialites from Mara’a (strongly and faintly laminated), and one sediment sample from Mara’a.

Fig. 41 Gas chromatogram (total ion current) of the fatty acid fraction from a Tiarei microbialite (TAH 15). Circles: n-alkanes; triangles: iso- and anteiso-fatty acids; diamonds: C₁₁₈:₁₄:₀ and C₁₈:₁₄:₀; is – internal standard, i – iso, ai – anteiso.
4.3.5 Discussion

*Interpretation of lipid biomarkers and stable isotopes*

Biomarker data of ancient reef-microbialites are very rare in the published literature (e.g., Reitner et al., 2000). To our knowledge, the present study is the first where lipid biomarkers of deglacial reef-microbialites have been successfully analyzed. A set of abundant molecular fossils has been detected, which include specific biomarkers that allow for deepening the understanding of the processes leading to microbialite development. Generally, the detected saturated (mainly C$_{14}$:0 and C$_{16}$:0) and unsaturated short-chain n-fatty acids (mainly C$_{18:1\,\omega9}$) are rather unspecific since they can be attributed to various marine autochthonous sources such as phytoplankton (e.g., Volkmann et al., 1989; Viso and Marty, 1993; Pond et al., 1998), zooplankton and diverse benthic organisms (e.g., Albers et al., 1996; Graeve et al., 1997), and marine bacteria (Parkes and Taylor, 1983; Gillan and Sandstrom, 1985), such as sulfide-oxidizing bacteria (McCaffrey et al., 1989; Grant, 1991) and cyanobacteria (e.g., Wakeham, 1995; Albers et al. 1996; Graeve et al., 1997).

Principally, long-chain n-fatty acids (C$_{24:0}$-C$_{30:0}$) are typically derived from higher land plant leaf waxes (Elington et al., 1968; Simoneit, 1978; Naraoka and Ishiwatari, 2000). Their occurrence is usually attributed to fluvial input or eolian transport (e.g., Birgell et al., 2004), but they are also known to be derived from marine bacteria or algae (Naraoka and Ishiwatari, 2000; Shi et al., 2001).

Terminally-branched fatty acids are common molecular fossils of various bacterial cellular and membrane lipids (e.g., Edlund et al., 1985; Goossens et al., 1986; Kaneda, 1991). Among those, various sulphate-reducing bacteria are known to produce *iso-* and *anteiso* fatty acids (C$_{15:0}$ and C$_{17:0}$; Fig. 41) (e.g., Perry et al., 1979; Taylor and Parkes, 1983; Wakeham and Beier, 1991; Elvert et al. 2003). Furthermore, they appear to be absent from cyanobacterial lipids (e.g., Cohen and Vonshak, 1991).

The stable oxygen and carbon isotope values of the calcium carbonate are close to those obtained on high-Mg-calcite cements that were precipitated in equilibrium with sea-water (e.g., Land and Goreau, 1970) and plot in a smaller area within the field of previously published values from the Tahitian microbialites (Camoin et al., 1999, 2006; Fig. 38). Similar values were reported from microbialites of Vanuatu (Cabioch et al., 2006) and cryptic microbialites of Lizard Island (Great Barrier Reef, Australia) and St. Croix (US Virgin Islands; Reitner et al., 2000).

*Putative deglacial microbial communities*

Microbialites from both sites studied here show almost similar abundances of marine (Tiarei: 44 to 49%; Mar'a: 42 to 65%), terrestrial (Tiarei: 8 to 9%; Mar'a: 7 to 21%) and bacterial (*iso-*/anteiso) lipid markers (Tiarei: 17 – 24%; Mar'a: 9 – 29%). The most extreme values in microbialites represent the samples TAH 11 (65% marine markers; 7%
terrestrial markers; 9% bacterial markers), TAH 12 (29% bacterial markers), and TAH 13 (21% terrestrial markers); (Fig. 40; Table 13). The high contents in the samples (cf., Fig. 41) and the abundance of the iso- and anteiso fatty acids of average 20% (Mara’a and Tiarei) of all fatty acids are unusual for modern coral-reef carbonates (Reitner et al., 2000). The loose inter-reef sediment shows a predominance of marine lipids (76%) over terrestrial (4%) and bacterial lipids (6%; Fig. 40; Table 13). The sediment represents the “normal” marine and terrigeneous background signal, which is clearly differentiated from the significant bacterial signal found in the microbialites.

Enzymatic carbon isotope fractionation of heterotrophic sulphate-reducing bacteria is low, which might explain the very small shift between the δ¹³C values from TOC (Mara’a: −19.3‰, Tiarei: −19.5‰, average: −19.4‰) to the compound-specific δ¹³C values of the iso- and anteiso fatty acids (Mara’a: −19.1‰, Tiarei: −19.3‰, average: −19.2‰) in the microbialites from both sites (Fig. 42). Experiments with pure cultures of four species of sulphate-reducing bacteria have shown that the carbon isotope fractionation process of three of the four heterotrophic grown sulphate reducers were small within a range of 0 to 2‰ between the substrates, acetate or lactate and CO₂, and the cell biomass (Londry and Des Marais, 2003; Londry et al., 2004).

![Graph](image)

**Fig. 42** Isotopic composition and of specific compounds (δ¹³C): iso-/anteiso- fatty acids C₁₅/₁₇, short-chain n-fatty acids C₁₆-2₃, and long-chain n-fatty acids C₂₄-₃₀, and of the total organic carbon (TOC). s lam – strongly laminated, f lam – faintly laminated, dend – dendritic, sed – sediment.

Alternatively, the slight shift from the δ¹³C values of the TOC towards higher δ¹³C values of the iso- and anteiso C₁₅/₁₇ could point to anaerobic phototrophic bacteria (Barghoorn et al., 1977; Sirevåg et al., 1977), which are also able to activate carbonate precipitation. However, clear signals for the involvement of anaerobic phototrophs in the Tahitian deglacial microbial community are not present. Earlier reports have supposed the participation of
cyanobacteria in the formation of Tahitian microbialites; however these studies are lacking data from biomarker analysis (Camoin et al., 1999; Gautret et al., 2006). During this study, no lipid biomarkers of cyanobacteria were found, such as n-heptadecane and methyl-branched heptadecanes (e.g., Han et al., 1968; 1969; Gelpi et al., 1970; Thiel et al., 1997). Depths profiles in modern hypersaline cyanobacterial mats show a rapid decrease of concentrations of heptadecanes within the upper 2 mm (Wieland et al., 2008). Thus, the absence of clear cyanobacterial marker could also be the result of microbial degradation and a later overprint of the phototrophic signature by heterotrophic processes within the microbial mat (Andres et al., 2006; Wieland et al., 2008).

Overall, the high portion of the bacterial biomarkers (iso-/anteiso C\textsubscript{15/17}), the very low carbon isotopic fractionation, and the framboidal pyrite, which was found in the microbialites (XRD results; see also SEM observations in Westphal et al. in prep) point to sulphate-reducing bacteria, which were involved in the post-LGM microbial community.

**Putative modes intensifying the primary productivity**

The Al and Si concentrations in the microbialites and the terrigeneous fraction, which mainly is composed of basalt-derived (pyroxene, plagioclase, and magnetite) and clay minerals, reflect the largely basaltic composition of the island of Tahiti (cf., Duncan and Mc Dougall, 1976). As for Al and Si, basalt and its weathering products are potential local sources for the elevated Fe contents in the microbialites. The solid-phase of biogenic Ba (barite, BaSO\textsubscript{4}) is formed in the upper ocean and sinks to the seafloor. The Ba export from the upper ocean is closely correlated with the export of organic carbon (Dymond et al., 1992). Because of the high burial efficiency (between 15 and 30%), higher than that of organic carbon, the Ba accumulation rates can be used as proxy for palaeoproductivity (Dymond et al., 1992). A correlation between marine barite accumulation rates and productivity in the equatorial Pacific was observed (Paytan et al., 1996). The dark laminae of the Tahitian microbialites are characterised by elevated concentrations of Al, Si, Fe, and Ba compared to the light-colored laminae. The clear lamination of dark- and light-colored laminae could point either to a cyclically intensified input of basalt-derived weathering products, or to a periodically increased carbonate precipitation under constant basalt-derived input (Westphal et al., in prep). One possibility is that increased humidity during the post-LGM, combined with the rapid sea level rise, which flooded the coastal regions of Tahiti, has led to periods of enhanced sediment supply relative to uniform microbialite growth that primarily created the lamination. In any case, the post-glacial terrigeneous influxes are assumed to have provided high amounts of dissolved inorganic nutrients to the reef-ecosystem off Tahiti. Increased dissolved inorganic nutrients-levels would have intensified the primary productivity during the post-LGM. A similar relationship with increased fluvial nutrient supply has been proposed for the development of the reef-microbialites off the volcanic island of Vanuatu during the last deglaciation (Cabioch et al., 2006).
**Microhabitats for microbialite formation in Tahitian coral reefs**

Microbioerosion in corals and encrusting microbialites revealed reducedillumination, which was explained by increased nutrient supply condensing the photic zonation (telescoping effect); (Heindel et al., in press). Intensified primary productivity could have led to the increased formation of so called marine snow, i.e. aggregate development through biological uptake by phytoplankton/zooplankton and bacteria, which convert DIN into particulate organic matter (e.g., Short et al., 1995; Fabricius and Wolanski, 2000; Yentsch et al., 2002). This would have reduced light penetration and therefore the lower depth limit for coral growth (e.g., Fabricius and Wolanski, 2000). When deposited on corals, marine snow buries the polyps, which try to survive by increasing the production of mucus. Experimental studies show that coral polyps could not remove marine snow by mucus exceeding specific quantities (e.g., Fabricius and Wolanski 2000; Fabricius et al., 2003; Wild et al., 2004; Weber et al., 2006). The development of anoxic microenvironments on the coral heads was observed in the marine snow-mucus-mixture that is inhabited by various bacteria (in particular heterotrophs) covering the coral heads (Meikle et al., 1988; Weber et al., 2006). While the increase of biomass probably stressed the zooxanthellate corals, it is assumed that the biomass supply was not ideal for bacteria. Cyanobacteria also would provide organic matter for bacteria of deeper layers in microbial mats (e.g., Teske et al., 1998; Fenchel et al., 1998; Paerl et al., 2001); however evidence for cyanobacteria was not found. Additionally, the relative high water energies in a coral reef could have influenced the anoxic milieu to bacteria’s disadvantage. Stressed bacterial cells are known to produce elevated EPS, probably for protective and metabolic functions (Dade et al. 1996; Decho, 2000; Riding, 2000). Recently, the sulphate reducers were found to produce large amounts of EPS, which promoted carbonate nucleation under laboratory conditions (Braissant et al., 2007). A similar scenario may apply for the deglacial Tahiti coral reefs.

Such anoxic microhabitats could have developed in cryptic niches with low water energy, some decimeters to a few meters below the coral reef-top, but within the photic zone. The photic setting is proven by endolithic chlorophytes and by coralline red algae intercalated in microbialites (Heindel et al., in press; Westphal et al., in prep.). The marine snow-mucus-mixture probably provided the habitat and the organic matter for sulphate-reducing bacteria, which produced high amounts of EPS. The carbonate precipitation might have been activated by different bacterial and/or chemical alterations of EPS, as introduced in the beginning. The level of microbialite growth kept pace with the deglacial reef accretion so that the growth level remained in the same relative position shortly below the coevally flourishing corals at the reef-top.

Most likely, the processes described in this study represent a part of the complete microbial activities; other types of microbes such as anoxogenic and oxygenic phototrophs might also be involved. A recent study on modern microbial mats from Tahiti postulates sulphate-reducing bacteria and iron oxidizers as major players (Warthmann, et al. subm).
Our results imply that it was not high concentrations of bacteria that produced the outstanding volume of microbialites in the post-LGM coral reefs off Tahiti, but a relatively specific community of stressed bacteria, dominated by sulphate-reducing bacteria, which were responsible for inducing the processes leading to carbonate precipitation.

4.3.6 Conclusions

Elevated sediment influx from the volcanic island of Tahiti to the barrier reef-ecosystem during last deglacial times has led to elevated trophic levels and thus to increased primary productivity. Increased availability of organic matter would have strongly promoted development and activity of microbial communities, which mediated carbonate precipitation in anoxic microhabitats. The present study shows for the first time by means of biomarker analysis, which microbes and processes probably have been involved in the microbialite formation. Sulphate-reducing bacteria were possibly accompanied by anoxygenic phototrophic bacteria and other microbes. The outstanding volume of microbialites appears to be the response of stressed heterotrophic bacterial communities to a moderate enrichment of the environment in organic matter that still allowed the corals to flourish. The new model of continuous cryptic reef-microbialite formation in a growth level immediately below the reef-top implies that the proposed scenario was “normal” for the last deglacial environment.

Acknowledgements. – This research used samples and/or data provided by the Integrated Ocean Drilling Program (IODP) as part of the IODP Expedition 310 Science Party research of H.W. and is part of K.H.’s PhD thesis. We are grateful to the 310 Science Party colleagues and co-chiefs for the collaboration. The Bremen Core Repository team is acknowledged for their unceasing support. The MARUM (DFG-Research Center / Excellence Cluster “The Ocean in the Earth System”) is acknowledged for providing infrastructure and support for this research. The GC-MS and isotopic measurements were performed at the MARUM; the LA-ICP-MS, XRD, and TOC analysis were done at the Geosciences Department of University of Bremen. We thank Brit Kockisch for the TOC measurements, Jim Hendry for fruitful discussions, Andreas Klügel for support at the LA-ICPMS, Christoph Vogt for XRD analysis, and Xavier Prieto Mollar for lab assistance. The study was funded by the Deutsche Forschungsgemeinschaft Project WE 2492/8 to HW and PE 847/5 to JP

Appendix, see following pages, including the Tables 12a, b and 13.
Table 1.2: Composition of the detected compounds (dry weight% and the compound-specific carbon isotope values, δ13C, 99% confidence interval)

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Note: The dry weight% and δ13C values are specific to the compounds detected in the samples. The confidence interval (99%) for δ13C values is also provided.

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| Table 12b: (continued) Contents of the detected compounds/fatty acids (ng lipid/g rock) and the compound-specific carbon isotopic values δ¹³C (%). s lam - strongly laminated, f lam - faintly laminated, dend - dendritic, sed - sediment, empty cell - trace amounts or not detected. |
### Table 13: Summary of all compound data (as a percentage)

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### Notes
- **Seire**: Percentages of Seire
- **Sample**: Percentages of Sample
- **Seminera**: Percentages of Seminera
- **Maria**: Percentages of Maria
- **Terra**: Percentages of Terra
- **N**: Number of samples
- **Compound groups**: Various compound groups listed
- **Type of sample**: Seire, Sample, Maria, Terra
- **She**: Various notes or comments related to the data
4.4 Microbialites as contemporaneous framework components of coral reefs – the trophic paradox (deglacial of Tahiti, IODP 310) (abstract)

Hildegard Westphal¹, Katrin Heindel¹, Marco Brandano², Jörn Peckmann¹, Guy Cabioch³

1) MARUM – Centre for Marine Environmental Sciences, University of Bremen, Leobener Straße, 28359 Bremen, Germany
2) Dipartimento di Scienze della Terra, Università di Roma “La Sapienza”, Ple Aldo Moro, 5. I-00185 Roma, Italy
3) IRD-Nouméa, BP A5, 98.848 Nouméa CEDEX, Nouvelle-Calédonie

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Abstract. – Marine microbialites associated with hermatypic corals are known from several intervals of Earth’s history, including the latest deglacial leading from the Pleistocene to the Holocene. In contrast, in the modern world no such massive occurrences are known to form. Here, deglacial microbialites from Tahiti (IODP 310) are studied. The paradox of the co-occurrence of oligotrophic corals with microbialites that generally favour elevated trophic levels has previously led to the assumption that the microbialites are considerably younger than the coral framework, and have formed in deeper storeys of the reef edifice; or that they represent a severe disturbance of the reef ecosystem. In contrast, the present study demonstrates that microbialite encrustation has taken place coeval to coral growth, which implies an encrustation horizon immediately below the reef-top. Encrustation has taken place under photic conditions, even though cyanobacteria appear not to play a role in the microbialite precipitation. This immediate encrustation explains the high in situ recovery of the IODP 310 cores – the reef has been stabilized instantaneously, leading to high robustness against reworking by storms, but also to a comparably low permeability that improved the drilling results. The question about the reasons for the voluminous development of microbialites in the deglacial reefs of Tahiti (up to 80% of the cores) is still not solved. An intensified primary productivity caused by fluvial or groundwater transport of erosional products from the volcanic hinterland, which increased microbial activities, appears to have been a possibly cause. However, the coral community seem to be undisturbed and no breaks in the development of the succession were detected. The fact, however, that voluminous deglacial reef-microbialites are restricted to volcanic islands, implies that moderately elevated trophic conditions favour this type of microbialite formation. Clearly, the genesis of the reef-microbialites of Tahiti did not follow a serious disturbance such as drowning. The microbialites are no “desaster forms”; rather their development represent a continuous process that appears to have been a normal part of the ecosystem at that time.
5 SUMMARY AND OUTLOOK

The following paragraphs summarise the major conclusions from the manuscripts, answer the questions phrased at the beginning (Chapter 3), address new questions that arose from the results and provide some perspectives for future work.

Most of the objectives pointed out at the beginning of this study were solved:

- **The photic zonation and the palaeobathymetry of the deglacial coral reef setting were reconstructed; additionally, the timing of the encrustation of the coral framework by microbialites was solved.**

  Microbioerosion indicates photic conditions during coral growth and microbialite formation. Moreover, detected ichnoecoenoses in corals, coralline algae, and microbialites are similar in the middle and top ranges of the deglacial reefs, which imply uniform photic conditions (dysphotic) and therefore uniform palaeobathymetries for coral growth and microbialite formation. Radiocarbon datings corroborate the finding that the encrustation was almost at the same time as coral growth. At the base, the endolithic traces in the corals indicate shallow euphotic zone II to deeper euphotic conditions, whereas towards the upper ranges of the post-glacial reefs the microbioerosion in corals implies deeper palaeobathymetries represented as dysphotic conditions. In contrast, ichnoecoenoses in coralline algae and microbialites from the base of the succession reflect dysphotic conditions, which indicate deeper palaeobathymetries than those indicated in the corals. Hence, reflecting the sea-level rise. Again this is corroborated by radiocarbon dates, which show a larger time gap between coral growth and the encrustation by microbialites compared to the top and middle ranges of the reefs. Throughout the entire deglacial reef sequence, microbioerosion shows an encrustation within the photic zone. This agrees with coeval coral growth and microbialite formation.

- **Evidence for changed trophic conditions and an intensified primary productivity during the last deglaciation was found. Accordingly, the previously proposed dependence of reef-microbialite development from the volcanic hinterland was confirmed.**

  The sea-level rise can not fully explain the unusual dominance of ichnotaxa typical for deeper photic zones. Consequently, a nutrient-driven reduction in illumination might have suppressed the development of the shallowest euphotic ichnoecoenoses. Some of the detected low-light specialists among the microbioeroders are known to prefer environments enriched in nutrients, supporting this theory. Enrichment in nutrients, derived from the volcanic island appears to have intensified the primary productivity, which is reflected in a telescoping effect. That would have strongly supported the sea-level driven shift from euphotic to dysphotic conditions along the deglacial succession. The elemental composition (Al, Si, Fe, Ba) of a laminated microbialite indicates a strong terrigeneous input of weathered basalt-derived minerals (pyroxene, plagioclase,
magnetite) from the volcanic island. Relative to carbonate precipitation rates, the accumulation of a large proportion of the minerals in horizontal layers is thought to have created the lamination of the Tahitian microbialites.

- **The Tahitian deglacial microbial community was partly identified. Due to this, the major process that initiated the formation of microbialites in the coral reefs during last deglaciation could be elucidated.**

Lipid biomarker analysis carried out on several microbialites from Tahiti reveal an unusually “fat” signal of terminally branched fatty acids (iso-anteiso-\text{C}_{15/17})\text{C}_{15/17}, which are typical biomarkers for sulphate reducers. Up to now, such high concentrations of iso-anteiso-\text{C}_{15/17} \text{C}_{15/17} lipids (up to 29% of all detected fatty acids) had not been found in authigenic carbonates from coral reefs. Carbon isotopic values of the total organic matter and the compound-specific δ\text{13C}\text{13C}-values of the iso-anteiso-\text{C}_{15/17} \text{C}_{15/17} fatty acids show an insignificant enzymatic fractionation of the carbon isotopes, which is characteristic for heterotrophic sulphate-reducing bacteria. The slight shift from the δ\text{13C}\text{13C} values of the TOC towards higher δ\text{13C}\text{13C} values of the iso- and anteiso \text{C}_{15/17} \text{C}_{15/17} fatty acids may alternatively point to anoxic phototrophic bacteria, which might be associated with sulphate reducers and therefore also involved in carbonate precipitation. The involvement of cyanobacteria in microbialite formation has been proposed in previous reports, but evidence for cyanobacteria was not found via lipid biomarker analysis. However, cyanobacterial markers might be degraded by other microbes or microbial processes and therefore are not detectable in such carbonates.

Concluding, the degradation of the increased biomass by sulphate reducing bacteria was most likely the major process, which induced the carbonate precipitation and therefore the genesis of the Tahitian microbialites.

- **A scenario involving the development of microhabitats for sulphate reducers and the putative sources of required biomass was proposed.**

The Tahitian deglacial scenario involves an enhanced primary productivity which is assumed to have led to the formation of so called marine snow. These aggregates are composed of organic matter derived from phyto- and zooplankton (primary producers) and of dissolved inorganic nutrients, which are provided in high quantities from the volcanic island. This marine snow is assumed to have been deposited on the corals in protected, cryptophotic niches (cryptic reefal habitat within the photic zone). Accumulation of marine snow on the coral heads resulted in an increased production of coral mucus, whereas the polyps try to remove the organic aggregates. It is suggested that anoxic microhabitats develop within the marine snow-mucus-mixture providing the appropriate habitat and the organic matter for bacteria. The suggested scenario requires stressed organisms: stressed zooxanthellate corals because of intensified biomass supply and stressed bacteria because of less ideal supply of biomass as well as not perfect conditions in the reefal habitat. Stressed bacteria, especially sulphate reducers are known
to produce high amounts of EPS. As described in the introduction (Chapter 1), EPS production and consumption initiates carbonate precipitation. This scenario leads to the assumption that a relatively specific community of bacteria, dominated by sulphate-reducing bacteria, induced the precipitation of carbonate in outstanding volumes.

To summarise, this study showed that the analysis of lipid biomarkers provides reliable results in identification of molecular fossils in authigenic reef-microbialites, similar to those of other types of fossil authigenic carbonates. The reliable usage of microbioerosion patterns for the evaluation of changes in trophic conditions was promisingly demonstrated during this research and is suggested for future applications. The presented investigations of diverse sedimentological, geobiological and geochemical patterns on these microbialites provide a better understanding of the environmental conditions and the genesis of the reef-microbialites during the post-LGM at Tahiti.

However, one objective is still open:

- **It still remains unclear, why this type of microbialite apparently stopped to form when the sea-level has stabilized.**

Apparently, the change in trophic conditions plays the major role in deglacial microbialite formation. Recent and past, Tahiti is located in the tropics influenced by a strong humid climate all-year. There are no obvious reasons for decreased erosional processes reducing the supply of basalt-derived nutrients to the modern coral reef ecosystems. Nevertheless, imaginable scenarios could be: (1) a reduced humidity compared to post-glacial climates, which reduced the fluvial influx of nutrient-rich sediments (even so, today humidity is high at Tahiti); and (2) changes in upward fluid migrations from the volcanic basement, which would reduce the intensity of basalt-seawater interaction and hence, decrease the nutrient-enrichment of the seawater.

Additionally, new questions arose which require further research:

- Did anoxygenic phototrophic bacteria play a significant role as member of the Tahitian post-glacial microbial community in microbialite formation?

- Did cyanobacteria in fact play no role or was their biomarker signature deleted by other bacteria and degradation processes?

- Could reef-microbialites of the “Tahitian type” be reliable proxies for past oceanographic and climatic reconstructions supplementary to zooxanthellate corals?

The analysis of the existing biomarker data-set for additional lipid biomarkers is suggested to solve the questions about the involvement of other microbes, such as anoxygenic phototrophs and cyanobacteria in carbonate precipitation. The microscopic zoom into the molecular level could also be used for the identification of microbial remnants in the microbial carbonates. Accordingly, the high-resolution technique of transmission microscopy (TEM) is proposed. Additionally, microbialites from the site Fa’a’a in the West
of Tahiti should be analysed for molecular fossils, microbiocerosion patterns, elemental composition, stable isotopic composition, microfabric, carbonate and TOC contents in order to compare with the interpreted environmental scenario at the sites Mara’a and Tiarei.

For evaluating the reliability of microbialites as climate proxy a high-resolution technique like micro-isotopic drillings is recommended to be performed at a MicroMill. These high-resolution measurements of oxygen and carbon isotopic values in microbialites are assumed to provide data on climate changes. However, the interpretation of isotopic variations in the microbial carbonates is far from trivial, taking in considerations that oxygen and carbon stable isotopes are strongly influenced by various factors and that the microbial carbonate is highly heterogeneous (including abundant carbonate of external origin; Chapter 2).

It is of most importance to follow up the question whether the reef-microbialites, which came up at several sites in the Pacific and Indian Ocean during the last deglaciation, are similar to the microbialites from Tahiti. A future project is proposed, which focus on the comparison of the reef-microbialites from Tahiti, Vanuatu and the Maldives. Drilled reef-cores from Vanuatu (South-West Pacific) and from the Maldives (Indian Ocean) exist, which contain microbialites. Few basic researches are available, focusing on these microbialites (Cabioch et al., 1999; 2006; Gischler, et al., 2008b). It is suggested, to extend these basic data-sets in order to gain a detailed sedimentological, geobiological and geochemical description to fully characterise these reef-microbialites, which seem to be a typical feature for post-LGM coral reefs in the Pacific and Indian Ocean. For that purpose, the application of the same multi-proxy approach is proposed, which was introduced in that thesis. Lipid biomarker analysis and the study of microbiocerosion patterns are applied to provide as reliable and promising data in the microbialites from Vanuatu and the Maldives as from Tahiti. The existing geochemical and sedimentological data-sets of the previous studies from Vanuatu and the Maldives should be extended by using more specific techniques like LA-ICP-MS (elemental composition), high-resolution micro-isotopic drillings performing at a MicroMill, and transemission microscopy.

Ongoing future investigations are an important pre-requisite to follow up phrased questions and to complete existing data-sets of microbialites. Especially the comparison of the different settings comprising reef-microbialites is needed for a full interpretation of the Tahitian and other reef ecosystems in terms of accurately reconstructing changing environments during the last thousands of years of Earth’s history.
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