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Microbialites and Micro-encrusters in Shallow Coral Bioherms (Middle to Late Oxfordian, Swiss Jura Mountains)

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KEYWORDS: MICROBIALITE – MICRO-ENCRUSTERS – HIGH-RESOLUTION PALAEOECOLOGY – CORAL BIOHERMS
– TROPHIC CONTROL – SWISS JURA – OXFORDIAN

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SUMMARY

Benthic microbial crusts (microbialites or microbolites) are an important component of Middle to Upper Oxfordian shallow-water coral bioherms in the Swiss Jura. They display stromatolitic (laminated), thrombolitic (clotted), and leiolitic (structureless) fabrics, which are distributed heterogeneously throughout the studied sections. The bioherms can be subdivided into coral-microbialite facies, microbialite-dominated facies, and sediment matrix.

Macroscopic and microscopic study reveals that microbialitic encrustations commonly occur in two layers. The first one is directly in contact with the substrate and composed of leiolite (locally stromatolite) and a well-diversified micro-encruster fauna; the second one fills the remaining porosity partly or completely with thrombolite and low-diversity micro-encrusters. The

growth of the first layer accompanies the growth of the coral reef and thus formed under the same environmental conditions. The second layer is the result of a moving encrustation front filling the remaining porosity (micro- and macrocavities) inside the reef, below the living surface. Both layers play an important role in early cementation. Phototrophic cyanobacteria probably intervene in the formation of the first encrustation zone, whereas heterotrophic bacteria associated to acidic, Ca²⁺-binding macromolecules in biofilms are thought to contribute to the thrombolite inside the reef body. When coral growth cannot take pace with microbialite development, the thrombolite front reaches the surface of the construction and finally covers the reef. The result is a thick interval of thrombolite, which can be interpreted as being related to an ecological crisis in coral-reef evolution.

A semi-quantitative analysis of the relative abundance of microbialite types and associated micro-encrusters permits to better constrain the processes leading to a reef crisis. Four micro-encruster associations can be distinguished, and each follows an evolutionary trend in the studied section: *Terebella-Tubiphytes* dominated, *Serpula-Berenicea* dominated, *Lithocodium* dominated, and *Bacinella* dominated. These trends are interpreted to reflect changes in environmental conditions. Bioerosion generally is at its maximum before and after abundant growth of microbialite.

According to microbialite-bioerosion relationships and shifts in micro-encruster associations, we propose that the evolution towards a coral-reef crisis involves four main phases: (1) An oligotrophic to low mesotrophic phase when low water turbidity and good oxygenation allow phototrophic metabolisms. This leads to a maximum of coral diversity and development of light-dependent micro-encrusters. (2) A low-mesotrophic phase when increased turbidity and slack water circulation reduce the photic zone and favor heterotrophic micro- and macrofauna. Bioerosion through bivalves increases. (3) A high-mesotrophic phase when environmental conditions are so bad that only microbialite can be

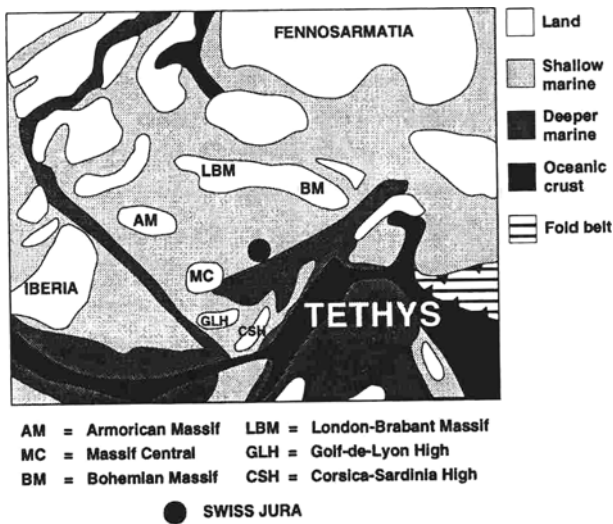


Fig. 1. Palaeogeography of the northern Tethys margin for the Oxfordian to Tithonian (modified from ZIEGLER, 1988).

produced. (4) A eutrophic phase when carbonate production is inhibited by high nutrient input and clay flocculation as a result of increased terrestrial run-off.

The observed evolutionary trends are not directly linked to changes in bathymetry, but sea-level fluctuations played an important role in opening and closing the depositional environments on the shallow platform. Climatic changes contributed in modulating the influx of siliciclastics and nutrients, and the alkalinity of the water. Demise of coral reefs generally coincides with low sea level and humid climate. Sea-level and climatic fluctuations and, consequently, the crises in reef growth are linked to orbital cycles in the Milankovitch frequency band.

1 INTRODUCTION

In the Late Jurassic, environmental conditions along the northern margin of the Tethys ocean were favorable for reef development (see literature cited in FLÜGEL & FLÜGEL-KAHLER, 1992; LÖSER et al., 1994; FLÜGEL et al., 1996). Palaeoecological studies in western Europe define three major groups of reefs: coral-dominated, sponge-dominated, and microbial reefs (LEINFELDER et al., 1993a, 1993b, 1994, 1996; WERNER et al., 1994). INSALACO (1996a, 1996b, 1998) and INSALACO et al. (1997) published on coral-reef nomenclature, classification and palaeoecology, and comprehensive palaeoecological research has been carried out in the Paris basin (BERTLING & INSALACO, 1998). These studies also present models of environmental control on microbial crusts. A very detailed study on a coral-microbialite reef in NW Germany has been carried out by HELM & SCHÜLKE (1998).

The Oxfordian coral bioherms of the Swiss Jura have first been illustrated by, e.g., THURMANN (1851), HEER (1865), GREPPIN (1867, 1870), and KOPY (1881-1889), and their stratigraphical and sedimentological context has been given by PÜMPIN (1965), GYGI & PERSOZ (1986), GYGI (1992), PITTET et al. (1995), PITTET (1996), and STRASSER et al. (1996). These reefs contain important amounts of microbialites and encrusting organisms, but very little work on the distribution and palaeoecology of the crusts has been carried out so far (AILLUD & DUPRAZ, 1998).

The aim of this paper is to describe the microbial crusts and explain their role in the construction of the reef, analyse the large- and small-scale evolutionary trends of the encrusting fauna, and discuss the environmental factors responsible for the ecological changes.

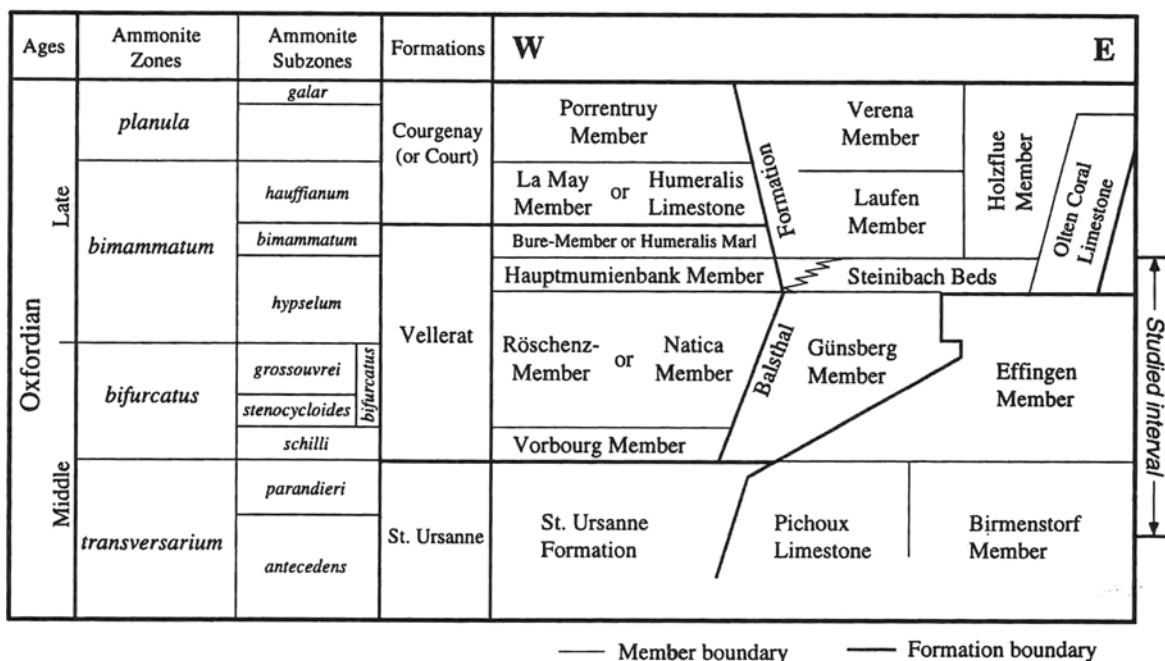


Fig. 2. Stratigraphy of the Middle to Upper Oxfordian (after GYGI & PERSOZ, 1986; GYGI, 1995).

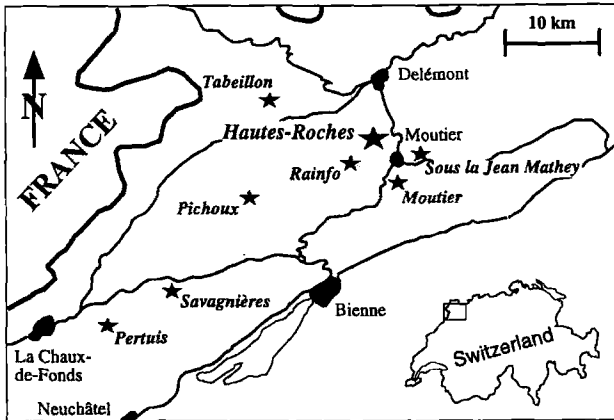


Fig. 3. Location of the studied sections.

2 PALAEOGEOGRAPHY AND STRATIGRAPHY

In the Middle to Late Oxfordien, the domain of today's north-western Swiss Jura mountains was part of a shallow carbonate platform surrounded by isolated land areas (Fig. 1). Within the precise biostratigraphic framework (Fig. 2) established by GYGI & PERSOZ (1986) and GYGI (1990, 1995), PITET (1996) performed a high-resolution correlation of various sections based on sequence stratigraphy and cyclostratigraphy. Position on the platform, age, and life-time of the Hautes-Roches patch-reef presented in this paper thus are well constrained. This reef belongs to the Vellerat Formation (Fig. 2) covering the *Schilli* to *Hypselum* ammonite subzones. The bioherms developed in a very shallow platform environment with episodic siliciclastic input. Variable morphologies with complex water-circulation patterns created fluctuations in energy, light, salinity, temperature, and sedimentation rate. Consequently,

the bioconstructions are not well developed. Furthermore, they display a relatively dark colour that may be due to incorporation of terrigenous material. Conditions for coral growth were better during deposition of the St. Ursanne Formation, and comparisons with the patch-reefs there will be made (sections indicated in Fig. 3).

3 METHODOLOGY

In order to perform a high-resolution palaeoecological analysis, 250 laterally and vertically densely-spaced samples have been taken in the 18-metres-thick patch-reef of Hautes-Roches (Fig. 5). All samples have been looked at on polished, etched or glazed slabs, and in thin sections. The relative abundances of thrombolitic, stromatolitic and leiolitic encrustations, micro-encrusters, bioerosion, and particles in the matrix have been assessed on a scale of 0 to 3 (for microbialite and bioerosion estimation on slices, for micro-encrusters in thin section: 0 = absent, 1 = present, 2 = common, 3 = abundant). In large samples, two or three thin sections have been made to better control the lateral variability. The log of the Hautes-Roches patch-reef in Figure 5 combines field observations and microscopic data. This reef is shown here as an example; the same approach has been used to analyse the bioherms of the other studied sections (Fig. 3; DUPRAZ, 1999).

Two-dimensional maps of distribution of some general parameters have been created on the computer, and curves of relative abundance of diagnostic textural and biological elements have been constructed. Because the samples are quite evenly spaced and can be considered to be representative of comparable surfaces, a moving average of 10 samples with steps of 5 samples has been chosen. This defines 43 intervals covering the patch-reef from bottom to top,

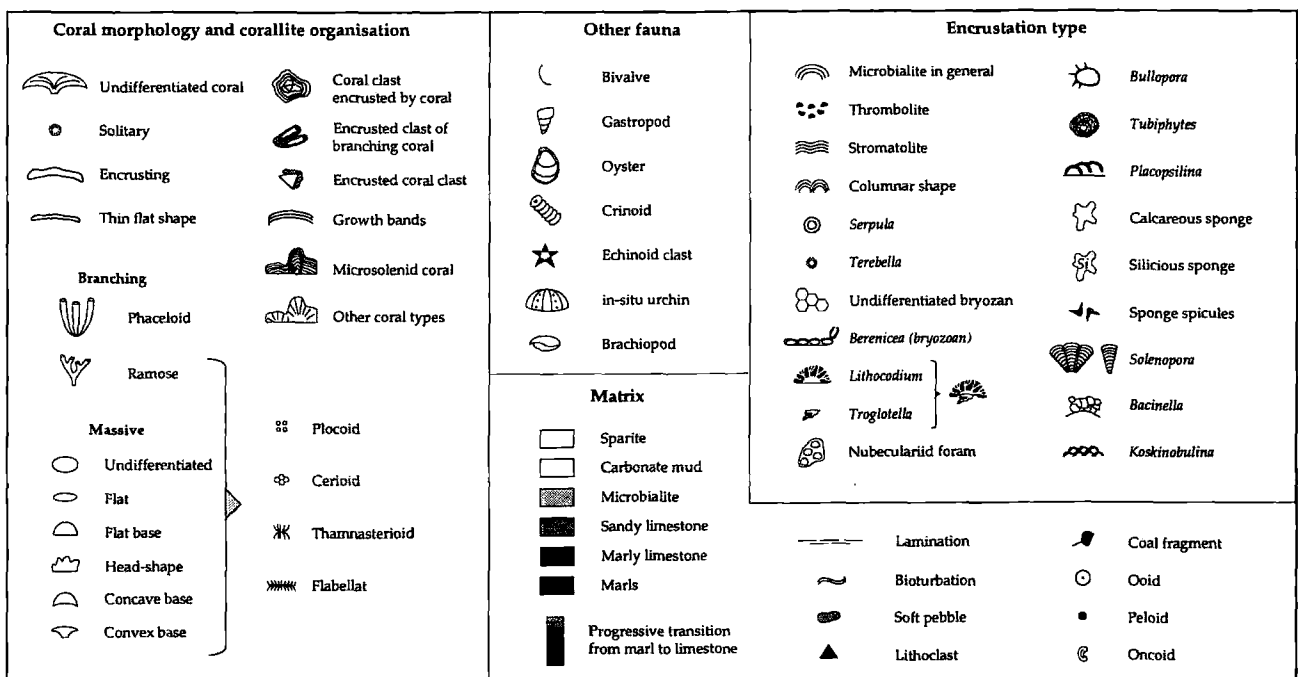
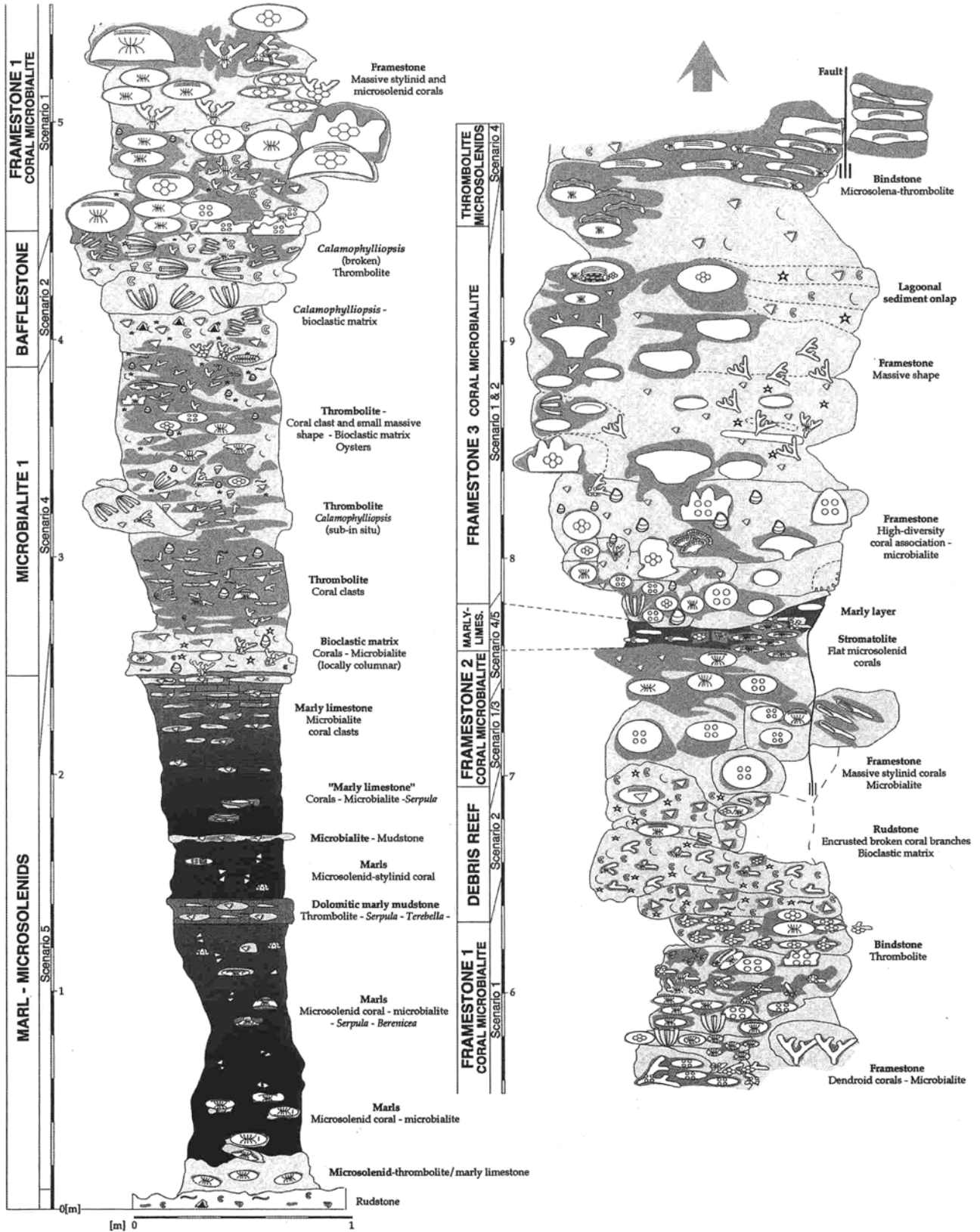


Fig. 4. Legend for sections and diagrams.

Fig. 5a. First part of the Hautes-Roches section.

**HAUTES-ROCHES PATCH-REEF
Part 1**



HAUTES-ROCHES PATCH-REEF
Part 2

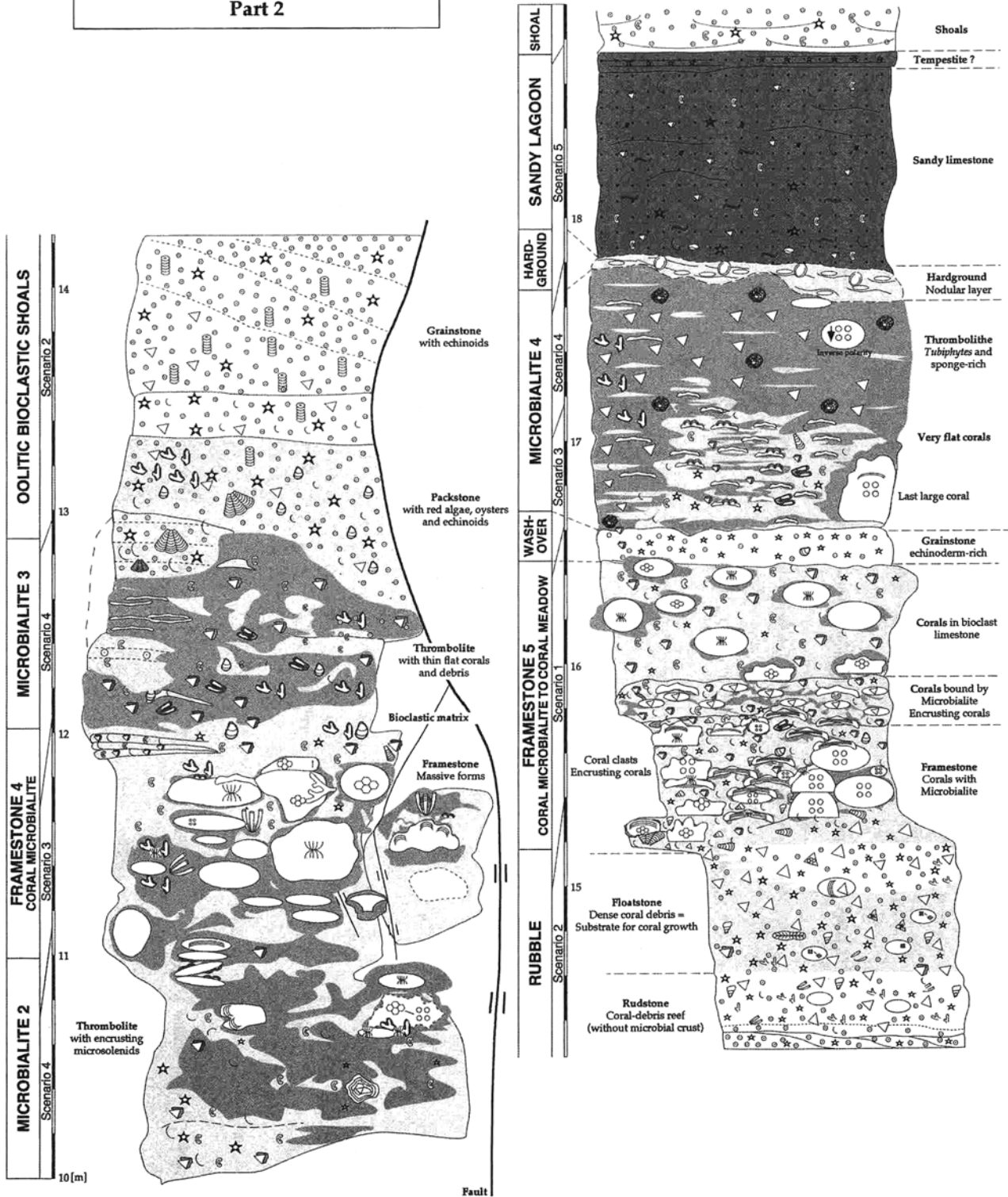


Fig. 5b. Second part of the Hautes-Roches section.

and for each interval an average value of relative abundance of the various parameters is attributed. Derived curves indicate the rate of change of composition. Organisms with similar ecological significance are grouped to describe trends in reef evolution. Finally, based on the observed fabrics and fauna, scenarios representing particular trophic stages are developed, and an ideal cycle of reef growth and demise is proposed.

Scanning-electron microscope (SEM) and energy-dispersive spectrometer (EDS) analyses have been used to identify microstructure and chemical composition of the encrustations. The corals have been determined at genus level and, where possible, at species level. Their morphological classification is based on ALLOTTEAU (1957) and ERRENST (1990).

4 COMPOSITION OF MICROBIAL CRUSTS

4.1 Microbialite types and cementation

Biomineralization

There are several direct (active) and indirect (passive) biomineralization mechanisms (e.g., NEUMEIER, 1998). It is now well established that certain bacteria induce carbonate precipitation through modification of the micro-environment by their metabolic activity (e.g., CHAFETZ, 1986; CHAFETZ & BUCZYNSKI, 1992; CASTANIER, 1987; CASTANIER et al., 1997; NEUMEIER, 1998). Photoautotrophic cyanobacteria remove CO₂ from the system and thus favor carbonate precipitation through an increase of alkalinity and pH in the proximity of the bacteria, thereby inducing mineralization (EHRlich, 1996; KRUMBEIN & SWART, 1983; PENTECOST & RIDING, 1986; VERRECCHIA et al., 1995). Heterotrophic bacteria (not directly associated to the photic zone) stimulate carbonate formation through ammonification of amino-acid or urea in aerobiosis, nitrate reduction, or sulphate reduction, which again lead to a higher pH

through CO₂-degassing or ammonia production (BERNER, 1971; CASTANIER, 1987; CASTANIER et al., 1997; CHAFETZ & BUCZYNSKI, 1992; EHRlich, 1996; NEUMEIER, 1998; PURVES et al., 1994). Carbonate precipitation by heterotrophic bacteria seems to increase with increasing organic matter content (CASTANIER et al., 1997; EHRlich, 1996; MITTERER, 1971), but phosphate above a critical concentration can inhibit carbonate precipitation (EHRlich 1996).

REITNER (1993), REITNER & NEUWEILER (1995), and REITNER et al. (1996) have shown that precipitation of carbonate in modern reef cavities is favored by acidic organic macromolecules (AOM). The spatial configuration of their terminal carboxyl groups is very similar to that of the carbonate anions, which explains the Ca²⁺-binding capacity of such macromolecules. The result is a crystal seed that will serve as nucleus for further mineralization. AOM occur in the organic mucilage (biofilm) that forms the uppermost layer of microbial crusts. AOM-induced biomineralization appears to be significant also in ancient microbial carbonates (NEUWEILER et al., 1996).

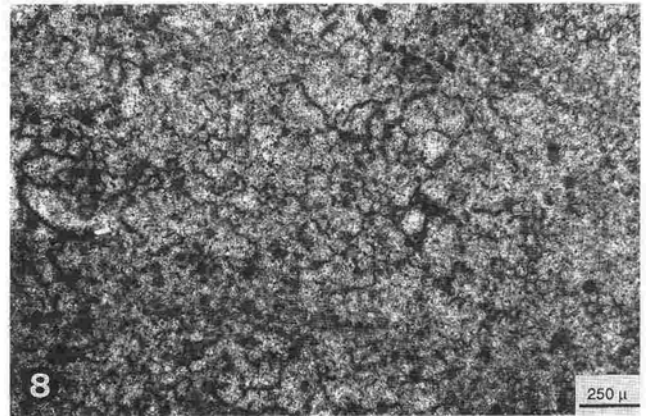
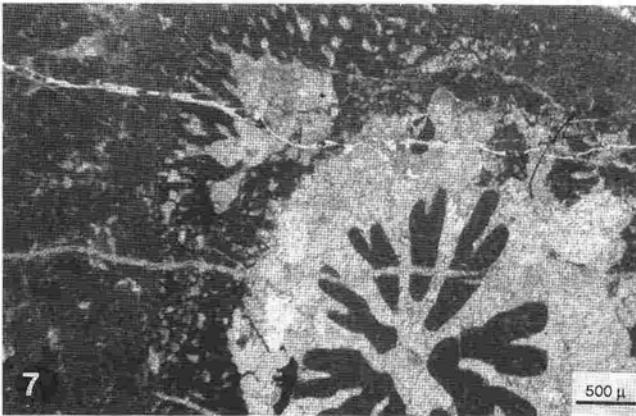
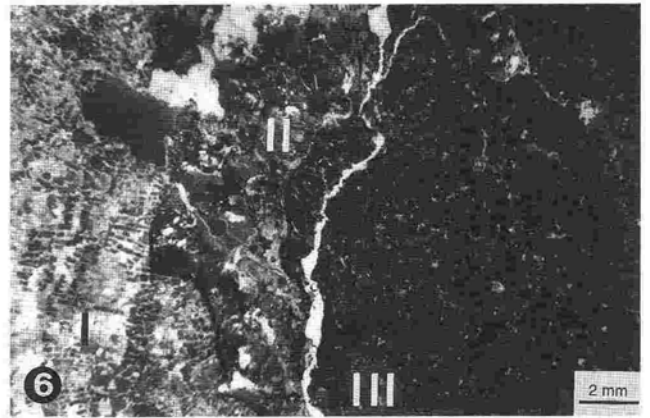
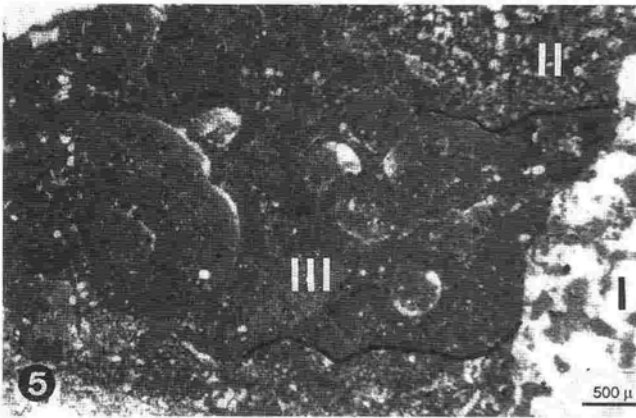
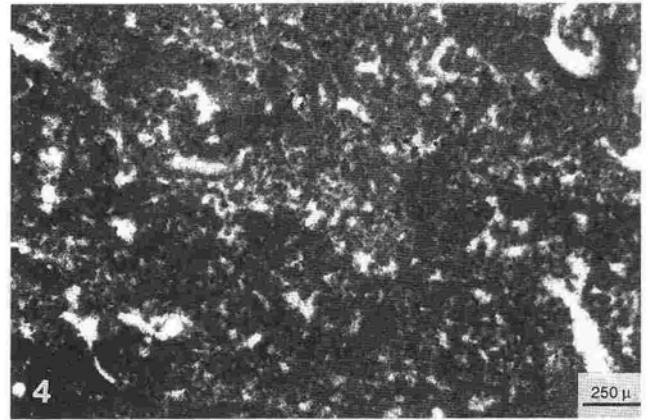
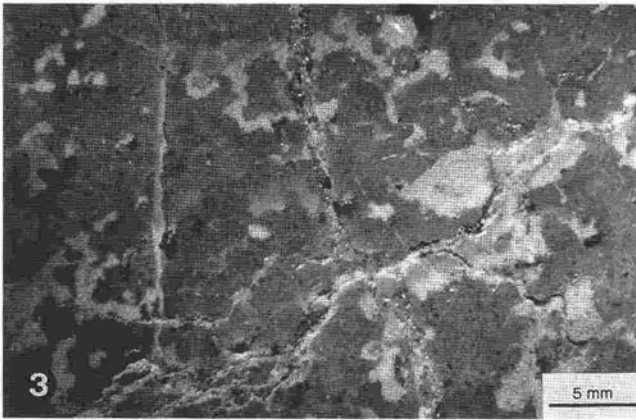
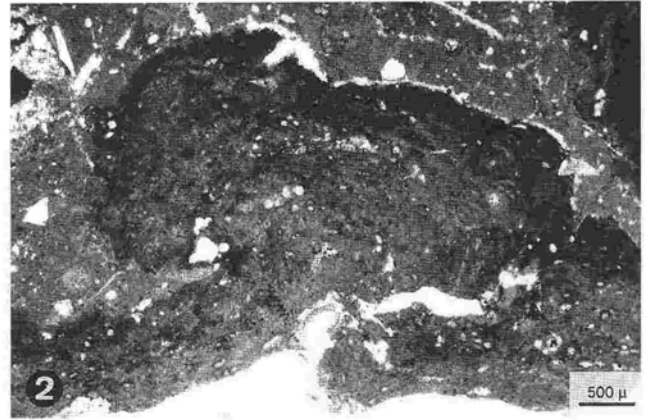
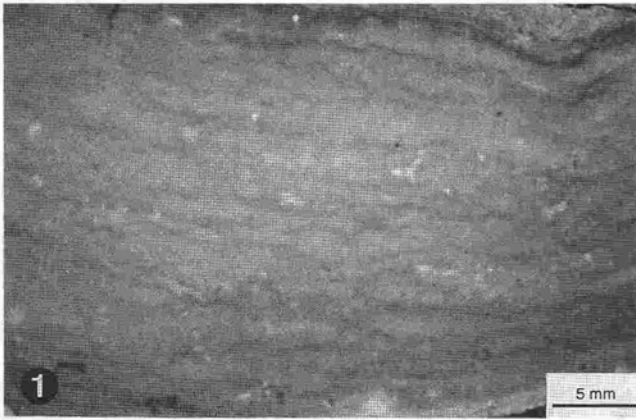
Many microbial crusts contain micropeloids with a diameter of approximately 30 µm. Several authors evoke abiogenic precipitation of carbonate (e.g. MACINTYRE, 1985; MARSHALL, 1983), whereas CHAFETZ (1986) found bacterial mediation and REITNER (1993) involvement of AOM to be important.

Classification

Microbial crusts develop in marine, fresh-water, and terrestrial depositional environments. RIDING (1991) presented a classification and introduced the word "microbolite" in place of "microbialite" (BURNE & MOORE, 1987) as a general term for benthic microbial deposits. Although "microbialite" was originally used for laminated deposits, it is commonly applied to include all types of benthic microbial deposits (e.g., REITNER, 1993). The term

Plate 11 Microbialites and micro-encrusters in Middle to Late Oxfordian shallow coral bioherms of the Swiss Jura Mountains.

- Fig. 1. Skeletal stromatolitic encrustation with fuzzy laminations. Sample HR101 (Hautes-Roches), Günsberg/Röschenz Member. Polished slab.
- Fig. 2. Columnar cryptic microbial crust. This encrustation starts to grow between coral fragments. The remaining porosity is filled by bioclastic matrix. Sample HB18 (Hautes-Roches), Steinibach Beds. Thin section.
- Fig. 3. Thrombolitic encrustation. The clotted fabric is well visible with mesoclots and micritic matrix. Sample HR21 (Hautes-Roches), Günsberg/Röschenz Member. Polished slab.
- Fig. 4. Peloidal fabric of thrombolite. Sample T9 (Tabeillon), St. Ursanne Formation. Thin section.
- Fig. 5. Encrustation displaying two layers. The first one directly encrusts the coral substrate (I) and is composed of *Bacinella-Lithocodium* (II), the second one fills the remaining porosity and consists of *Terebella* and peloidal thrombolite (III). Sample T19 (Tabeillon), St. Ursanne Formation. Thin section.
- Fig. 6. Encrustation with two layers: coral (I), a first encrustation (II) with high micro-encruster diversity (*Placopsilina*, *Serpula*, *Berenicea*) but without *Lithocodium* and *Bacinella*, and a second layer (III) composed of peloidal thrombolite with some *Tubiphytes*. Sample HR102' (Hautes-Roches), Günsberg/Röschenz Member. Thin section.
- Fig. 7. *Lithocodium aggregatum* encrusting *Stylosmilia* (phaceloid branching coral). Sample T69 (Tabeillon), St. Ursanne Formation. Thin section.
- Fig. 8. *Bacinella* invading the red alga *Solenopora*. Sample HR81 (Hautes-Roches), Günsberg/Röschenz Member. Thin section.



“automicrite” can be used for autochthonous, micritic *in-situ* mineralization, in contrast to “allogenic micrite” formed by allochthonous carbonate mud (WOLF, 1965). “Organomicrite” defines an automicrite where AOM played an important role in mineralization (REITNER et al., 1995). In the present paper, we mainly use the term “microbialite”.

RIDING (1991) proposed to use the term “cryptic microbial carbonate” for benthic microbial crusts that display micritic, clotted, peloidal, or sparitic microfabrics but lack distinctive macrofabrics. “Leiolite” was introduced by BRAGA et al. (1995) and is defined as a microbial crust that agglutinates particles but does not show any differentiated macrofabric. SCHMID (1996) uses this term for all microbial crusts without macrofabrics, and more specifically “cryptic microbial carbonate” if a dense microstructure is present. In our paper, we use the term “leiolite”.

In the definition of microbialite, macro- and microfabrics are included (Fig. 6). Macroscopically, three different fabrics are distinguished: laminated (stromatolitic), clotted (thrombolitic), and structureless (leiolitic). Microscopic fabrics are described as containing trapped and agglutinated particles, as peloidal, or as densely micritic. Peloidal and micritic fabrics are formed through a Ca-binding matrix and bacterially-induced mineralization, and/or biomineralization (*sensu* RIDING, 1991). Intermediate stages between these different end-members are common (Fig. 6; see also RIDING, 1991; BRAGA et al., 1995; LEINFELDER et al., 1996; SCHMID, 1996).

Stromatolites

Recent stromatolites are composed of layers of varying bacterial composition depending on oxygenation, dis-

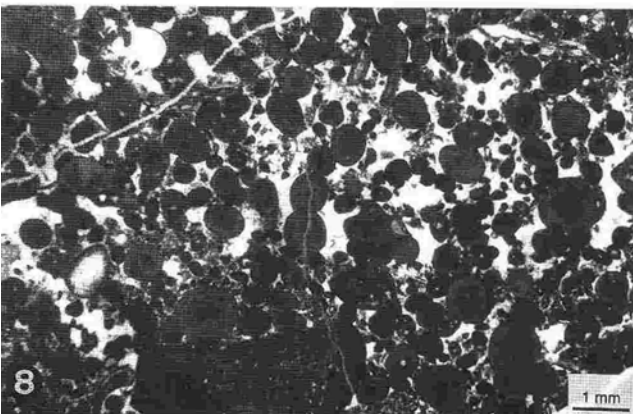
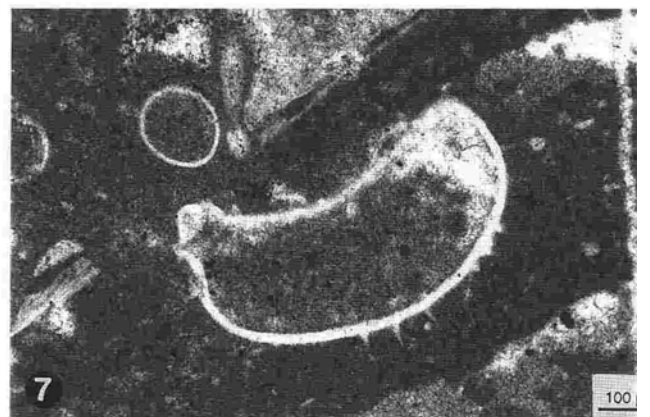
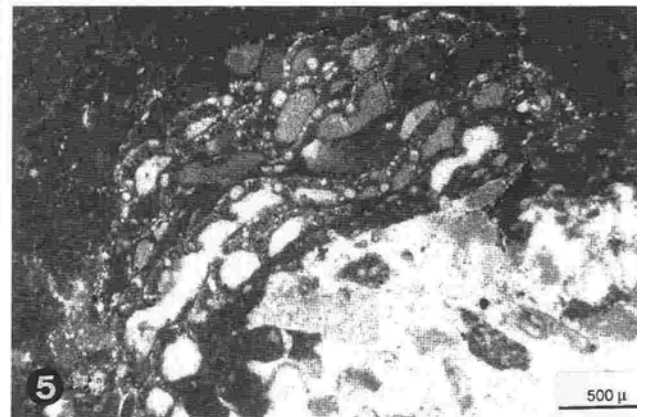
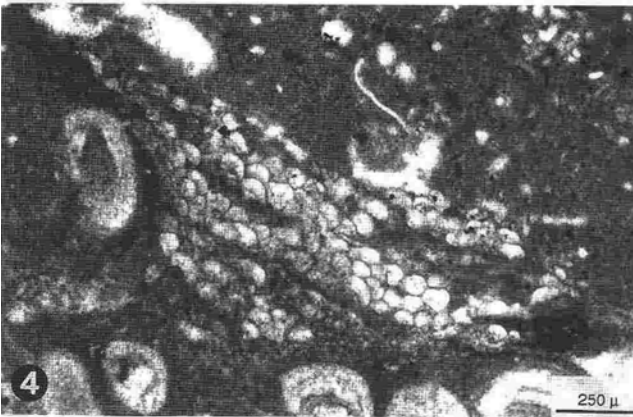
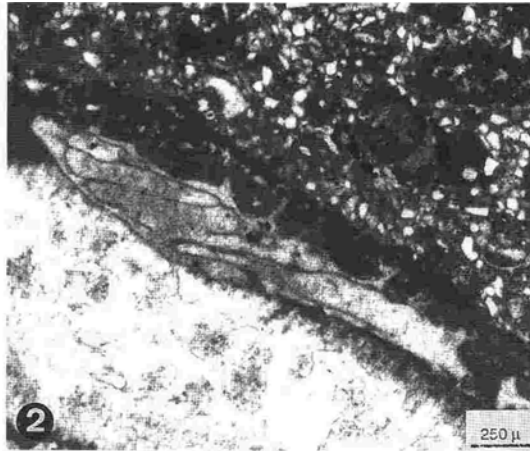
solved H₂S, and light intensity (BAULD, 1981), but also algae and metazoans may participate in the laminated structure (RIDING, 1997; FELDMANN & MCKENZIE, 1998). Experiments suggest that carbonate formation is very efficient a few centimetres below the surface in the aphotic zone. There, the cyanobacteria are dead but heterotrophic bacteria abundant, forming the micritic clotted fabric typical of fossil skeletal stromatolite (CHAFETZ & BUCZYNSKI, 1992; KNOLL & AWRAMIK, 1983). In Recent reef cavities as well as in saline lakes, biomineralization at the base of AOM-containing biofilms associated with heterotrophic bacteria has been observed (REITNER, 1993; REITNER et al., 1996).

The few stromatolites found in the studied Oxfordian reefs (Plate 11/1) generally present a peloidal to densely micritic microfabric. In some cases, the laminations are underlined by very thin layers of clay minerals, visible only in SEM and by EDS mapping (presence of Al, Si, and K). The periodic clay input and the general lack of micro- and macrofauna suggest formation in the intertidal zone (see also FELDMANN & MCKENZIE, 1998). No coarse agglutinated stromatolites have been observed.

The term “columnar encrustation” has been given to millimetre- to centimetre-sized domal structures (Plate 11/2). They generally start with flat laminations and then develop a columnar shape. This type of encrustation is commonly associated with nubeculariid foraminifera and *Tubiphytes* (see 4.2), and frequently occurs on corals that are otherwise little encrusted. In some cases, development of strongly dendroid encrustation forms have been observed and are interpreted as an answer to high sedimentation rates (see also SCHMID, 1996).

Plate 12 Microbialites and micro-encrusters in Middle to Late Oxfordian shallow coral bioherms of the Swiss Jura Mountains.

- Fig. 1. *Troglotella incrustans* WERNLI perforating a coral in its first stage of ontogenesis. Sample Ra16e (Rainfo), Günsberg/Röschenz Member. Thin section.
- Fig. 2. *Troglotella incrustans* WERNLI in an aberrant shape, living inside a *Lithocodium* cavity. Sample SJM03 (Sous la Jean Mathey), Steinibach Beds. Thin section.
- Fig. 3. Longitudinal section of *Tubiphytes morronensis* CRESCENTI. Note the two layers of the organism (porcelaneous and dark micritic to micropeloidal). Sample HR108 (Hautes-Roches), Günsberg/Röschenz Member. Thin section.
- Fig. 4. Longitudinal section of *Koskinobulina socialis* CHERCHI & SCHROEDER, with enigmatic encrustation (lower right) called “Krustenproblematikum” by SCHMID (1996). Sample HR45 (Hautes-Roches), Günsberg/Röschenz Member. Thin section.
- Fig. 5. *Placopsilina* agglutinating quartz grains and rhaxellid microscleres. Sample HR92b (Hautes-Roches), Günsberg/Röschenz Member. Thin section.
- Fig. 6. Nubeculariid foraminifera in peloidal thrombolite. Sample T123 (Tabeillon), St. Ursanne Formation. Thin section.
- Fig. 7. *Bullopore tuberculata* with its typical spine-covered test. Sample P69 (Pichoux), Vorbourg Member. Thin section.
- Fig. 8. Large agglutinated foraminifer (affinity with *Alveosepta*) incorporating ooids, thus contributing to the stabilization of the sediment. Sample T5'' (Tabeillon), St. Ursanne Formation. Thin section.
- Fig. 9. Coral (*Allocoenia*) growing on *Solenopora* substrate. The *Solenopora* has been broken and bioeroded before being colonized. Note the presence of *Bacinella* on and inside the red alga. Sample HR203 (Hautes-Roches), Günsberg/Röschenz Member. Thin section.



Thrombolites

Thrombolites in the studied reef sections display the typical features first described by AITKEN (1967). They are composed of millimetre- to centimetre-size clots separated by patches of micrite, sand-size sediment, or sparry cement (Plate 11/3; KENNARD & JAMES, 1986). The peloidal to dense micrite fabric, obvious in thin section (Plate 11/4), is attributed to carbonate precipitation stimulated by various metabolic activities of heterotrophic cocci- or baci-bacteria in aerobic to anaerobic settings (KENNARD & JAMES, 1986; LEINFELDER et al., 1996; RIDING, 1991). According to CAMOIN et al. (1997), LAURENTI & MONTAGGIONI (1995), and LEINFELDER et al. (1996), thrombolites are generally formed by various sciaphile (shadow-prefering) bacteria in environments characterized by very low water energy and low sedimentation rate in aerobic to anaerobic conditions. However, AOM-induced mineralization in biofilms containing decayed organic matter can produce thrombolite also without direct microbial activity and under completely anaerobic conditions (REITNER, 1993).

The studied Oxfordian thrombolites are commonly found associated with microfauna that do not support high water energy and can live in the shade. Consequently, these thrombolites tolerate low light intensity in deep and/or turbid water, and in reef cavities.

Leiolites

In the studied reefs, thin layers of leiolite cover many corals. They develop in association with photoautotrophic micro-encrusters and may represent a first phase of encrustation, before the reef cavities are infilled by thrombolite. Similar successions have been observed in Recent reef cavities where they translate the passage from lighter to darker conditions (REITNER, 1993).

4.2 Micro-encrusters

Micro-encrusters are abundant in thrombolites and leiolites, but rare or absent in stromatolites. Cavity-dwelling micro-encrusters have also been named "coelobites" (GINSBURG & SCHROEDER, 1973), or "cryptobionts" (KOBLOUK, 1988).

Bacinella-Lithocodium and Troglotella incrustans

Bacinella irregularis RADOICIC occurs quite commonly in the studied encrustations (Plate 11/5). It presents an irregular vesicular shape and is commonly associated with *Lithocodium agregatum* ELLIOT (Plate 11/7). First presented as two parts of a single organism (such as a codiacean alga: SEGONZAC & MARIN, 1972; BANNER et al., 1990), *Lithocodium* is now interpreted as a foraminifer (Luftusiacea; SCHMID & LEINFELDER, 1996), and *Bacinella* as being related to cyanobacteria (CAMOIN & MAURIN, 1988; NOSE, 1995; SCHMID, 1996). The fact that the two forms are found separately in our sections strengthens this latter interpretation.

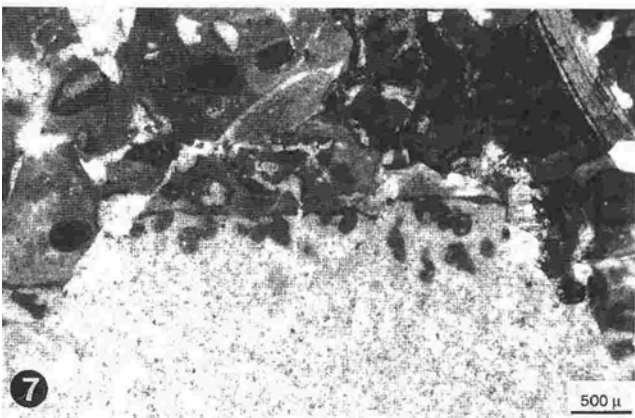
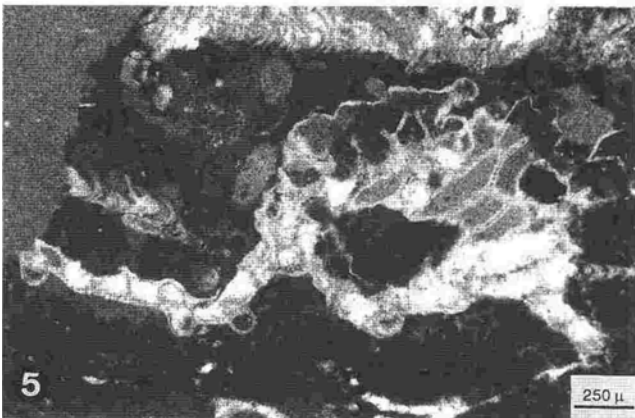
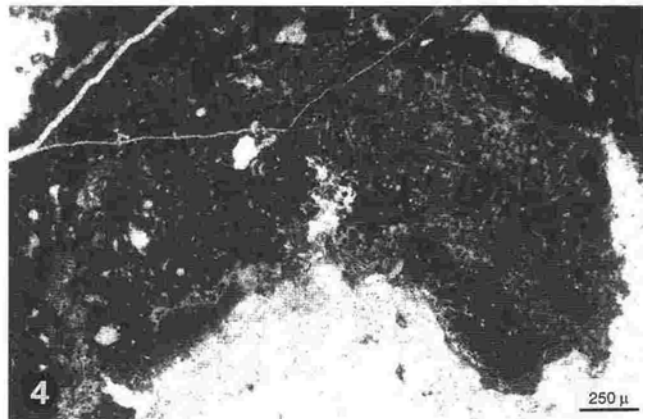
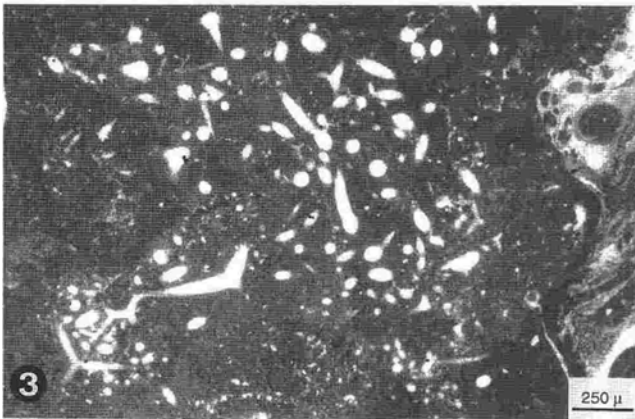
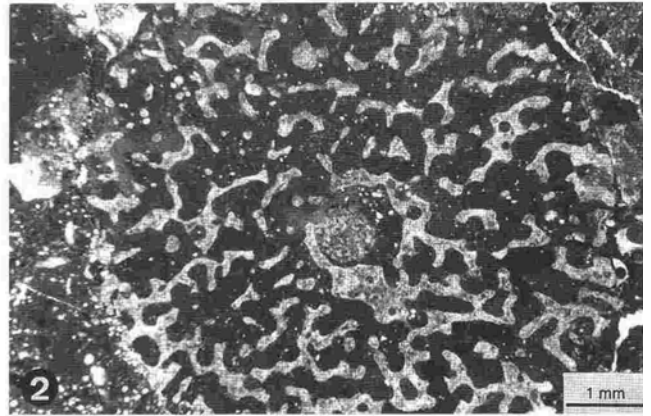
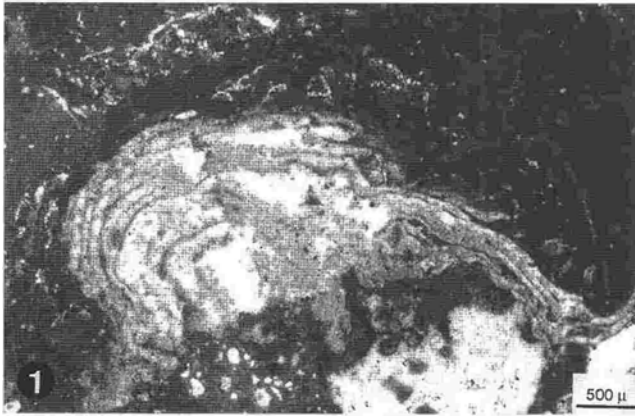
Bacinella has been seen destroying the reticular structure of the red alga *Solenopora* (Plate 11/8). SCHMID (1996) proposed that *Lithocodium* contains symbiotic, photosynthetic algae in the alveoles of the epiderm, thus explaining its affinity with shallow and clear water. *Lithocodium* also develops a commensalism with the boring telamminid foraminifer *Troglotella incrustans* WERNLI (WERNLI & FOKES, 1992; SCHMID & LEINFELDER, 1996). At a first stage of ontogenesis, this foraminifer has a regular growth and can perforate a substrate (Plate 12/1). In further development, it forms irregular chambers and reaches aberrant morphologies (Plate 12/2).

Tubiphytes

The species *Tubiphytes morronensis* CRESCENTI (Plate 12/3) develops a two-layered test: the first layer is porcelaneous, the second micritic to micropeloidal. It is interpreted as a symbiotic construction of a foraminifer and a dense microbial envelope by FLÜGEL (1981), as a sponge with a central tube by RIDING & GUO (1992). SCHMID (1995) identified it as a miliolid foraminifer with endosymbiotic algae constructing an outer test. This symbiotic association implies that the thickness of the outer test should decrease with water depth or with increased water turbidity. Most *Tubiphytes* encountered in the studied Oxfordian reefs have relatively thin micritic to peloidal envelopes, suggesting low light intensity.

Plate 13 Microbialites and micro-encrusters in Middle to Late Oxfordian shallow coral bioherms of the Swiss Jura Mountains.

- Fig. 1. Problematic recrystallized micro-encruster (affinity with the encrusting alga *Archeolithoporella* ENDO). Sample HR158 (Hautes-Roches), Günsberg/Röschenz Member. Thin section.
- Fig. 2. Pharetronid calcareous sponge. Note the osculum in the centre. Sample HR74 (Hautes-Roches), Günsberg/Röschenz Member. Thin section.
- Fig. 3. Siliceous demosponge in peloidal thrombolite. Sample P62 (Pichoux), Vorbourg Member. Thin section.
- Fig. 4. Perforating siliceous sponge *Aka*. Sample T51 (Tabeillon), St. Ursanne Formation. Thin section.
- Fig. 5. Longitudinal to oblique section of *Berenicea* sp. Sample Ra29a (Rainfo), Günsberg/Röschenz Member. Thin section.
- Fig. 6. Bioerosion by lithophag bivalve, interpreted as a perpendicular cross-section of a lithophag following coral growth. Sample Ra31'' (Rainfo). Günsberg/Röschenz Member. Thin section.
- Fig. 7. Bioerosion by sponge (*Entobia*). Sample HB17 (Hautes-Roches), Steinibach Beds. Thin section.
- Fig. 8. Para- or cryptoendolithic agglutinated foraminifera in a recrystallized coral. Sample HR206 (Hautes-Roches), Günsberg/Röschenz Member. Thin section.



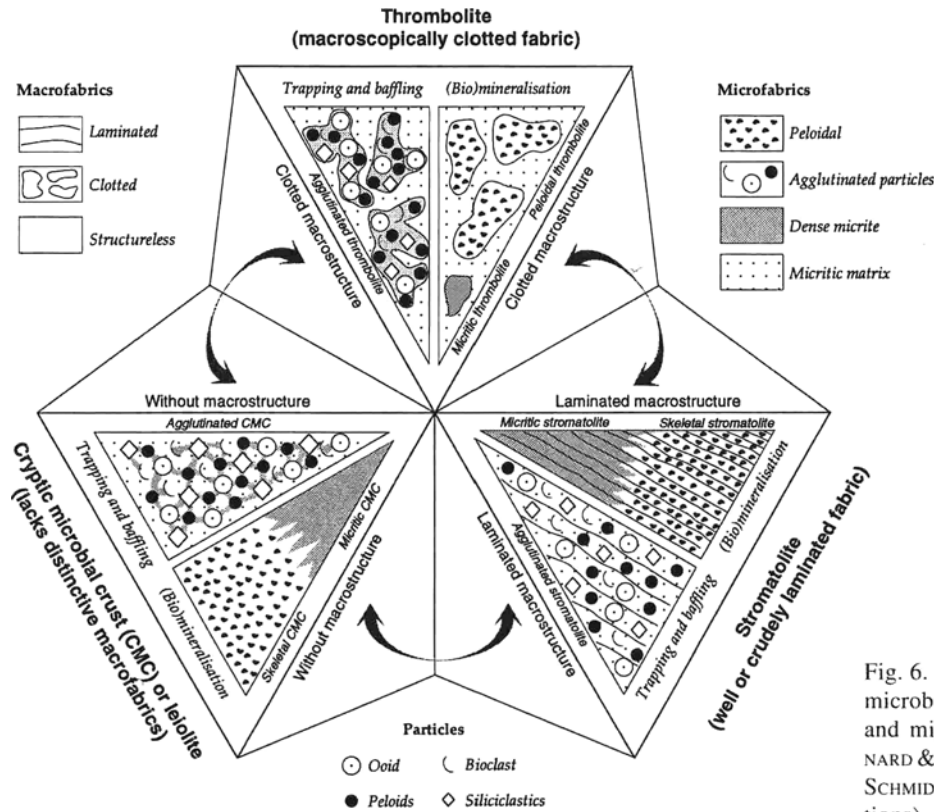


Fig. 6. Classification of Jurassic microbialites based on their macro- and microfabrics (based on KENNARD & JAMES, 1986; RIDING, 1991; SCHMID, 1996; and own observations).

Koskinobulina

Koskinobulina (CHERCHI & SCHROEDER, 1979) is an enigmatic organism. This fossil is composed of numerous small (50 to 100 μm) hemispherical to spherical "chambers" with perforated sparitic or micritic walls (Plate 12/4). The perforated wall is not always visible, and only a micritic sheath appears. This organism has been interpreted as an acervulid foraminifer (e.g., GISIGER, 1967; WERNLI & SEPTFONTAINE, 1971), and as "cyanobacteria or algae or foraminifer" for its resemblance with the problematic form *Wetheredella* WOOD (CHERCHI & SCHROEDER, 1985; COPPER, 1976; RIDING, 1977). SCHMID (1996) proposes a rotaliid foraminifer such as *Milletia* because the narrowings observed in *Koskinobulina* look like "chamberlets by longitudinal partitions" of *Milletia*. Elongated sections of such a foraminifer have never been observed in this study. *Koskinobulina* always presents a round shape with few narrowings. The fact that connections between the chambers have never been noted in our samples rather points to a colony of organisms.

Encrusting foraminifera

Placopsilina D'ORBIGNY is a lituolid foraminifer that preferentially agglutinates siliciclastic particles. Sometimes it picks up sponge microscleres to build its test (Plate 12/5), and quartz grains may be absent in the perimeter around the foraminifer but concentrated in its test. *Placopsilina* is abundant in the microbial crusts and in oncoids of the studied Oxfordian sections.

Vinelloidea crussolensis CANU is a foraminifer of the Order Miliolida and synonymous to *Nubeculinella bigoti* CUSHMAN (VOIGT, 1973). Because of the difficulty to determine the exact genus *Vinelloidea*, the general term "nubeculariid foraminifer" is used in this paper (Plate 12/6). It is in some cases difficult to differentiate between *Tubiphytes* with a little developed outer test and a nubeculariid foraminifer.

Bullopore QUENSTEDT (Order Lagenida) appears with different species in the Upper Jurassic (e.g., *B. rostrata*, *B. laevis*, and *B. tuberculata*; SCHMID, 1996; WERNER et al., 1994). *Bullopore* is composed of small, ball-shaped chambers linked by stolon-like necks and has a calcareous, perforate test. *B. tuberculata* is characterized by spines on the test (Plate 12/7). This foraminifer is attached to the substrate and rarely displays a regular shape.

Associated agglutinated foraminifera (not directly encrusting)

Pseudocyclamina, *Alveosepta* and *Ammobaculites* are commonly found in the siliciclastic lagoonal facies of the Oxfordian. They can trap coarse particles such as ooids or bioclasts to build their tests. Agglutinated ooids forming large chambers are found in the last centimetre of oolitic shoal deposits, thus stabilising the mobile sediment and serving as substrate for bioconstructions (Plate 12/8). Micritic bridges between the agglutinated grains may resemble meniscus cement, but do of course not imply a vadose diagenetic environment (HILLGÄRTNER et al., 1999).

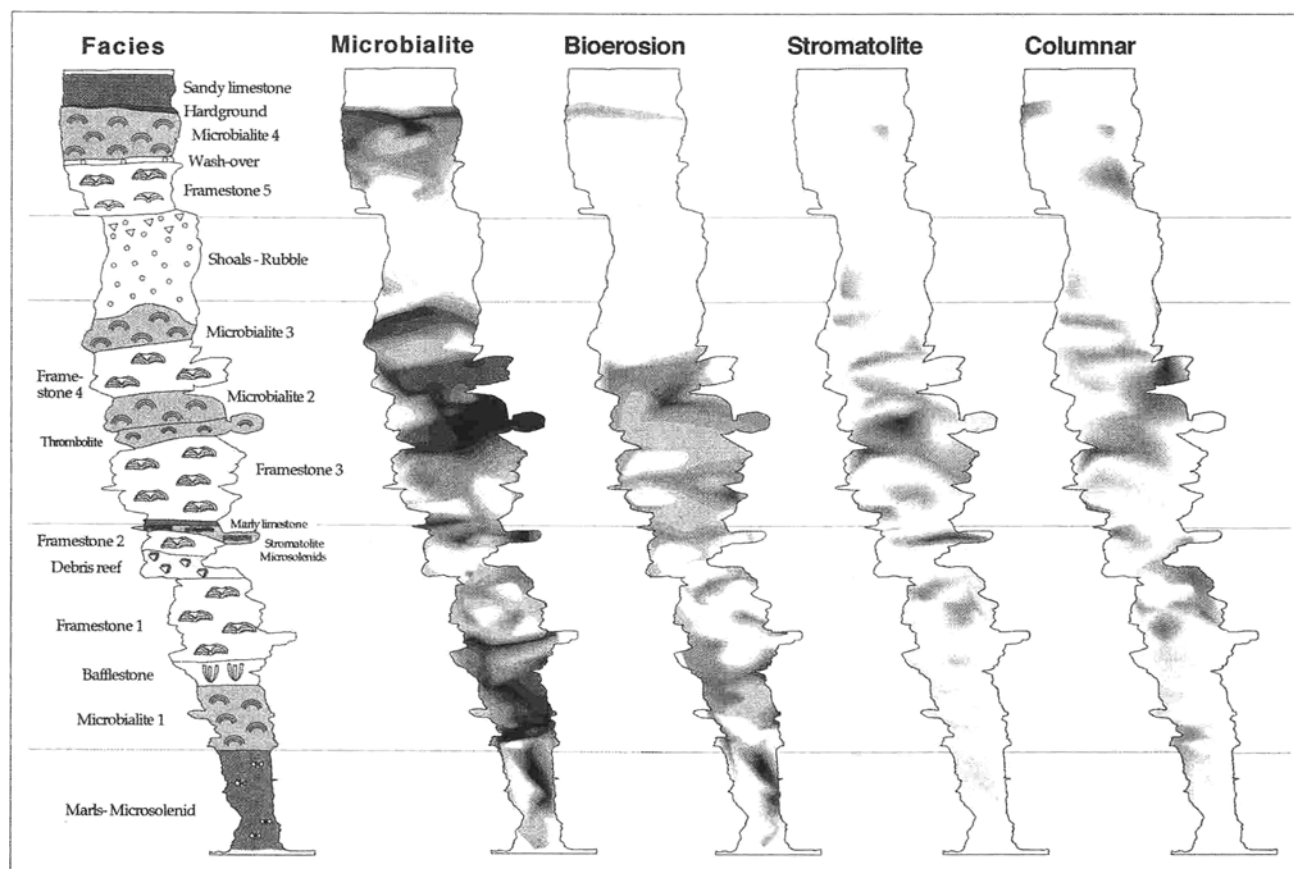


Fig. 7. Mapping of Hautes-Roches section showing the relative abundance of microbialite, bioerosion, stromatolite, and columnar encrustations (black = abundant, white = absent). Simplified facies distribution based on Figure 5.

Red algae and Green algae

Red algae occur only infrequently in the studied sections. They are generally represented by *Solenopora* and appear in high-energy facies. *Bacinella* and *Lithocodium* are commonly associated and indicate oligotrophic, relatively shallow depositional environments. *Solenopora* can serve as a substrate for coral growth (Plate 12/9), and it may be invaded by *Bacinella irregularis* (Plate 11/8; see also HELM & SCHÜLKE, 1998). *Solenopora* biostromes or *Solenopora*-rich levels commonly overlie coral-reef cores (Fig. 5b; GEISTER & LATHUILIÈRE, 1991; HELM & SCHÜLKE, 1998; SCHMID, 1996). A form resembling the Palaeozoic alga *Archeolithoporella* ENDO has been observed in a few samples. It is interpreted as a cyanobacterium or a red alga (Plate 13/1; FLÜGEL et al., 1991).

Green algae are rare in the Oxfordian sediments. The only representative of the group found in our samples is *Thaumatoporella* PIA.

Sponges

Sponges are important components in many Oxfordian bioherms and contribute to encrustation and bioerosion. Comprehensive studies on coral reefs *versus* sponge and thrombolite reefs have been undertaken by, e.g., LEINFELDER et al. (1993a, 1993b, 1994, 1996), WERNER et al. (1994), and KEUPP et al. (1996) showing zonations related to

bathymetry, sedimentation rate, energy, and trophic level. However, no real sponge reefs have been observed in our sections. The only sponges found are encrusting pharetronid calcareous forms (Plate 13/2), possible sphinctozoans, and demosponges (Plate 13/3) including the bioeroding genus *Aka* (Plate 13/4; REITNER & KEUPP, 1991). The bathymetry of the studied depositional environments was shallow to very shallow (PITTET, 1996; PITTET & DUPRAZ, 1995; PITTET et al., 1995; STRASSER et al., 1996), and the deeper-water conditions for the growth of hexactinellid sponges were never met.

Round to bean-shaped rhaxellid microscleres (rhaxes) are abundant in the studied bioherms (HASLETT, 1992; REIF, 1967). When a sponge dies, the small spicules are easily detached from the sponge body and dispersed, which explains their presence within thrombolite crusts and allomicrite. The spicules are also used to build *Placopsilina* tests (Plate 12/5) or *Terebella* walls. Originally in silica, the spicules are always preserved as calcite.

It has been shown that modern Mediterranean sponges contain up to 60% (volume) symbiotic, heterotrophic bacteria (SCHUMANN-KINDEL et al., 1996, 1997). During the degradation of the sponge tissue, sulfate-reducing bacteria increase the alkalinity, thus inducing calcification of the sponge tissue and formation of micropeloids (REITNER, 1993; REITNER & SCHUMANN-KINDEL, 1997; SCHUMANN-KINDEL et al., 1997). This last process is one possible

explanation for the peloidal microstructure of the Oxfordian thrombolites, which are commonly associated with small sponges. In Recent sponges, also AOM intervenes in the mineralization process (REITNER & GAUTRET, 1996).

Annelids

Annelids are represented mostly by serpulid and terebellid worms. Serpulids precipitate a hard tube, whereas Terebellids (Plate 11/5) produce an agglutinated wall. Many species of the latter are present, in particular *Terebella lapilloides* MÜNSTER, which can have an important significance for the environmental interpretation (see 6.3).

Recent serpulids do not support turbid water and low oxygen levels (BOSENCE, 1979). In the studied sections, serpulids and microbialites encrust microsolenids in marly sediments that imply high clay input and dysoxic to anoxic conditions. This may be explained by an episodic interruption of detrital input, and by a symbiotic relationship where the serpulid worms use the oxygen produced by cyanobacteria living in the microbial mats (CIRILLI, 1997).

Bryozoans

In the studied sections, this group is represented mainly by the cyclostomate *Berenicea* LAMOUREUX (Plate 13/5; e.g., CUFFEY & EHLEITER, 1984; LANG, 1989). Several cyclostomate bryozoans are attributed to the "*Berenicea*-group" (e.g., *Plagioecia*, *Oncousoecia*, *Stomatopora*) because it is difficult to differentiate them in thin section. *Berenicea* commonly is ladder-shaped without distinct zooecial apertures (see also SCHMID, 1996). If they are recognizable, *Stomatopora* can be interpreted as an opportunistic organism, whereas *Berenicea* needs optimal ecological conditions (TAYLOR, 1979).

4.3 Bioerosion

Bioerosion results from mechanical or chemical grazing, and from etching or perforating of a hard substrate. It plays a paramount role in the carbonate budget of a reef, which maintains an equilibrium between carbonate production and bioerosion (PEYROT-CLAUSADE et al., 1995). Bioerosion intensity is an indicator of trophic conditions and thus represents indirect evidence for nutrient influx (HALLOCK, 1988; see also 6.2 and 7). Numerous ichnogenera and ichnospecies describe the different traces resulting from the activities of eroding organisms (BROMLEY, 1994; BROMLEY & ASGAARD, 1993a, 1993b; BROMLEY & MARTINELL, 1991).

The epilithic fauna is mainly represented by grazers such as echinoids and gastropods. Their traces are difficult to identify in the fossil record, but their presence is indicated by bioclasts in the surrounding sediment.

Among the endolithic organisms, boring bivalves (lithophags) are the most efficient bioeroders. The corresponding ichnogenus is *Gastrochaenolites* (Plate 13/6),

which mainly occurs in shallow water (e.g., BROMLEY, 1994; LEINFELDER et al., 1994, 1996). These bivalves are euendolithic and apply chemical substances to dissolve the substrate. They are found in hard coral skeletons as well as in microbial crusts of the studied reefs, which implies a rapid cementation of the microbialites. Perforation depths vary between 2 mm and 3 cm. In some cases, the lithophags keep up with coral growth by successively closing the shell below them, forming stacked shell layers (Plate 13/6; KLEEMANN, 1994).

Sponges encrust but also perforate the substrate. Although not abundant in the studied patch-reefs, some good examples of sponge borings by the genus *Aka* (Adociidae) have been found (Plate 13/4). In Recent reefs, the genus *Cliona* creates similar bioerosion in very shallow and high-energy environments (REITNER & KEUPP, 1991). The corresponding ichnogenus is *Entobia* (Plate 13/7; BROMLEY & ASGAARD, 1993b).

Foraminifera perforate a substrate for protection, parasitism, test building, and feeding (VÉNEC-PEYRÉ, 1996). In the studied sections, perforations by *Troglotella incrustans* WERNLI have been observed (Plate 12/1). Some agglutinated foraminifera have been found enclosed in coral skeletons (Plate 13/8). These forms are not borers, but seem to adopt a paraendolithic or cryptoendolithic behavior.

In Recent reef cavities, favored by eutrophic conditions, Fe-Mn biofilms participate in the corrosion of microbial crusts by electro-chemical dissolution (REITNER, 1993). In some cases, such processes are responsible for up to 40% of crust destruction. It is not excluded that biofilms contributed to the erosion of Oxfordian microbialites, but no evidence could be found.

5 HAUTES-ROCHES PATCH-REEF

The 60-metres long Hautes-Roches section crops out along a forest trail to the South-West of the village of Hautes Roches in the Swiss Jura (Fig. 2). It covers the Middle to Late Oxfordian Vellerat Formation (Fig. 3; PITTET et al., 1995). For the purpose of this paper, only the reefal part is presented here (Fig. 5, legend in Fig. 4).

In the marly interval, microsolenid corals are the dominant fauna (Marl-Microsolenids; Fig. 5a). They commonly use thrombolite or leiolite as substrate, or grow on thin washover deposits. A few marly limestone intervals are present. Clay input then decreases, and carbonate sedimentation resumes gradually. This results in thrombolite-dominated facies (Microbialite 1; Fig. 5a) with some microsolenids and a few displaced *Calamophylliopsis* (phaceloid branching corals).

Calamophylliopsis become the main components in the following interval (Bafflestone; Fig. 5a) where they first form an *in-situ* colony, then appear as broken and encrusted branches. These serve as a substrate for the first coral-microbialite framestone level (Framestone 1; Fig. 5a), which is dominated by massive corals, in particular by

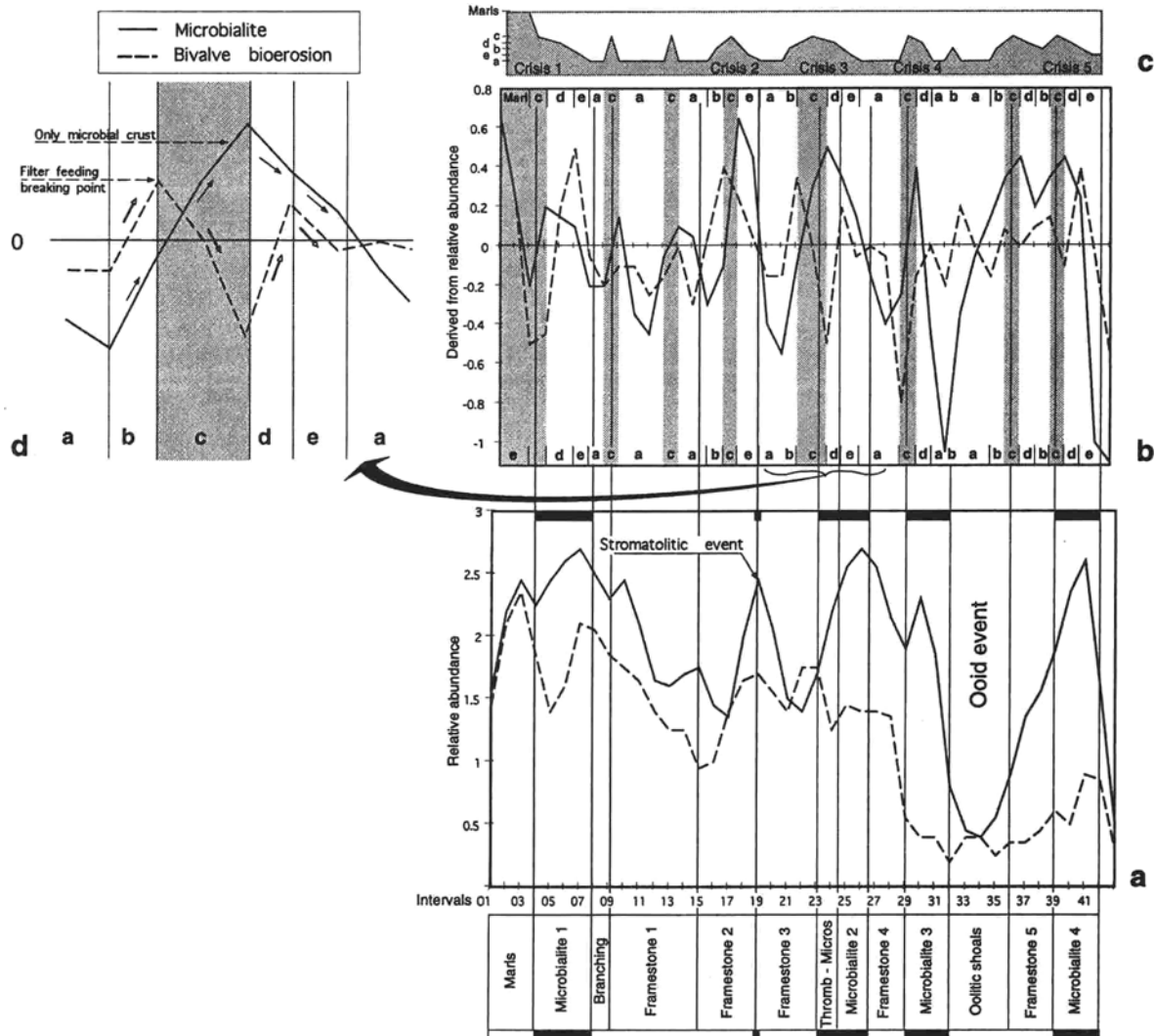


Fig. 8. Trends in microbialite growth and bioerosion activity in the Hautes-Roches section:

- (a) Changes of relative abundance along section (from left to right). Major facies intervals correspond to the ones defined in Fig. 5; the numbers represent the steps (every 5 samples) of a 10-sample moving average.
- (b) Rates of change in microbialite growth and bioerosion activity derived from the curves in Figure 8a (calculated by subtracting the relative abundance at step n from the value at step $n+1$). Zones a to e are defined in Figure 8d and discussed in the text.
- (c) Distribution of zones a to e along section, suggesting reef crises (see also Fig. 13).
- (d) Definition of zones a to e based on the combined rates of change of microbialite growth and bioerosion.

stylinid forms (*sensu* GILL, 1977). Corals grow on top of each-other forming a solid framestone, and microbialite fills and cements the cavities. This construction evolves into a reef dominated by dendroid coral morphologies, and finally into a debris-reef composed of encrusted broken branches (Debris Reef; Fig. 5a). This reef rubble could correspond to a fore- or back-reef deposit, or to a storm layer that later was encrusted by thrombolite. Massive globular stylinid corals install themselves on this layer (Framestone 2; Fig. 5a). They are associated with an important growth of microbialite, evolving from thrombolite to skeletal stromatolite. The stromatolite coexists with flat, bioeroded microsolenids and is sealed on the top by a marly layer.

The following interval (Framestone 3; Fig. 5a) corresponds to the most diverse reef community of the section, including microsolenid, isastreid, rhipidogyrid, stylinid,

and thamnasteriid corals. Lagoonal sediment locally onlaps the bioherm. Microbialite (mostly thrombolite) concentration is high. On the top of the buildup, the microbial encrustations develop small columnar shapes, then pass into an interval of skeletal stromatolite to thrombolite with flat microsolenid corals (Thrombolite-Microsolenids; Fig. 5a). The content of thrombolite increases upwards (Microbialite 2; Fig. 5b), and only a few *Microsolenia* encrusting bioeroded coral clasts occur. Progressively, a new microbialite-coral framestone develops (Framestone 4, Fig. 5b), which is once more capped by thrombolite containing thin platy thamnasteriid corals (Microbialite 3, Fig. 5b). Oolitic and bioclastic shoal deposits then cover the bioherm. Mollusk and echinoderm fragments are accompanied by the red alga *Solenopora*.

This facies evolves from grainstone to rudstone and floatstone, with an upward increase of coral clasts (Rubble;

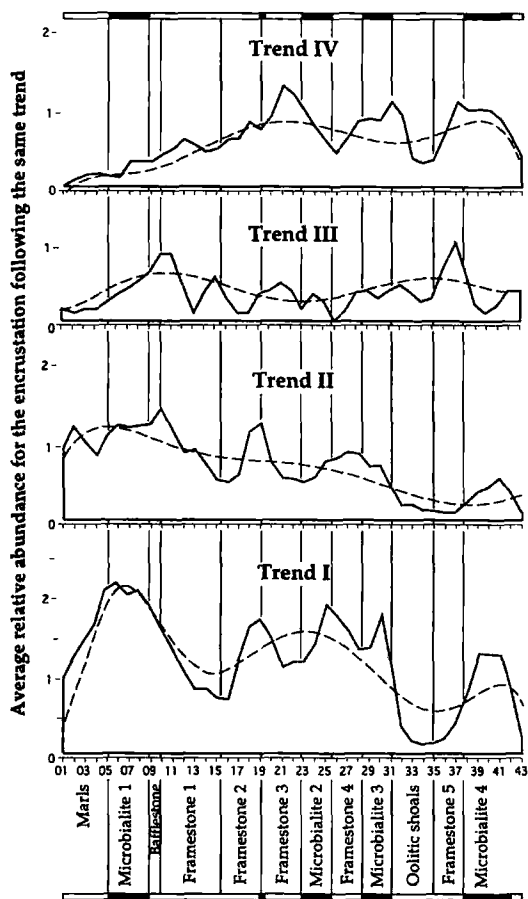


Fig. 9. Four main trends determined by the relative abundance of selected micro-encrusters. Trend I: *Terebella*, *Tubiphytes*, nubeculariid foraminifera, demosponges. Trend II: *Serpula*, *Berenicea*, other bryozoans, *Vinelloidea*. Trend III: *Lithocodium*, *Koskinobulina*. Trend IV: *Bacinella*, red algae, *Placopsilina*, calcisponges, rhaxellid microscleres. Major facies correspond to the ones defined in Figure 5, numbered intervals to the ones in Figure 8.

Fig. 4b). Thus, a substrate is created for a new microbialite-coral framestone (Framestone 5; Fig. 4b). A coral meadow develops in a bioclastic lagoon and is covered by a bioturbated, echinoid-rich grainstone interpreted as a wash-over or storm deposit. The reefal part of the Hautes-Roches section ends with thrombolites and associated *Tubiphytes*, bryozoans, and sponges (Microbialite 4; Fig. 5b). After a bioperforated hardground, facies changes completely and is now represented by bioturbated, quartz-rich limestones with coal fragments.

6 ENCRUSTATION TRENDS

6.1 Microbialite

In the Hautes-Roches section as well as in the other studied bioherms, microbialite is an important constituent. In spite of lateral variations, it is concentrated in well-defined intervals (Fig. 7). Microbialite is associated with microsolenid corals in the marly facies. In framestones, microbialite encrustations are less abundant, with the exception of the fourth framestone interval (Figs 7 and 8a)

where corals are surrounded by thick layers of thrombolite (Fig. 5b). Stromatolitic microfabric is found in several intervals (Figs 5 and 7). The fact that encrustation morphology repeatedly evolves from micro-columnar to laminated may indicate periodic changes from a shallow-subtidal to an intertidal environment. Leiolite is omnipresent in coral-rich levels where it directly covers the coral surface, but thick layers have never been observed.

Thin sections and EDS mapping reveal that quartz, feldspar, and clay minerals constitute up to 10% of the microbialites. This suggests that the depositional environments were influenced by terrigenous input also during reef growth.

6.2 Bioerosion and its relation with microbialite

Bioerosion and microbialite are closely related and are not necessarily synonymous of reef crisis. In any reef, living corals represent only the upper part of the bio-construction. The inner part is composed of dead corals, which furnish a substrate for encrustation and bioerosion in the cavities connected to the reef surface, and inside the reef body.

Bioerosion is omnipresent in the studied patch-reefs. In Figure 8a, the relative abundances of microbialite and bioerosion (mostly represented by *Gastrochaenolites*) in the Hautes-Roches section are plotted (Fig. 8a). The curves in Figure 8b are derived from Figure 8a and represent the speed of increase (positive values) or decrease (negative values) in microbialite growth and bioerosion through bivalves. Bivalve bioerosion shows a fairly good positive correlation with the relative abundance of microbialite (Fig. 8a), but the derived curves are somewhat out of phase: bioerosion by bivalves increases just before the maximum of microbialite (Fig. 8b). This is related to the fact that perforation occurs already in the living corals (paraendolithic activity) and in dying corals on the reef surface.

Five ecologically significant zones can be defined, based on the trends of microbialite abundance and bioerosion (Fig. 8d):

- * Zone a: both trends are negative, i.e. encrustation and bioerosion activity are present but "normal". This zone generally correlates with the initial growth of coral-framestones and implies a relatively balanced coral community.
- * Zone b: while microbial encrustation remains stable (negative values), bioerosion activity increases, attesting to a change in the environmental conditions and hampered coral growth.
- * Zone c: the filter-feeding bivalves suffer ecological stress and decrease their activity, while microbial encrustation reaches positive values and eventually dominates. This zone develops in the middle to upper parts of some framestones and indicates degrading environmental conditions.
- * Zone d: microbial growth slows down, bioerosion increases again.

* Zone e: both microbial growth and bioerosion activities decrease, and the starting point for renewed balanced coral growth is reached.

This analysis of microbialite *versus* bivalve-erosion ratios suggests that environmental changes influence already the upper part of the framestone facies. Some intervals in the studied section fit well this theoretical, cyclical pattern, but many intervals do not display the complete succession of zones. Additional parameters such as the evolution of micro-encrusters must be considered.

6.3 Micro-encrusters

General trends

Micro-encrusters are present throughout the boundstone facies of the Hautes-Roches section. Their relative abundances have been assessed systematically, and four trends can be identified (Fig. 9):

* Trend I summarizes the relative abundances of *Terebella*, *Tubiphytes*, nubeculariid foraminifera, and demosponges, which all covary along the section. Each maximum of this composite trend correlates with a maximum in microbialite development (Figs 8a and 9). There is a slight general decrease in abundance from bottom to top of the section.

* Trend II describes the evolution of relative abundances of *Serpula*, *Berenicea* (and a few other, undifferentiated bryozoans), and the foraminifer *Vinelloidea*. It is characterized by a general decrease of relative abundance along section, which is related to the transition from marl-dominated to carbonate-dominated facies. The peak at step 19 is due to the recurrence of marls after Framestone 2 (Fig. 5a). In the marly facies, periodic interruption of clay input permits the installation of microsolenid corals, which offer a substrate for opportunistic, filter-feeding organisms such as *Serpula* and bryozoans. The *Calamophylliopsis* bafflestone shows relatively little encrustation, probably because sedimentation rate was high and rapid coral growth outpaced microbial encrustation. *Serpula* and *Berenicea* rapidly colonized the coral branches.

* Trend III includes the evolution through time of *Lithocodium* and *Koskinobulina*. This trend shows a good correlation with the coral framestone facies, with a maximum in the presence of branching corals and in the rubble of Framestone 5. The relatively clear water permitting coral growth also favors *Lithocodium* that lives in symbiosis with a photosynthetic alga (SCHMID, 1996).

* Trend IV is followed by *Bacinella*, red algae, *Placopsilina*, calcisponges, and rhaxellid microscleres. This trend is in opposition to trend II as it increases along section and correlates relatively well with the framestone facies. The associated micro-encrusters are negatively influenced by siliciclastic input and turbid water.

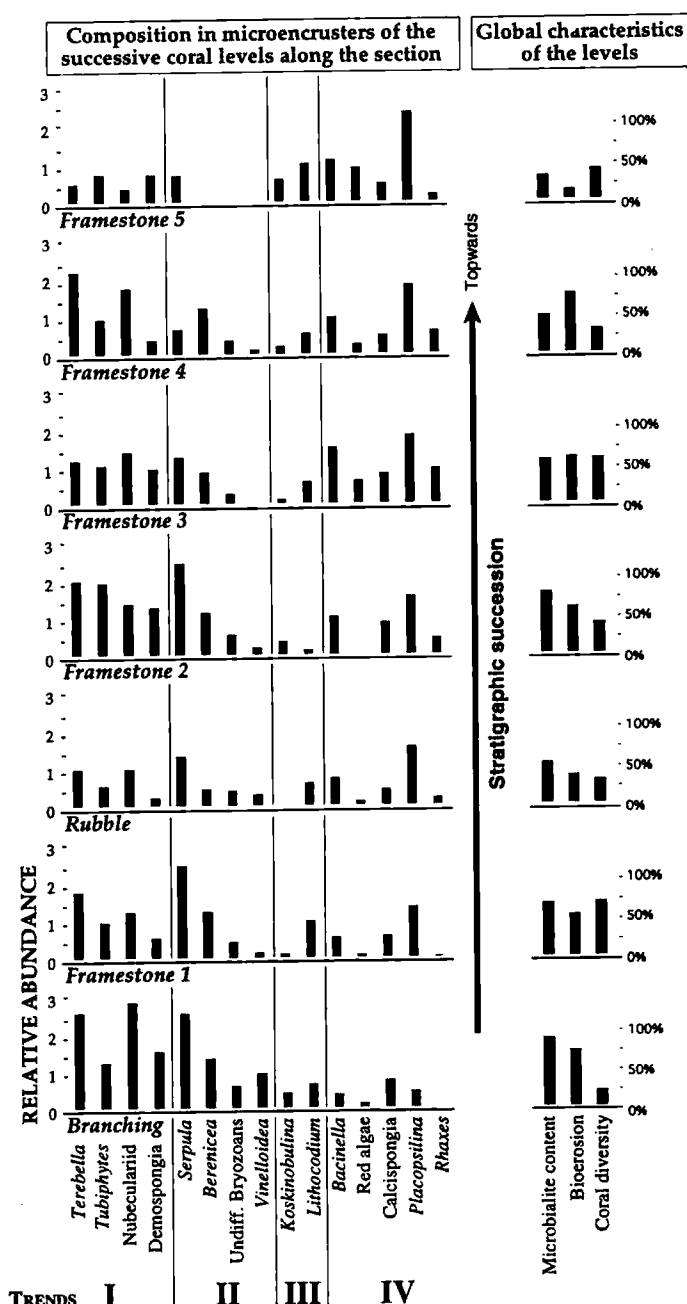


Fig. 10. Distribution of selected micro-encrusters for the different coral levels in the Hautes-Roches section (see facies distribution in Fig. 5). Trends I to IV (Fig. 9) are indicated on the x-axis. At right, general information on the coral levels (relative abundance of microbialite and bioerosion, and coral diversity based on coral genera present in the level compared to all genera found in all studied sections).

Figure 10 summarizes the occurrences of micro-encrusters in each coral-rich interval of the Hautes-Roches section. It becomes clear that, beyond the trends displayed in Figure 9, there is much variation between the various levels, implying changing environmental conditions. Framestone 5 is particular in having a low microbialite content and low values of trends I and II, whereas trends III and IV are well marked. This may be explained by a relatively high sedimentation rate inhibiting encrustation and rapidly filling the reef cavities. The organisms of

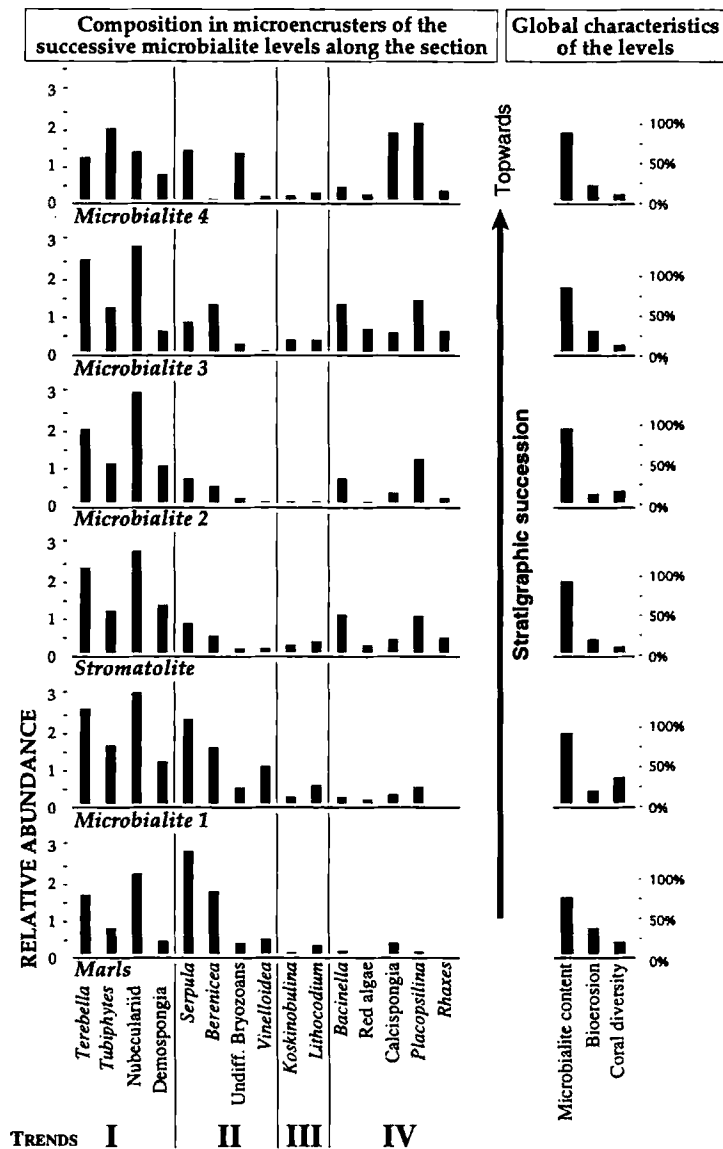


Fig. 11. Distribution of selected micro-encrustors for the different microbialite levels in the Hautes-Roches section (for explanation of parameters refer to legend of Fig. 10).

trends III and (partly) IV have the same requirements for light as the corals and generally appear in coral-rich facies.

Figure 11 represents the microbialite-rich intervals along section and the associated micro-encrustors. The dominant corals in these levels are microsolenids. Micro-encrustors defining trends I and (partly) II are well represented, whereas the organisms from trends II and IV generally are less abundant. The marly interval at the bottom of the section displays a low micro-encruster diversity but a high content in opportunistic organisms.

Trends related to reef crises

The methodology used to analyse the microbialite-bioerosion relationship has also been used for the detailed study of the different micro-encruster trends shown in Figure 9. *Terebella-Tubiphytes* have been chosen to represent trend I, the *Berenicea*-group trend II. *Bacinella* and *Lithocodium* have a quite similar evolution and are grouped to represent trends III and IV. The evolution through time of these associations is shown in Figure 12. As already

evidenced in Figure 9, the *Bacinella-Lithocodium* trend generally is out of phase with the *Terebella-Tubiphytes* and *Berenicea* trends. The derived curves (rates of change: Fig. 12b) show a good correlation between the c-zones determined in Figure 8b and the peaks of the *Terebella-Tubiphytes* association, a correlation between the framestone facies and the *Bacinella-Lithocodium* association, and an intermediate position of the *Berenicea* trend. A systematic succession of fastest increase of *Bacinella-Lithocodium*, fastest increase of *Berenicea*, then fastest increase of *Terebella-Tubiphytes* is observed (Fig. 12c).

Bacinella and *Lithocodium*, directly encrusting coral surfaces, are correlated with episodes of maximum coral diversity, whereas *Terebella* and *Tubiphytes*, which are rarely found directly on the surface of corals, are correlated with abundant growth of microbialites. This suggests that the living conditions for these encrustors have not been very different from the ones of their respective substrates. *Bacinella-Lithocodium* need oligotrophic, oxygenated, shallow, normal-marine water as do the corals, and *Terebella-Tubiphytes* can tolerate the same conditions

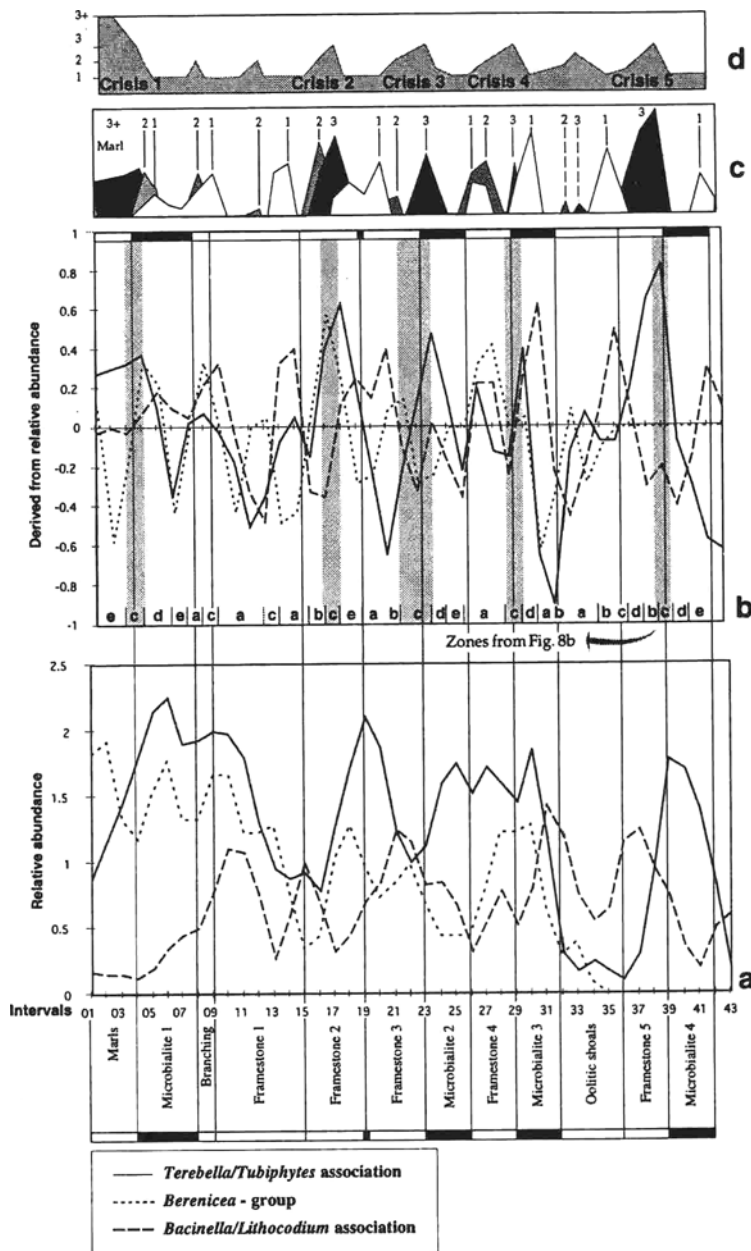


Fig. 12. Evolution of the *Terebella-Tubiphytes* association, the *Berenicea*-group (bryozoans), and the *Bacinella-Lithocodium* association.

(a) Changes of relative abundance along section. For explanation of intervals refer to legend of Figure 8.

(b) Rates of change along section. Zones a to e correspond to the ones defined in Figure 8.

(c) Synoptic representation of the positive halves of the curves in (b). 1: *Bacinella-Lithocodium*; 2: *Berenicea*; 3: *Terebella-Tubiphytes*. Note the repeated succession of maximum change for the three parameters.

(d) Periods of reef crises interpreted from (c). For explanation refer to text.

that favor microbialites. The *Terebella-Tubiphytes* and *Bacinella-Lithocodium* associations are also interpreted as having a bathymetrical significance (e.g., LEINFELDER et al., 1993a, 1993b, 1996; WERNER et al., 1994): *Terebella-Tubiphytes* colonize deeper environments and are equally found in dysoxic conditions where *Terebella* dominates (LEINFELDER et al., 1996). The filter-feeding *Berenicea*-group is found directly on coral surfaces. Its evolutionary trend (Fig. 12a, b) is situated between that of the *Bacinella-Lithocodium* and *Terebella-Tubiphytes* associations, thus implying "intermediate" environmental conditions.

Consequently, the succession in time of fastest increase of *Bacinella-Lithocodium*, fastest increase of *Berenicea*, then fastest increase of *Terebella-Tubiphytes* (Fig. 12c) represents the evolution from photoautotrophic to heterotrophic behavior. Dominance by heterotrophic

organisms can be interpreted as a crisis in the reefal ecosystem (Fig. 12d), and the repetition through time of these crises corresponds to the environmental evolution already postulated by the distribution of microbialites and bioerosion (Fig. 8c).

Figure 13 summarizes the results of the microbialite versus bioerosion analysis and that of the micro-encrusters. It implies periodic changes of the reef environment through time: five major crises of reef growth and three smaller ones can be identified. The small crises are underlined by c-zones in a framestone facies (Fig. 8). They produced less microbialite than the bigger crises and contain a relatively high amount of *Bacinella-Lithocodium* and, consequently, less *Terebella-Tubiphytes*.

The same trends have been observed so in the other studied sections of the Swiss Jura.

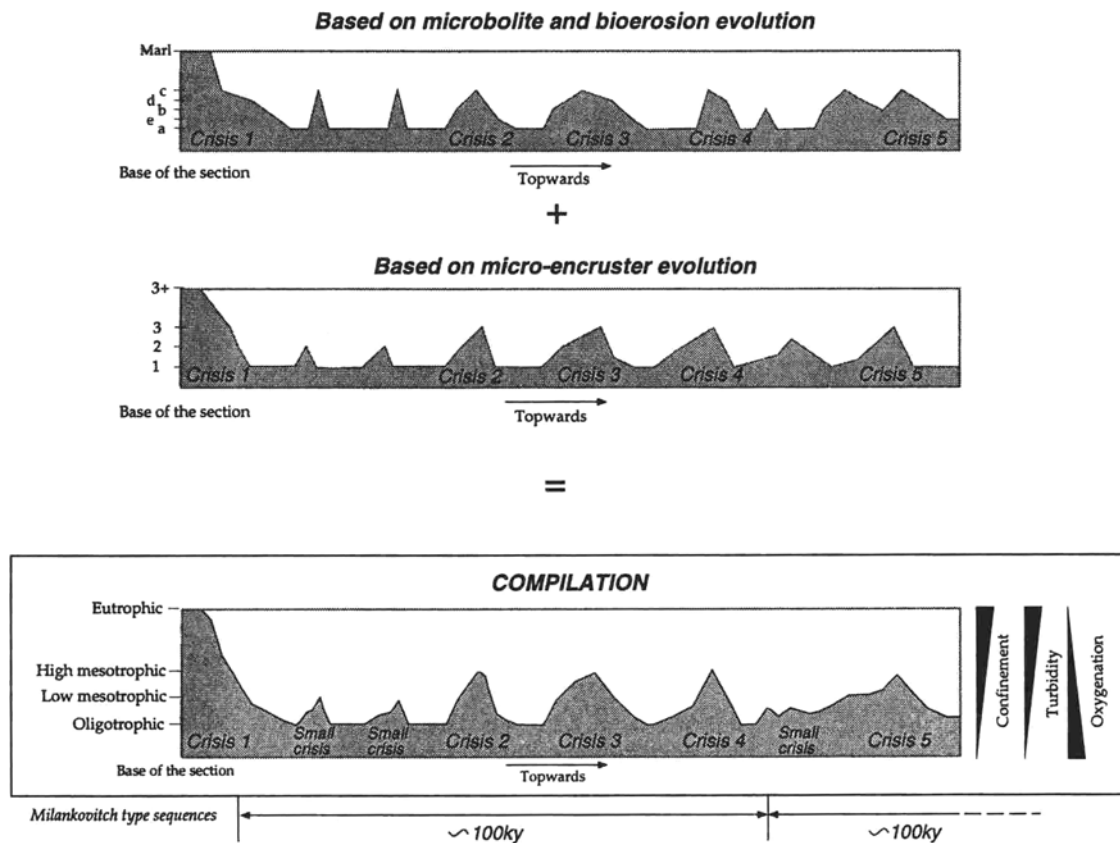


Fig. 13. Compilation of crises in reef evolution based on the interpretation of microbialite and bioerosion (Fig. 8c), and micro-encruster variation (Fig. 12d). Five major and three smaller crises are identified and attributed to trophic levels depending on environmental confinement, water turbidity, and oxygenation. Milankovitch-type sequences are indicated based on the work of PITTET (1996).

7 INTERPRETATION OF DEPOSITIONAL ENVIRONMENTS

7.1 Environmental parameters

During the formation of the reefs presented in this paper, bathymetry never exceeded a few metres (PITTET, 1996) and can thus not be the only responsible factor for the observed facies changes. However, even slight fluctuations in sea level can open and close shallow lagoons behind barrier systems and thus strongly modify water energy, oxygenation, salinity, temperature, and sediment transport. Climatic changes induced by Milankovitch orbital cycles caused rainy periods and thus periodic input of siliciclastics and nutrients into these shallow lagoons (PITTET & DUPRAZ, 1995; PITTET et al., 1995), which in turn led to fluctuations in water turbidity, hampering of carbonate production through clays, and varying trophic conditions.

Various factors controlled the evolution through time of Oxfordian coral bioherms, depending on the depositional environment. Different models have been proposed in the literature. LEINFELDER et al. (1994, 1996) gave a facies zonation for a ramp setting where bathymetry, oxygen availability, and eutrophication determine the distribution of corals, sponges, and microbialites. INSALACO et al. (1998) classified Oxfordian reefs according to their dependence on light intensity, hydrodynamic energy, and sediment balance. For KEUPP et al. (1990, 1996), sea-level

change, sedimentation rate, bathymetry, and light intensity control the spongiolite megafacies as well as microbial crusts that can tolerate higher trophic levels. The same authors have also suggested that textural changes in microbialite facies are controlled by hydrodynamic events and episodic oxygen fluctuations. CIRILLI (1997) explains that growth of thrombolites and stromatolites are mainly controlled by light intensity, water depth, and sedimentation rate.

The low sedimentation rates required for the growth of microbialite (LEINFELDER et al., 1996; NEUWEILER et al., 1996) are obtained in protected areas such as small reef cavities, and inside sponge bodies. Sediment starvation can also be related to rapid sea-level rise or fall, or to low carbonate production through eutrophication (NEUWEILER et al., 1996). High alkalinity is another important factor for microbialite growth. It can be produced by sulfate reduction in micro-environments, and by continental run-off (KRUMBEIN & SWART, 1983; NEUWEILER, 1993; NEUWEILER et al., 1996).

Nutrient availability has a great influence on carbonate production and defines oligotrophic, mesotrophic, and eutrophic conditions (HALLOCK, 1987; BRASIER 1995a, 1995b). Increase in nutrients can activate plankton blooms that diminish water transparency and thus the depth of the photic zone, potentially forcing benthic life from a phototrophic to a heterotrophic mode (CAPLAN et al., 1996;

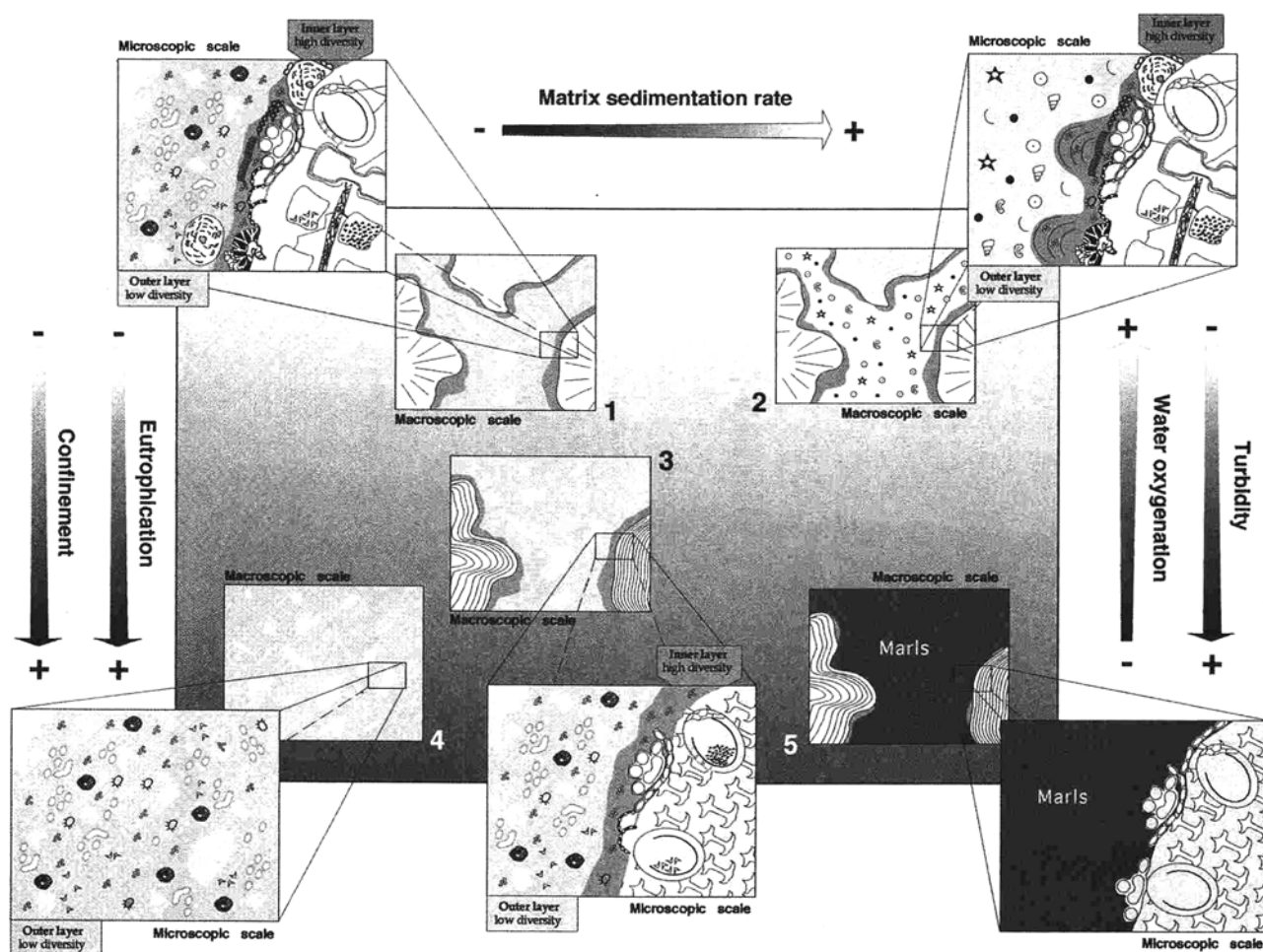


Fig. 14. Scenarios of encrustation related to environmental factors. Micro-encrusters commonly form a first layer covering the coral substrate. The second, thrombolite-dominated layer fills the remaining primary porosity. For discussion refer to text, for legend to Figure 4.

HALLOCK & SCHLAGER, 1986; HALLOCK, 1987). Fine-grained siliciclastics and particulate organic matter washed in from the continent equally increase water turbidity. Point sources and the complex morphology of the shallow platform increase the spatial heterogeneity (HALLOCK, 1987) in the distribution of siliciclastics and nutrients.

Modern reefs prefer nutrient-poor water (e.g., HALLOCK, 1997). The fact that the studied Oxfordian reefs occur in environments with a relatively high terrigenous content suggests that they were quite tolerant to nutrients. This may be explained by a weakly developed relation between symbiotic algae and the coral hosts, which is suggested by the low growth rates and weak growth-band contrasts (NOSE & LEINFELDER, 1997). Microsolenid corals display a dense structure of perforated septa with penulae suspected to have supported a complex gastro-vascular system that may have permitted a heterotrophic (suspension-feeding) mode of life comparable to the modern deeper-water *Leptoseris fragilis* (GILL & SANTANTONIO, 1995; SCHLICHTER, 1992). Microsolenids thus probably supported light and nutrient fluctuations and could therefore live in extreme environments such as muddy lagoons (AILLUD & DUPRAZ, 1998; FÜRSICH et al., 1994; INSALACO, 1996a).

In most studied samples of the Oxfordian in the Swiss Jura, the microbialite crusts can be subdivided into two distinct layers: a first one generally rich in micro-encrusters and directly covering the coral surface, and a second one with less micro-encrusters and filling partially or completely the cavities of the bioherms (Plate 11/5, /6). Five main scenarios are recognized, which are interpreted to be related to confinement of the depositional environment, eutrophication, sedimentation rate, water turbidity, and oxygenation (Fig. 14). Salinity changes certainly occurred but probably were minor: no clearly brackish or freshwater facies were found in the studied sections. In pure microbialites, the absence of fauna does not allow to interpret the salinity. Temperature changes also are difficult to assess, and it cannot be excluded that they constituted an additional ecological factor.

7.2 Oligotrophic to low-mesotrophic environments

Encrustation scenario 1

In the first scenario (1 in Fig. 14; distribution in Fig.), light-dependent organisms such as *Bacinella* and *Lithocodium* encrust the coral surfaces, indicating relatively clear water

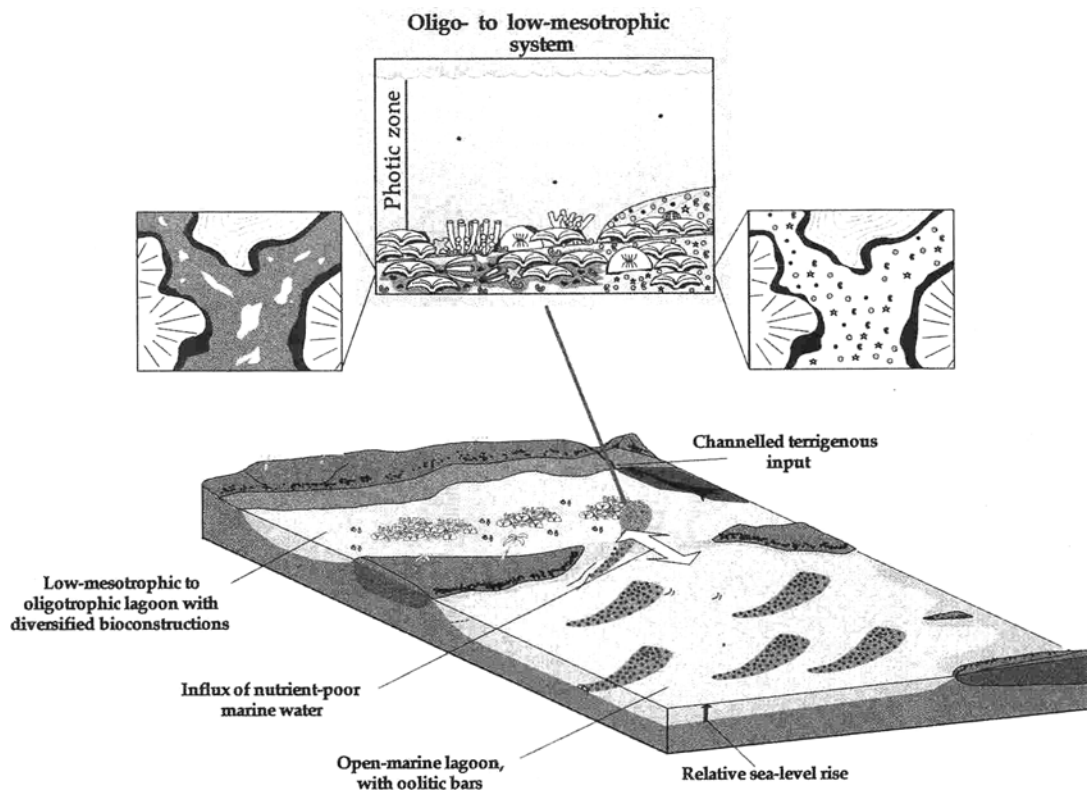


Fig. 15. Sketch of an oligotrophic to low-mesotrophic depositional system (based on Fig. 14). Note that the photic zone reaches the sea floor (inset inspired from CAPLAN et al., 1996). For legend see Figure 5.

and oligotrophic conditions. They correlate with a well diversified coral fauna (e.g., stylinid, thamnasteriid, amphiastroid, dermosmiliid, and microsolenid forms) and a generally low microbialite content. Associated are heterotrophic forms such as the opportunistic serpulids and bryozoans of the *Berenicea* group. The filter-feeding *Berenicea* always occurs below the surface of the bioherm in shadowy areas and has no competitors for space except *Serpula*. The agglutinated foraminifer *Placopsilina* is common and lives on the surface of the bioherms where it can develop its probable symbiotic relationship with photosynthetic algae. These micro-encrusters can be associated with leiolite and, locally, with laminated crusts. In some cases, small columnar fabrics occur. This type of encrustation is associated with the living corals and does not indicate any environmental crisis. The polarity of encrustation and the associated bioerosion suggest shallow water (LATHULIÈRE, 1982).

The outer microbialite layer fills the cavities of the bioherm. It is composed mostly of thrombolite in association with *Terebella* and *Tubiphytes*. This encrustation still is contemporary to the living corals. As a migrating front, it follows coral growth but stays below the bioherm surface. Photosynthesis there is not possible, and heterotrophic metabolism and possible AOM in biofilms induce carbonate precipitation. Similar thrombolitic cavity fills and cementation induced by sciaphile organisms have also been described in Recent reefs of French Polynesia (CAMOIN & MONTAGGIONI, 1994; CAMOIN et al., 1997; LAURENTI & MONTAGGIONI, 1995), and in the Oxfordian of the Paris

Basin (BERTLING & INSALACO, 1998). A comparable micro-encrusters and microbialite replacement sequence has been described by HELM & SCHÜLKE (1998) in the Upper Oxfordian of NW Germany. Zonations between lit and shadowy environments have been observed in Recent cavities but involve other kinds of micro-organisms (REITNER, 1993). These encrustations play an important role in the cementation of the bioconstructions and thus help to create a positive relief. Corals growing directly on top of each other to form a dense framestone are rare in this scenario.

Encrustation scenario 2

In this case (2 in Fig. 14; distribution in Fig. 5), only one layer with a high micro-encruster diversity directly covering the coral surface is observed. The composition is similar to the one in scenario 1, but more columnar morphologies are present. The development of microbial crust is weak due to a higher sedimentation rate. High sedimentation rate may be related to higher carbonate productivity under favorable environmental conditions, and/or storms and tidal currents may wash more carbonate grains into the lagoon. Because all primary porosity is filled by carbonate mud and sand, no cavity-filling thrombolite can develop. Debris-reefs mainly composed of large coral clasts and grainstone matrix also belong to this scenario. The coral rubble shows thin crusts generally composed of *Serpula*, *Bacinella*, *Lithocodium*, and *Solenopora*. This facies is interpreted to correspond to the most open depositional environment.

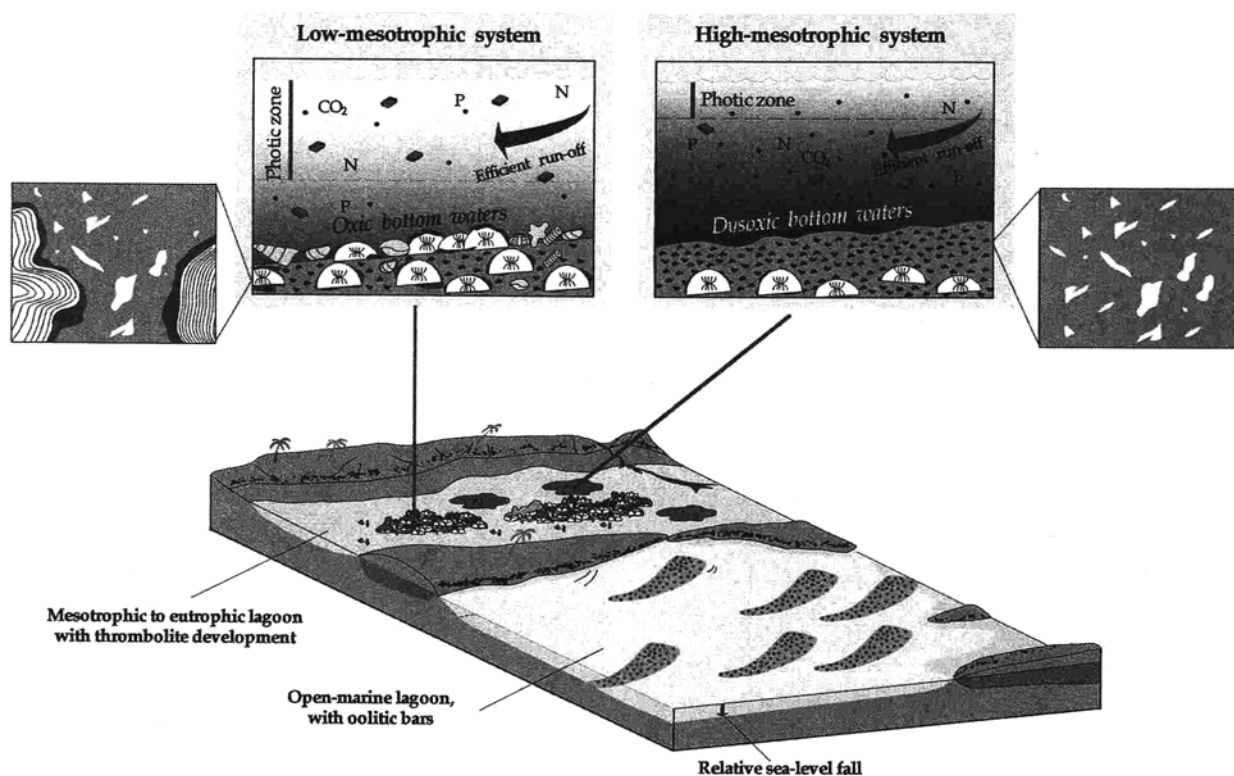


Fig. 16. Sketch of depositional system passing from low-mesotrophic to high-mesotrophic conditions (based on Fig. 14). Clay and nutrient input causes higher turbidity, and the photic zone diminishes. Thrombolite first grows inside the reef, then reaches the bioherm surface and finally covers all corals.

Depositional environments

Bioconstructions displaying scenarios 1 and 2 form in relatively well-oxygenated lagoons (Fig. 15). Coral diversity (genera, species, and morphologies) is high. The clear water permits the settlement of photoautotrophic and photosynthetic benthic fauna on the bioconstructions as well as on the lagoon floor. Carbonate productivity is high and contributes to a high sedimentation rate. Terrigenous input is present but subordinate. Some areas of the lagoons are more restricted and allow development of some microbialite, other areas are at least periodically in contact with the open-marine realm.

7.3 Low-mesotrophic to high-mesotrophic environments

Encrustation scenario 3

Two encrustation layers are differentiated (3 in Fig. 14; distribution in Fig. 5), but the composition in micro-encrusters is different from scenario 1. Light-dependent encrusters generally are missing: *Serpula*, *Berenicea*, and nubeculariid foraminifera colonize the coral surfaces. *Placopsilina* may be present. The second, cavity-filling layer is mainly composed of thrombolite with *Terebella*, *Tubiphytes*, and nubeculariid foraminifera. Coral diversity is reduced and dominated by microsolenids. Stylinid corals (*sensu* GILL, 1977) generally are absent. Bioerosion is well developed.

Encrustation scenario 4

The few corals present are microsolenids, and their

surfaces may locally be encrusted by serpulids. Only the second encrustation layer is well developed in this scenario (4 in Fig. 14; distribution in Fig. 45): between 75 to 90% of the rock are composed of thrombolite with associated *Terebella* and *Tubiphytes*. Sponge spicules and, in some cases, lithistid sponges can be found. Bioerosion is reduced to the minimum, but relatively more abundant on top of the microbialites.

Depositional environments

In scenarios 3 and 4, the scarcity of phototrophic fauna such as zooxanthellate corals and *Bacinella-Lithocodium* associations indicates environmental conditions that reduced the photic zone (Fig. 16). Increased water turbidity due to progressive closing of the lagoon could be a cause. This would induce dysoxic conditions and a decrease in drainage of terrigenous material out of the lagoon (not necessarily implying an increase of terrigenous input into the lagoon). The system thus shifts from low- to high-mesotrophic conditions. The high concentration in nutrients and organic matter provokes algal and microbial blooms. For a certain time, the heterotrophic filter feeders can follow this environmental degradation, and lithophag bioerosion as well as bryozoan populations of the *Berenicea*-group increase. Grazing and filter-feeding macrofauna (gastropods, oysters, brachiopods, and boring sponges) equally find good living conditions. Such an evolution from phototrophic to heterotrophic conditions through nutrient increase has been described by several authors (e.g., BIRKELAND, 1987; CAPLAN et al., 1996; HALLOCK, 1987).

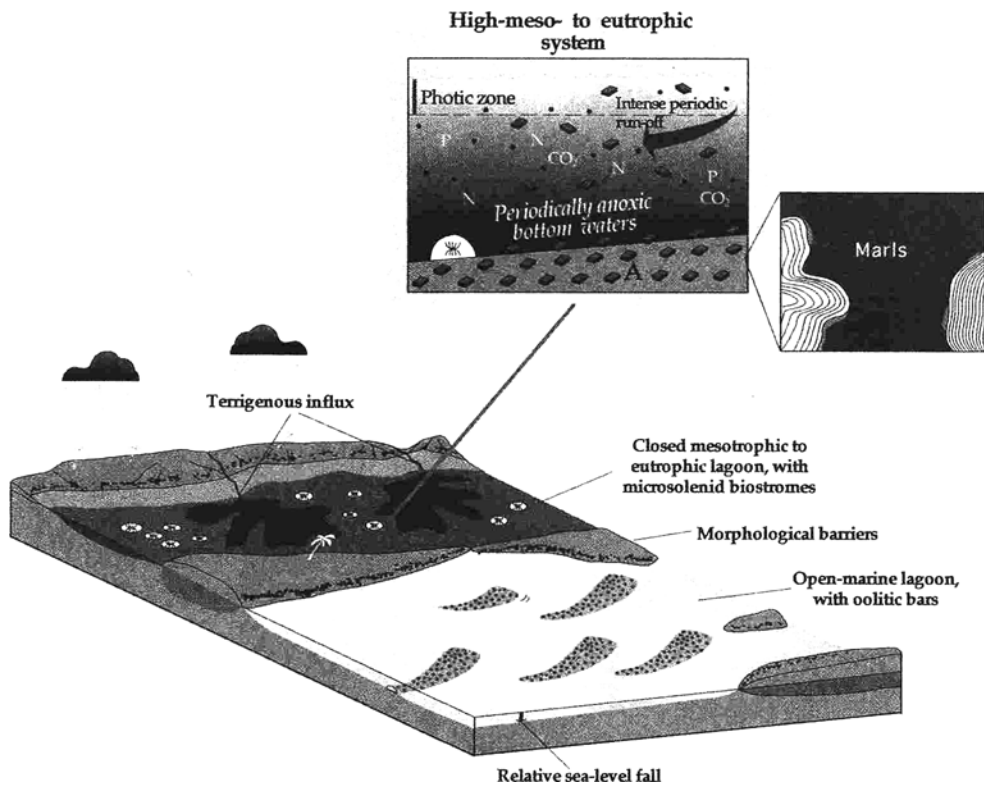


Fig. 17. Sketch of depositional system with high-mesotrophic to eutrophic conditions (based on Fig. 14). Clay and nutrient input is high but fluctuating, which allows for periodic colonization by microsolenid corals.

In low-mesotrophic conditions, thrombolite is confined to filling cavities inside the bioherms. However, if coral growth is hampered through increasing eutrophication, bioerosion outpaces carbonate production, the thrombolite growth-front reaches the top of the bioherm, and finally covers and seals it. RIDING et al. (1991) describe the evolution from a "thicket reef" to a composite crust containing microbialite in a Messinian fringing reef in Spain. Even if the ecological setting is different from that of the Oxfordian, the consequences are comparable: once coral demise is induced by environmental factors, then encrustation by opportunistic organisms takes over and kills the reef.

7.4 Fluctuating eutrophic environments

Encrustation scenario 5

This last scenario is represented by a few opportunistic micro-encrusters on the surfaces of microsolenid corals (5 in Fig. 14; distribution in Fig. 5). The poor diversity (mainly *Berenicea* and *Serpula*) and the scarcity is due to the abundance of clay minerals. Microbialite has been observed locally, but never is abundant. Bioerosion generally is important. In some cases, oysters growing on microbialite serve as substrate for massive, mushroom-shaped microsolenid colonies. Some relatively thickly encrusted microsolenids occur in the marls. This indicates that the clay input slowed down periodically in order to permit microbial growth and bioerosion by bivalves.

Depositional environment

Important, eustatically and/or climatically controlled

clay input into the shallow lagoon and the associated high nutrient levels inhibit carbonate production (EHRlich, 1996). High nutrient content also increases primary productivity, which creates oxygen-depleted bottom water following bacterial decomposition of organic matter (HALLOCK & SCHLAGER, 1986; HALLOCK, 1987). Seasonality changes or shifting point sources modulate the terrigenous input, creating poikiloaerobic conditions (OSCHMANN, 1991) that periodically allow for the installation of microsolenid colonies. Telling from the thickness (4-6 cm) of the microsolenid colonies, the growth periods last about 10 years. These corals present a relatively flat base, no important surface relief, and no lateral partial mortality typical for corals having to cope with a high sedimentation rate (BERTLING, 1993). FÜRSICH et al. (1994) describe such coral meadows that are mainly controlled by sedimentation rate.

8 SEQUENCE STRATIGRAPHY AND CYCLOSTRATIGRAPHY

The Hautes-Roches section and the bioherms of the other sections studied in the Swiss Jura can be placed in the time framework derived from high-resolution sequence stratigraphy and cyclostratigraphy (PITTET, 1996; PITTET & STRASSER, 1998). The reefal facies of Hautes-Roches (Fig. 5) contains one complete small-scale composite sequence *sensu* STRASSER et al. (1999). As implied from lateral correlations, this sequence corresponds to the first cycle of orbital eccentricity with a duration of about 100 ky. Five environmental crises have been identified in this sequence (Fig. 13), and it is well possible that they are related to the

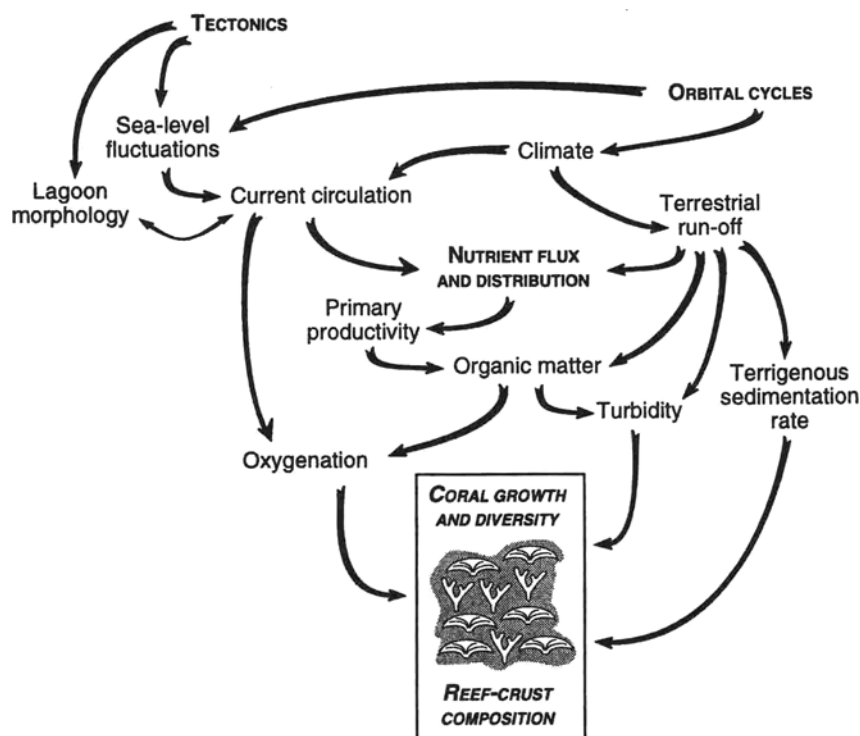


Fig. 18. Flow-chart of the main factors controlling, directly or indirectly, reef evolution.

cycle of the precession of the equinoxes with a duration of about 20 ky (BERGER et al., 1989).

Sea-level fluctuations linked to the 100-ky orbital cycle apparently were not strong enough to create emersion levels and evident sequence boundaries in the Hautes-Roches reef complex. However, trends in facies evolution, encrustation content and micro-encruster associations indicate a general opening of the system that reaches its maximum with the oolite shoals, then a closing that leads to restricted-lagoonal facies with quartz and coal fragments (Fig. 5). This general "transgressive-regressive" trend correlates laterally with other sections (PITTET & STRASSER, 1998). Elementary (20-ky) sequences in coral reefs generally are better preserved in the transgressive phase when accommodation space is created and preservation potential enhanced by rapid microbial cementation. Early highstand deposits still contain bioherms, whereas the late highstand is characterized by sandy lagoonal facies. The low-amplitude sea-level changes related to the 20-ky orbital cycles did not directly influence the reef system, but probably opened and closed lagoons and thus modified water circulation and oxygenation, and through climate changes controlled terrigenous run-off and nutrient availability. The possible complex feed-back mechanisms are illustrated in Figure 18.

On the 100-ky as well as on the 20-ky scale, oligotrophic waters and subsequent coral growth are related to rising relative sea level (Fig. 15), whereas mesotrophic to eutrophic conditions follow a sea-level fall (Figs 16 and 17). PITTET (1996) and PITTET & STRASSER (1998) showed that, for the 100-ky periodicity in the Oxfordian of the Jura Mountains, rainy periods with increased terrigenous run-off coincided with low sea-level stands, thus enhancing eutrophication and water turbidity in the already restricted lagoons. In the case of the studied bioherms, it is therefore

suggested that reef crisis corresponds to low sea level and humid or strongly seasonal climate.

9 CONCLUSIONS

In the Oxfordian coral constructions of the Swiss Jura, the equilibrium between coral growth, bioerosion, and microbial encrustation is delicate. In contrast to modern reefs, benthic microbial encrustation is dominant in these bioherms. Microbialites contribute actively to reef growth and play an important role in its cementation and preservation.

Cyanobacteria can participate in carbonate precipitation in patch-reefs and in skeletal stromatolites within the photic zone. However, many of the studied microbialites occur in reef cavities where light is not available, and where conditions may be dysaerobic. They are therefore thought to have formed mainly by bacterial activity and by mineralization induced by Ca-binding macromolecules in biofilms. Encrustations of the same texture and composition but covering the reef surface imply low light levels and dysoxic conditions that are probably related to terrigenous input and eutrophication of the depositional environment.

The succession through time of corals, microbialite types, bioerosion, and micro-encruster associations in the studied section allows to propose the following model:

Periodic and relatively high input of siliciclastics and associated nutrients, and alkaline water are the major controlling factors for reef development. Bathymetry played a subordinate role on the very shallow Jura platform, but opening and closing of lagoons linked to low-amplitude sea-level fluctuations as well as fluctuating terrigenous run-off created periodic changes in trophic conditions. An ideal reef sequence can be reconstructed:

(1) A well-oxygenated lagoon with low water turbidity allows for coral growth with relatively high diversity. Microbial crusts and micro-encrusters are associated with the living corals. Autotrophic organisms dominate, and thrombolite is formed only inside the patch-reef framework.

(2) The second stage is the confining of this lagoon, forcing the evolution toward dysaerobic and low-mesotrophic conditions. Water turbidity increases due to terrestrial run-off and algal-microbial blooms, and the photic zone consequently does not reach the sea floor any more. Bioerosion activity increases as well as the abundance of heterotrophic micro-encrusters. Thrombolite progressively reaches the surface of the bioconstructions.

(3) The lagoon becomes more restricted and high nutrient concentration induces high primary productivity, which in turn induces oxygen consumption through bacterial decomposition of organic matter. The resulting dysoxic to anoxic environment favors pure thrombolite-dominated microbialites associated with *Terebella* and *Tubiphytes*.

(4) In extreme cases, high clay and nutrient input strongly reduces carbonate production.

Five major and three smaller periods of environmentally controlled crises in coral-reef growth can be identified. Lateral correlation by high-resolution sequence stratigraphy and cyclostratigraphy suggests that these crises are probably orbitally controlled: insolation cycles induced by the precession of the equinoxes (20-ky periodicity) caused low-amplitude sea-level fluctuations that opened and closed lagoons, and climatic changes that controlled siliciclastic run-off and nutrient input. The studied Oxfordian reefs generally grew well during high sea level and dry climate, but suffered when low sea level and high rainfall in the hinterland caused eutrophication, water turbidity, and dysoxic conditions. Once coral growth slowed down and bioerosion further weakened the bioherm, microbialites took over and finally killed the reef. Consolidated through bacterially mediated cementation, however, microbialites also served as substrate for renewed coral growth once the environmental conditions allowed for it.

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