Nutritional Modes in Coral—Microbialite Reefs (Jurassic, Oxfordian, Switzerland): Evolution of Trophic Structure as a Response to Environmental Change

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Detailed study of Oxfordian coral-microbialite reefs in the Swiss Jura Mountains has identified major paleoecological variations in space and time, which are attributed to environmental changes. Micro- and macroscale semi-quantitative analyses of microbialite types, micro-encrusters, bioerosion, corals, and other macrofauna composing the reefal facies were performed. Three main trophic structures (dominant nutritional modes) were recognized: phototrophic-dominated, balanced photo-heterotrophic, and heterotrophic-dominated. A phototrophic (light-dependant) fauna dominated reefs growing in pure carbonate and nutrient- poor environments, where sedimentation rate was the main factor controlling reef growth. In mixed siliciclastic-carbonate platform environments, a balanced photo-heterotrophic fauna with periodical shifts to heterotrophic-dominated associations was induced by freshwater and sediment run-off into closed, shallow lagoons. In this case, the main factors controlling reef growth were the distribution and accumulation of terrigenous sediment on the platform and/or associated nutrient availability. The balanced photo-heterotrophic structure found in mixed carbonate-siliciclastic settings produced the most diversified reefs, suggesting that these Oxfordian reefs preferentially thrived in water moderately charged with nutrients (mesotrophic environment). In the case of strong siliciclastic accumulation and/or strong increase in nutrient availability, coral reef diversity dropped drastically and heterotrophs dominated the trophic structure. A model of the evolution of trophic structure in these reefs as a function of the governing environmental factors is proposed. Focusing on the dominant nutritional mode at each step in reef evolution allows a detailed characterization of reefal structure and a better understanding of the processes leading to coral reef settlement, development, and demise.

INTRODUCTION

Reconstruction of trophic structure is a key to better understand the ecology of paleocommunities (e.g., Scott, 1978; Stanton and Nelson, 1980). In coral reef ecosystems, the distribution of phototrophic and heterotrophic fauna in benthic communities is a function of complex interactions between nutrient availability, sediment supply, light conditions, and oxygenation (Hallock and Schlager, 1986; Hallock et al., 1988; Föllmi et al., 1994; Brasier, 1995a, b; Caplan et al., 1996; Birkeland, 1997). On shallow carbonate platforms adjacent to land, rivers may transport freshwater, sediment, and nutrients into the coral ecosystem, which may result in an increase of water turbidity, changes in water temperature and salinity, and modification of the trophic structure through nutrient excess (Carannante et al., 1988; Weissert, 1989; Hallock et al., 1993; Föllmi et al., 1994; Woolfe and Larcombe, 1998, 1999). Nutrient effect on Recent coral reef growth and development of fleshy algae remains controversial among specialists, although good examples of faunal replacement triggered by naturally or anthropogenically induced excess of nutrients and sediment have been published for example by Tomascik and Sanders (1987), Rogers (1990), and Hallock et al. (1993). Studies on Recent reefs, however, are performed over a relatively short period of time, with surveys covering a few tens of years. Fossil reefs, on the other hand, offer a time perspective that is impossible to achieve in the Recent, although the rock record presents far less detail about the initial living communities.

Coral-microbialite patch reefs of the Middle to Upper Oxfordian in the Swiss Jura Mountains offer the opportunity to study coral reef ecosystems on a carbonate-dominated platform periodically influenced by terrigenous input (e.g., Gygi and Persoz, 1986; Pittet and Strasser, 1998; Strasser et al., 1996). Point sources of terrestrial sediment and complex bottom morphologies increased the spatial heterogeneity in the distribution of siliciclastics and nutrients and, thus, created sub-environments that varied in their hospitality for reef growth. The aim of this paper is to (1) analyze these reefal communities; (2) interpret the spatial and temporal evolution of their trophic structure; and (3) present a possible model of growth, development, and demise of lagoonal coral reefs.

GENERAL SETTING

The biostratigraphic and sequence stratigraphic frameworks of the studied sections are well established (Fig. 1; Gygi and Persoz, 1986; Gygi, 1995; Pittet and Strasser, 1998; Gygi, 2000). The reefal facies belong to the St-Ursanne and Vellerat Formations, covering the *luciaeformis*

Ages	Ammonite zones	Ammonite sub-zones	Formations	Sequence boundaries
Late	bimammatum	hauffianum	Cour-genay	
		bimammatum		Ox7
		hypselum	Vellerat	
				Ox6
Middle	bifurcatus	grossouvrei		
		stenocycloides		
		rotoides		
		schilli		Ox5
	transver-sarium	luciaeformis	St-Ursanne	
		antecedens		

OXFORDIAN

☐ Studied interval

FIGURE 1—Stratigraphy, biostratigraphy, and third-order sequence boundaries of the Middle to Upper Oxfordian in the Swiss Jura based on Gygi and Persoz (1986) and Gygi (1995, 2000). Gray shade represents the studied interval.

to *hypselum* ammonite subzones (Fig. 1). The St-Ursanne Formation is up to 90 m thick and characterized by almost pure carbonate deposits. The Vellerat Formation has a mean thickness of about 55 m and represents shallow platform environments with episodic siliciclastic input. Two third-order sequence boundaries can be recognized in the studied interval (Fig. 1): boundaries Ox 5 (157 Ma according to Hardenbol et al., 1998) and Ox 6 (155.8 Ma) occur at the top of the St-Ursanne Formation and within the Vellerat Formation, respectively. Figure 2 shows the locations of the nine studied sections in the Swiss Jura Mountains and an additional one in France. The detailed study includes a total of 12 reef bodies. Three examples are presented in the first part of the data description, illustrating one reef in a pure carbonate setting and two reefs subject to different types of terrigenous influence.

METHODS

In this paper, the term 'communities' refers to 'paleocommunities' as used in paleoecology, which represent an incomplete record of the original living communities. Uncertainties related to taphonomical distortion are inherent in such a study, and caution is required when interpretations of paleocommunities are extrapolated to original living communities. A very high-resolution paleoecological analysis, including semi-quantitative estimation of faunal diversity and abundance, was carried out to characterize the paleocommunities in as much detail as possible. Nine hundred samples, laterally and vertically densely spaced, were taken from nine sections, using a sampling grid with squares 25 cm in diameter. Polished, etched, or varnished slabs and thin sections were used for binocular and microscopic analysis. The relative abundances of each reef component (macroscopic and microscopic) were assessed on a scale from 0 to 3 (0 = absent, 1 = present, 2 = common, 3
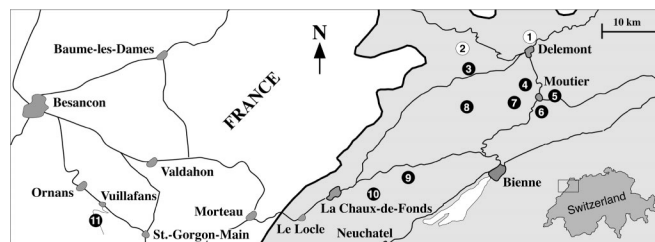

FIGURE 2—Location map of the studied sections (numbers): (1) Vorbourg, (2) St-Ursanne, (3) Tabeillon, (4) Hautes-Roches, (5) Sous-la-Jean Matthey, (6) Moutier, (7) Rainfo, (8) Pichoux, (9) Savagnières, (10) Pertuis, (11) Chateauvieux-les-Fosses. Vorbourg and St-Ursanne (white circles) represent two additional sections not studied in detail, but used for paleogeographical reconstruction.

= abundant). Lateral variability was evaluated by comparing 2 or 3 thin sections of large samples. Results were compiled on logs, combining field observations, macroscopic mapping on slabs, and microscopic data from thin sections. The quality of the outcrops did not permit continuous mapping based on digitized photographs. Two-dimensional distribution maps of reefal components were computer generated, based on the assessment of the relative abundances of these components by analyzing densely and evenly spaced samples (slabs and thin sections). Curves of relative abundances of diagnostic textural and biological elements (from bottom to top of the studied sections) were drawn using a moving average. The steps used for the moving average construction vary as a function of the total number of samples in the section (generally an average made on 10 samples with a step of 5). As the samples are spaced quite evenly and can be considered to be representative of comparable surfaces, an average value of relative abundance of the various parameters was attributed for each step.

Scanning-electron microscope and energy-dispersive spectrometer analyses were used to identify microstructure and chemical composition of the encrustations.

REEFAL COMPONENTS

The studied reefs are comprised of six main components: corals, microbialite, micro-encrusters, bioerosion features, macrofauna (other than corals), and sedimentary matrix. The diagnostic features of these components are outlined below.

Corals were identified on polished slabs and in thin sections at genus level and, where possible, at species level. Coral microstructure was studied in thin sections. Classification of the recognized coral genera is based on Alloiteau (1952), but many updates were made at all hierarchical levels based on more recent publications (e.g., Roniewicz, 1966; Beauvais and Beauvais, 1975; Roniewicz and Barbulescu, 1976; Gill, 1977; Beauvais, 1994; Morycowa and Roniewicz, 1990, 1995). Significant changes since Alloiteau (1952) include the creation of the sub-order Microsolenina (Morycowa and Roniewicz, 1995), the sub-order Rhipidogyrina (Roniewicz and Barbulescu, 1976), and a new regrouping of stylinid corals (Gill, 1977). Important results on ontogenetic evolution, populations, and species variability were furnished by Lathuilière (1988, 1996), as well as a repertory of species synonymies for Jurassic cor-

als (Lathuilière, 1989). Coral taxonomy and systematics are presented and discussed in Dupraz (1999).

Microbialite is defined as organosedimentary deposits of benthic microbial communities (Burne and Moore, 1987; equivalent to "microbolite" of Riding, 1991), and represents the second most important component of Oxfordian reefal facies after corals. Macroscopically, microbialite is recognizable by a generally darker color compared to the allochthonous matrix. It either has well-defined boundaries, or it gradually passes into the matrix. Three main microbialite macrostructures are observed in the studied reefs: clotted (thrombolite: Aitken, 1967; Kennard and James, 1986; Turner et al., 2000; Shapiro, 2000), laminated (stromatolite: e.g., Monty, 1977), and structureless (leiolite: Braga et al., 1995). Microbialite locally shows dendritic morphologies. All these macrostructures can have micropeloidal, densely micritic, or agglutinated microfabrics (Riding, 1991). Thrombolite-type microbialite is dominant in this study. Thrombolite generally is observed encrusting corals or other macrofauna (e.g., brachiopods, bivalves), but it can represent the principal facies component (over 70%) of the entire stratigraphic interval of the build-up (e.g., sections of Hautes-Roches A, Pichoux, and Moutier).

Micro-encrusters commonly are associated with the corals and microbialites. Micro-encrusters occurring in cavities can be compared to the "coelobites" of Ginsburg and Schroeder (1973), or to the "cryptobionts" of Kobluk (1988). They directly encrust the coral substrate or are found inside the microbialite. Micro-encrusters are abundant inside thrombolite and leiolite, but are nearly absent in the stromatolite facies. Micro-encrusters include different species of red algae, foraminifera, bryozoans, annelids, and sponges that were studied in detail by Dupraz (1999) and Dupraz and Strasser (1999).

Bioerosion features are ubiquitous. The most common forms are borings by bivalves reflected by the ichnogenus *Gastrochaenolites* (Kelly and Bromley, 1984). Borings by sponges (ichnogenus *Entobia*) and by foraminifera (e.g., *Troglotella incrustans* Wernli and Fookes, 1992) also have been observed.

Macrofauna other than coral and the *sedimentary matrix* found in the reefal and peri-reefal environment (Fig. 3) are important for the interpretation of the paleo-ecosystem in its entirety. The term "matrix" will be used for all sediment filling the primary porosity of the reef. Its analysis is important because it provides clues about the depositional environment surrounding the patch reefs. The term "terrigenous input" involves all material derived from continental erosion. The run-off onto the carbonate platform in the Swiss Jura Mountains was controlled mainly by rivers (Gygi and Persoz, 1986).

DESCRIPTION OF THE STUDIED REEFS

To illustrate the detailed methodology and provide the data needed for the final discussion, the description of the reefs will follow two steps: (1) presentation of three examples of detailed stratigraphical logs, each representing a reef in a particular depositional environment (pure carbonate, and two different types of terrigenous influence); and (2) an overview of the distribution of characteristic macro- and microfauna in the facies of all studied reefs. Detailed logs of all reefs are available in Dupraz (1999).

Examples of Detailed Reef Studies

Tabeillon Patch Reef

This reef is representative of those forming in a pure carbonate depositional environment (no terrigenous input). The 53 m-long Tabeillon section crops out along a small trail in the Combe de Tabeillon near the village of Glovelier in the Swiss Jura (Fig. 2). It belongs to the upper part of the St-Ursanne Formation (Fig. 1) and displays two reefal intervals (Dupraz, 1999). The younger one is shown in Figure 4. It is documented by 115 samples. The bioherm consists of a central core composed of domestone facies (dominated by dome-shaped massive corals: Insalaco, 1998) and bafflestone, with lateral onlap of peri-reefal sediment. The packstone bank at the reef base shows abundant large agglutinated foraminifera binding sand grains (Dupraz and Strasser, 1999; Hillgärtner et al., 2001). Sediment on the right side of the build-up is composed of mudstones to wackestones with reefal debris, whereas oo-biosparites to oo-biomicrites dominate on the left side (Fig. 4). This facies distribution suggests a current control on sedimentation, resulting in a protected low-energy flank (right side, "back patch reef" deposit) and a high-energy flank (left side, "fore patch reef" deposit). The reef probably had positive relief, protecting the back-reef area from impact of currents.

The coral fauna is dominated by phaceloid corals (*Stylosmilia* and *Calamophylliopsis*). Other important coral groups include microsolenids, stylinids (*Stylina*, *Pseudocoenia*), and actinastraeids (*Allocoenia*). The microbialite is composed mainly of light, poorly-structured thrombolite and leiolite. The micro-encrusters are dominated by the foraminifer *Lithocodium aggregatum* Elliot (Schmid and Leinfelder, 1996) and by *Bacinella irregularis* Radiocic (interpreted as cyanobacteria: Camoin and Maurin, 1988; Schmid, 1996).

The distribution of corals and encrustations is heterogeneous (Fig. 5). Stylinid and actinastraeid corals, and the micro-encrusters *Bacinella irregularis*, *Lithocodium aggregatum*, and *Placopsilina*, colonize the upper and lateral parts of the bioconstruction (Fig. 5A). Microsolenid corals, the bulk of microbialite, and the micro-encrusters *Terebella lapilloides* Munster and *Tubiphytes morronensis* Crescenti are situated in the central lower part of the reef (Fig. 5B). Phaceloid corals have a more heterogeneous distribution (Fig. 5C), as do serpulid worms and, to some extent, bryozoans of the "*Berenicea*" group.

Pichoux Patch Reef

This reef is representative of those formed in a mixed siliciclastic-carbonate environment. Terrigenous sedimentation was relatively low and dominated by quartz.

The section is situated along the road in the Gorges du Pichoux (Fig. 2). The reefal interval (Fig. 6) belongs to the Vorbourg Member of the Vellerat Formation (Fig. 1). The bioconstruction is under- and overlain by intertidal facies, implying a very shallow depositional environment.

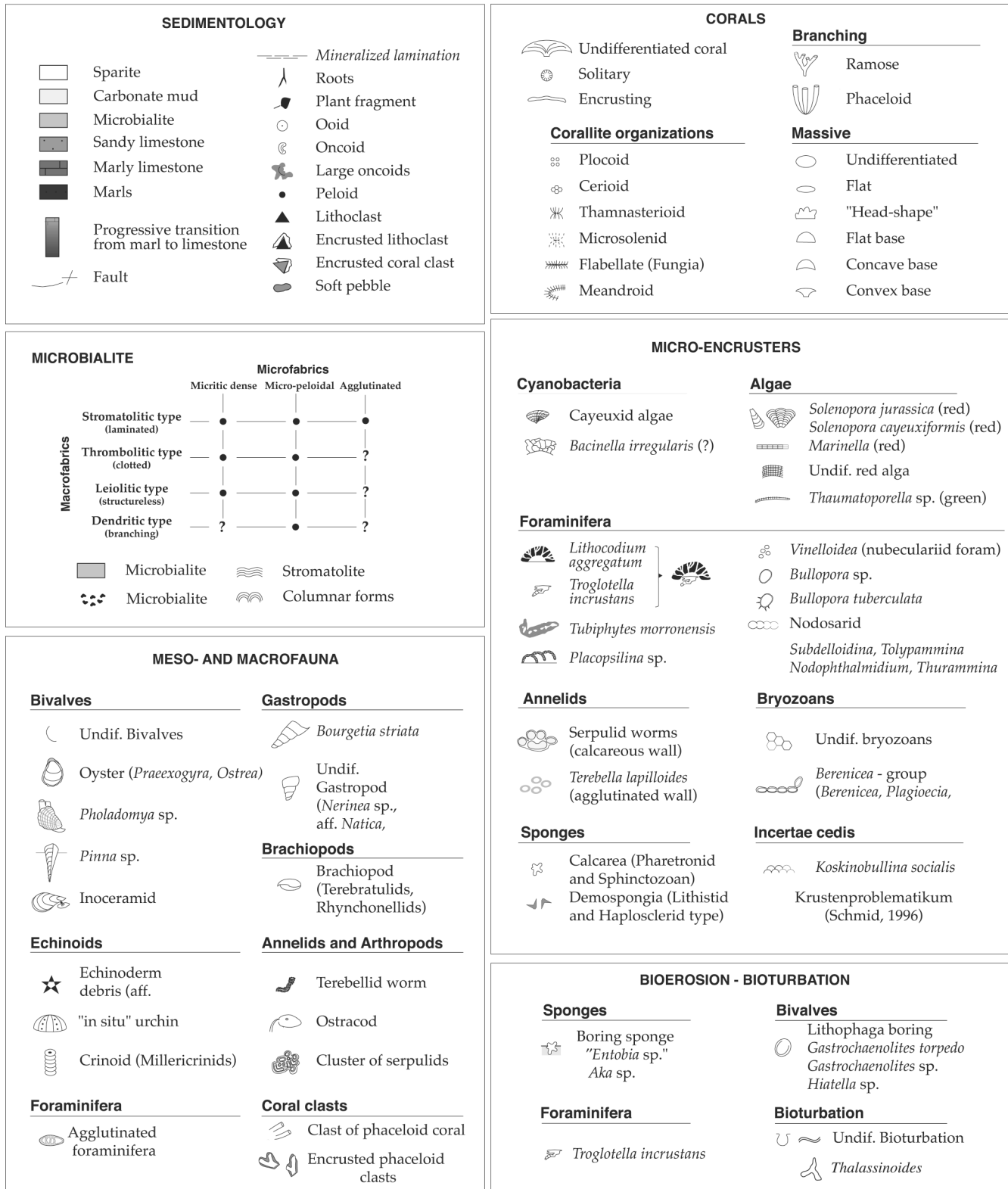Based on 145 samples, the patch reef is seen to be dom-

SEDIMENTOLOGY

- Sparite
- Carbonate mud
- Microbialite
- Sandy limestone
- Marly limestone
- Marls
- Progressive transition from marl to limestone
- Fault

- ----- *Mineralized lamination*
- Roots
- Plant fragment
- Ooid
- Oncoid
- Large oncoids
- Peloid
- Lithoclast
- Encrusted lithoclast
- Encrusted coral clast
- Soft pebble

CORALS

- Undifferentiated coral
- Solitary
- Encrusting

Corallite organizations

- Plocoid
- Cerioid
- Thamnasterioid
- Microsolenid
- Flabellate (Fungia)
- Meandroid

Branching

- Ramose
- Phaceloid

Massive

- Undifferentiated
- Flat
- "Head-shape"
- Flat base
- Concave base
- Convex base

MICROBIALITE

Microfabrics

Macrofabrics

	Micritic dense	Micro-peloidal	Agglutinated
Stromatolitic type (laminated)	●	●	●
Thrombolitic type (clotted)	●	●	?
Leiolitic type (structureless)	●	●	?
Dendritic type (branching)	?	●	?

- Microbialite
- Microbialite
- ≈ Stromatolite
- ⌢⌢ Columnar forms

MICRO-ENCRUSTERS

Cyanobacteria

- Cayeuxid algae
- *Bacinella irregularis* (?)

Foraminifera

- *Lithocodium aggregatum*
- *Troglotella incrustans*
- *Tubiphytes morronensis*
- *Placopsilina* sp.

Annelids

- Serpulid worms (calcareous wall)
- *Terebella lapilloides* (agglutinated wall)

Sponges

- Calcarea (Pharetronid and Sphinctozoan)
- Demospongia (Lithistid and Haplosclerid type)

Algae

- *Solenopora jurassica* (red)
  Solenopora cayeuxiformis (red)
- *Marinella* (red)
- Undif. red alga
- *Thaumatoporella* sp. (green)

- *Vinelloidea* (nubeculariid foram)
- *Bullopora* sp.
- *Bullopora tuberculata*
- Nodosarid
- *Subdelloidina, Tolypammina Nodophthalmidium, Thurammina*

Bryozoans

- Undif. bryozoans
- *Berenicea* - group (*Berenicea, Plagioecia,*

Incertae cedis

- *Koskinobullina socialis*
- Krustenproblematikum (Schmid, 1996)

MESO- AND MACROFAUNA

Bivalves

- Undif. Bivalves
- Oyster (*Praeexogyra, Ostrea*)
- *Pholadomya* sp.
- *Pinna* sp.
- Inoceramid

Echinoids

- Echinoderm debris (aff.
- "in situ" urchin
- Crinoid (Millericrinids)

Foraminifera

- Agglutinated foraminifera

Gastropods

- *Bourgetia striata*
- Undif. Gastropod (*Nerinea* sp., aff. *Natica,*

Brachiopods

- Brachiopod (Terebratulids, Rhynchonellids)

Annelids and Arthropods

- Terebellid worm
- Ostracod
- Cluster of serpulids

Coral clasts

- Clast of phaceloid coral
- Encrusted phaceloid clasts

BIOEROSION - BIOTURBATION

Sponges

- Boring sponge "*Entobia* sp." Aka sp.

Foraminifera

- *Troglotella incrustans*

Bivalves

- Lithophaga boring *Gastrochaenolites torpedo Gastrochaenolites* sp. *Hiatella* sp.

Bioturbation

- Undif. Bioturbation
- *Thalassinoides*

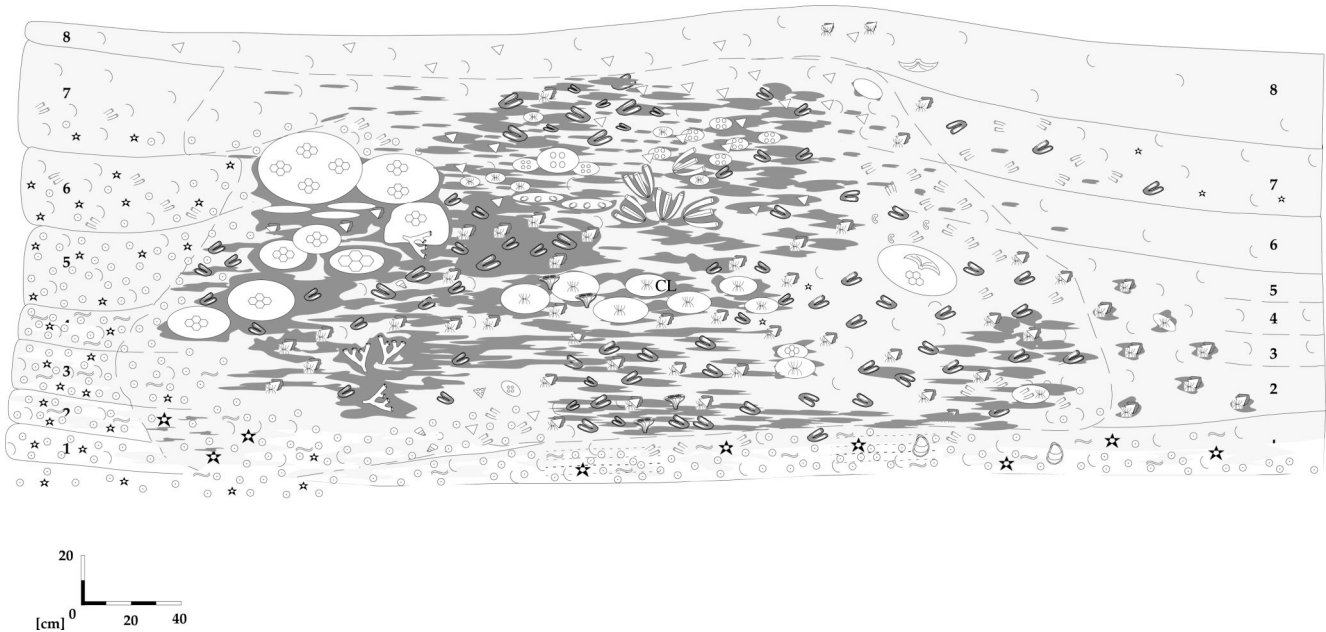**FIGURE 3**—Main components of the studied reefal facies. Symbols are used in sections and graphs.

FIGURE 4—Tabeillon patch reef (for legend see Fig. 3).

inated by microbialite facies, mainly thrombolite. Microbialite developed directly on soft carbonate mud. The section displays five main facies: patchy microbialite with oysters; dense microbialite; dense coral-microbialite framestone (*Clausastraea parva* Milne-Edwards); microbialite and corals (*Microsolena*); and alveolar microbialite.

Coral diversity is low, dominated by the genera *Microsolena* and *Clausastraea*. In the dense framestone level in the middle of the section, *Clausastraea* is practically the only coral found. A few *Isastraea* have been observed at the top of the section and are related to grainstone deposits. Also on the top, some *Allocoenia* (small cerioid forms) encrust strongly bored *Clausastraea* clasts. Stylinid corals are completely absent.

Trends in relative abundances (Fig. 7) demonstrate that microbialite is omnipresent in the section, and that bioerosion by bivalves (*Gastrochaenolites* sp.) is important. Quartz is abundant with the exception of the dense framestone level and the very top of the section. There is a good correspondence between peaks of quartz and *Terebel-*
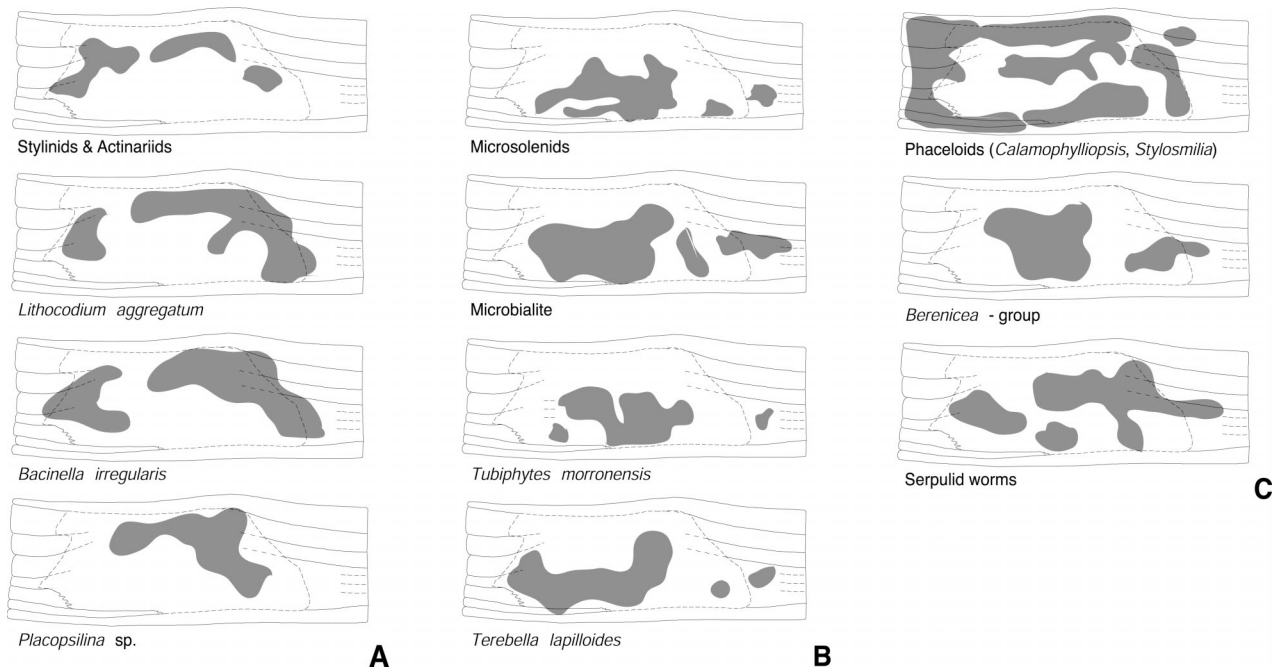

FIGURE 5—Distribution of diagnostic organisms (shaded) in the Tabeillon patch reef. For discussion refer to text.
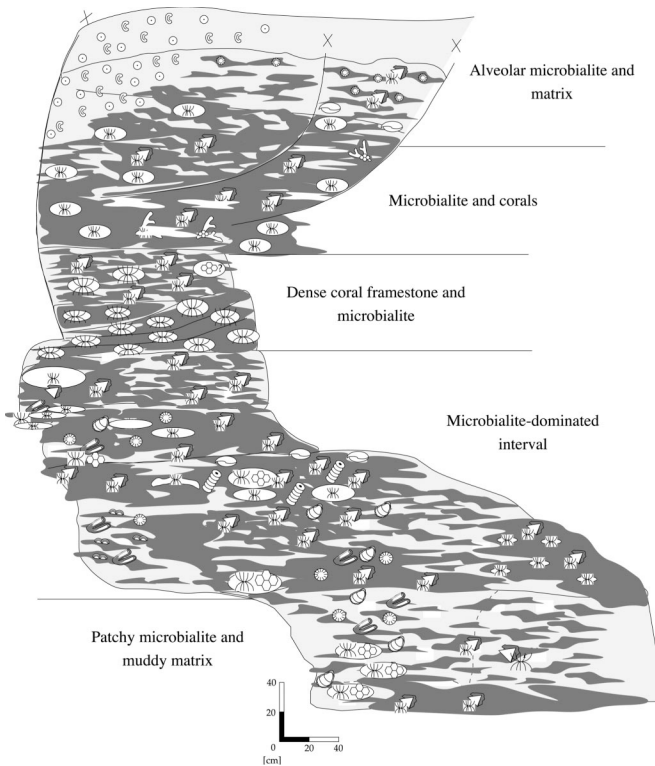
FIGURE 6—Pichoux patch reef (for legend see Fig. 3).

la lapilloides, and there is some correspondence between quartz and the filter-feeders of the "*Berenicea*" group as well as with the serpulids (Fig. 7). Only a few *Lithocodium* and *Bacinella* have been found in the top of the section: they are correlated negatively with the filter-feeding fauna and especially with the *Terebella-Tubiphytes* association (Fig. 7).

Rainfo Patch Reef

This reef is characterized by mixed siliciclastic-carbonate sedimentation with high terrigenous accumulation, dominated by clays. The section is located to the west of Moutier, along a dirt road passing through Rainfo forest (Fig. 2). The reefal part of the section (Fig. 8) is time-equivalent to the middle part of the Vellerat Formation (Fig. 1). This patch reef contains abundant marls. The paleoecological analysis is based on 78 samples and several tens of macrofossils (gastropods and echinoids) collected in the marls. The section starts with bioturbated sandy beds preserving ostracods, bivalve and echinoid fragments, mud clasts, and numerous agglutinated foraminifera (*Alveosepta* and *Pseudocyclammina*). The following interval contains two superposed sequences that show the facies evolution from marl through marly limestone with microsolenid corals to coral framestone. The top of the section displays fossil-rich marls.

The clayey marls at the base of the section ('Marls 1' to 'Marly Limestone' in Fig. 8) preserve large numbers of the grazing gastropod *Bourguetia saemanni*, associated with millericrinoid and echinoid-spine fragments. With the onset of carbonate deposition, the first microsolenid corals are observed, flat at the beginning, and more massive
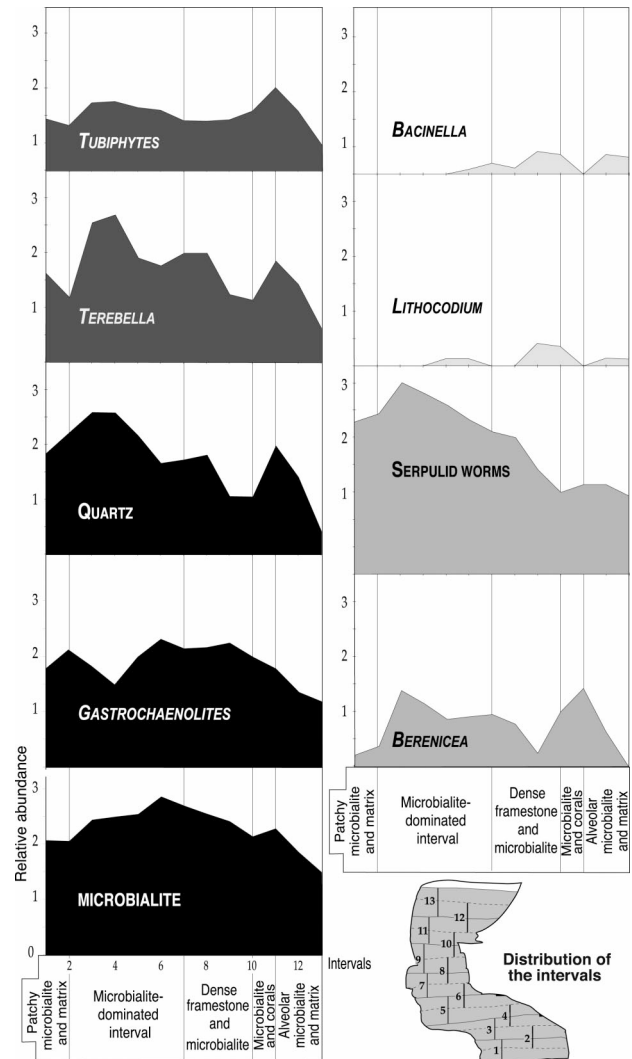

FIGURE 7—Relative abundances of selected components in the Pichoux patch reef.

afterwards. *In situ* echinoids are found in the 'Marls-Microsolenids' 1 interval (Fig. 8). Clasts of corals are encrusted by columnar microbialite rich in nubeculariid foraminifera and *Placopsilina* (quartz-agglutinating foraminifera). 'Framestone 1' (Fig. 8) is dominated by microsolenid corals (Fig. 9). This coral type again is found in the following marly interval ('Marls-Microsolenids 2') as well as in the overlying floatstone (Fig. 8). 'Framestone 2' is characterized by numerous stylinid corals. The compositional difference between the two framestone levels is emphasized in Figure 10, that shows the shift from microsolenid domination ('Framestone 1') to the predominance of small cerioid and plocoid forms ('Framestone 2').

The micro-encrusters are dominated by *Terebella*, nubeculariid foraminifera, and serpulids, but also include *Placopsilina*, *Tubiphytes*, and siliceous sponges. *Lithocodium* and *Bacinella* are practically absent. Serpulid worms are common in the marly facies, generally associated with bryozoans from the "*Berenicea*" group and calcareous sponges.
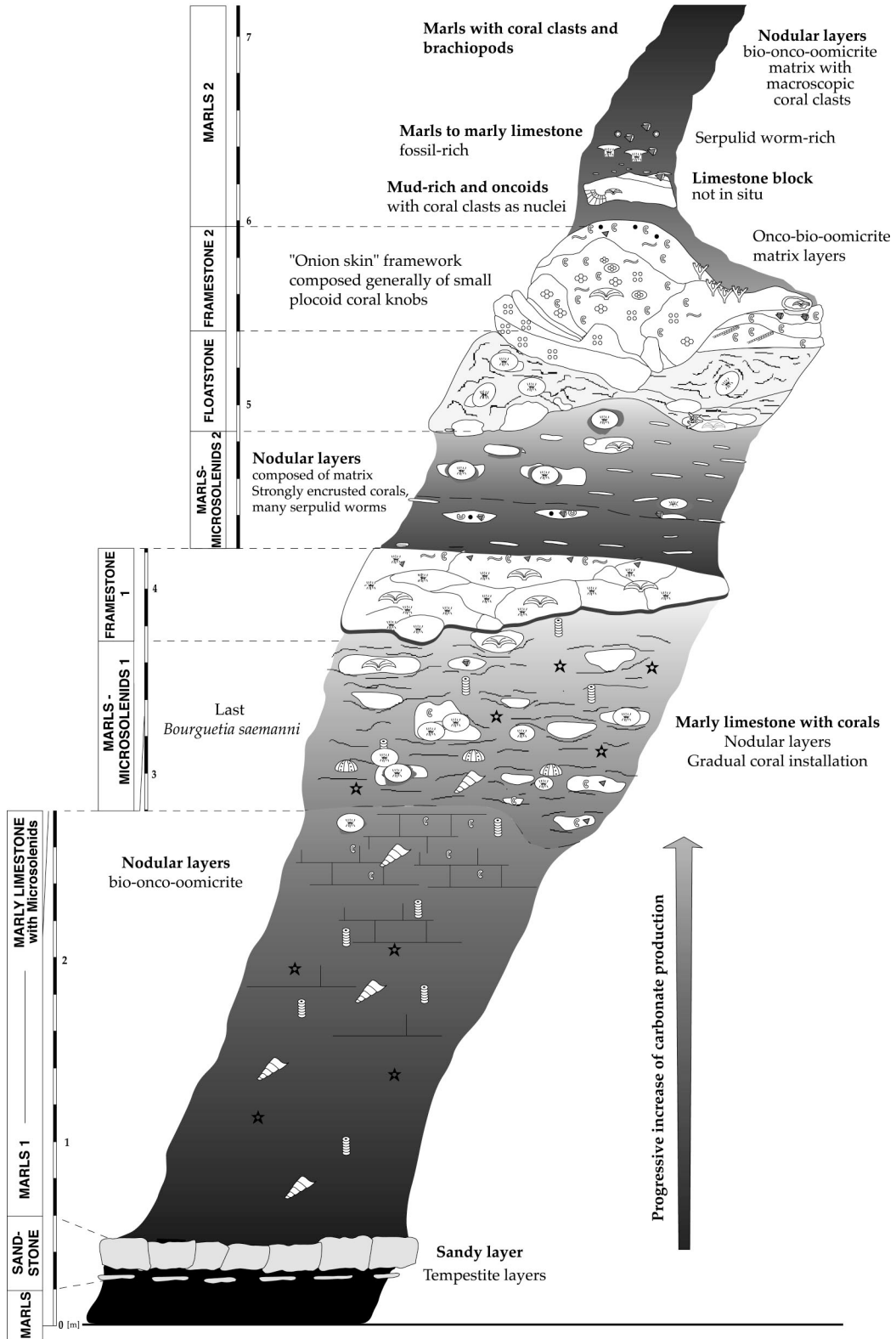
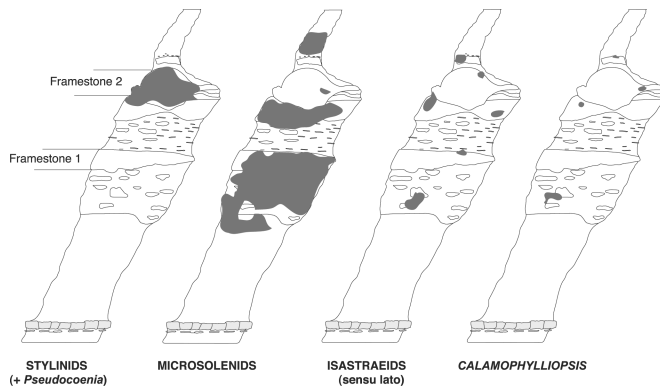**FIGURE 8**—Rainfo patch reef (for legend see Fig. 3).

FIGURE 9—Distribution of the main coral groups (shaded) in the Rainfo patch reef (see Fig. 8).

FIGURE 10—Relative importance of the main coral groups in the three coral-rich levels of the Rainfo patch reef (see Fig. 8).

Faunal Distribution in All Studied Reefs

Figure 11 provides an overview of the faunal distribution in each characteristic facies comprising the studied sections, based on the abundances of corals, microbialite, micro-encrusters, bioerosion, terrigenous content, and significant macrofauna. The facies designations denote the dominant facies in each reef.

Corals

Coral diversity is generally higher in framestone facies than in other facies. Microsolenid corals are the best represented family in the studied sections, and *Microsolena* is the most common genus of this family (Fig. 12). Microsolenids are present in all framestone facies, but they also are dominant in microbialite and marly facies (Fig. 11). This coral family prevails when total coral diversity is low (Fig. 11). In Rainfo, Hautes-Roches A, and Chateauvieux A, microsolenids are almost the only corals found in marls, showing mushroom to massive morphologies. In contrast, stylinid corals are absent in marly and microbialite facies. In this study, the term stylinid follows the definition given by Gill (1977), emphasizing a special septal ornament called an 'auricula' (Fig. 12). Stylinids are found in framestones and rubble with low terrigenous content (Fig. 11), such as in Tabeillon A and B, Chateauvieux A, Hautes-Roches A, and Rainfo (only in the second framestone interval, see Fig. 8). Stylinid corals are not observed in framestones dominated by carbonate mud as in Tabeillon B.

Phaceloid corals, incorporating the delicate genus *Stylosmilia* and the sturdier *Calamophylliopsis*, are associated with mudstone facies in Tabeillon A, Tabeillon B, and Hautes-Roches A (Fig. 11). Isastreid corals are found in many facies, but are more abundant in rudstones and floatstones as shown in Hautes-Roches A and B, Rainfo, and Chateauvieux A. *Clausastraea parva* Milne Edwards (montlivaltiid) and *Amphiastrea piriformis* Gregory (amphiastraeid) are observed only in Pichoux and Sous-la-Jean Mattheys, respectively. In these two cases, they represent the dominant genus in the sections (almost monospecific).
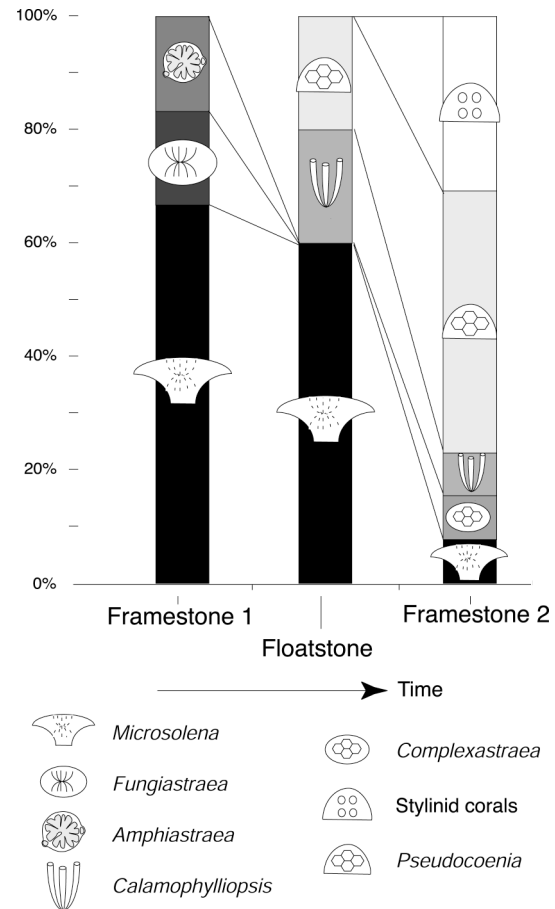
Microbialite

Microbialite is more abundant in the mixed carbonate-siliciclastic environments than in pure carbonate settings. Generally, it is associated with high quartz and low marl contents. Nature and color of the microbialite change as a function of terrigenous content in the sections (Fig. 11). In pure carbonate facies, such as in Tabeillon A and B, light leiolite is often difficult to differentiate from allochthonous micrite with the naked eye (Fig. 13A). This leiolite, however, displays a clear micropeloidal microstructure under the microscope (Fig. 13B). The thrombolite found in terrigenously influenced reefs is darker, showing more contrast between the mesoclots (Kennard and James, 1986; Shapiro, 2000) and the interstitial, unbound micrite. Energy-dispersive spectrometry (EDS) shows that dark thrombolite includes more elements coming from siliciclastics such as Si, Al, Mg, and K, as well as more S, Fe, and locally P and Ti (Dupraz, 1999). The darker thrombolite occurs in Pichoux, where it is associated with high quartz content and plant fragments.

Thrombolite is also an important component of framestones (Fig. 11). Its importance drastically decreases in the marly and rubble facies, whereas the maximum of relative abundance is observed in quartz-rich intervals without marls (Pichoux, Hautes-Roches A, Moutier,

FIGURE 11 table — Compilation of diagnostic facies components (relative abundances on a scale 0–3; empty = 0, 1+ = 1.5).

Column key (Site : Facies):
1 SLJM:Marls · 2 SLJM:Coral Meadow · 3 HR-B:Marly Limestone · 4 HR-B:Framestone · 5 HR-B:Rudstone · 6 RAINFO:Marly Limestone · 7 RAINFO:Framestone · 8 RAINFO:Floatstone · 9 PICHOUX:Microbialite · 10 PICHOUX:Framestone · 11 PICHOUX:Rubble · 12 HR-A:Marls · 13 HR-A:Microbialite · 14 HR-A:Framestone · 15 HR-A:Rubble · 16 MOUTIER:Microbialite · 17 MOUTIER:Framestone · 18 CV-A:Marly Limestone · 19 CV-A:Rubble · 20 CV-B:Microbialite · 21 CV-B:Mud-Corals · 22 TAB-A:Carb. Mud · 23 TAB-A:Framestone 1 · 24 TAB-A:Framestone 2 · 25 SAV:Dendritic microb. · 26 SAV:Framestone · 27 SAV:Oncolites · 28 PERTUIS:Framestone · 29 PERTUIS:Perireefal · 30 Sum-Mixed:Marls · 31 Sum-Mixed:Microbialite · 32 Sum-Mixed:Framestone · 33 Sum-Mixed:Rubble · 34 Sum-Carb:Framestone · 35 Sum-Carb:Carb. Mud

Group	Facies	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
	Total diversity		1+		2	2	1+	2	1+	1+	2	2	1	1+	3	3	1	3	2	2+	1+	2	1+	2	2	1	2		2	2	1+	1+	2+	2	2	1+
Corals	Actinastraeid			1				1	1	1	1	1			2	1		1							2		3					1	1+	1	1+	
Corals	Amphiastraeid		3				1																								-					
Corals	Cyathophorid																		1																-	
Corals	Stylinid							1+	1						2	3		1	1	3		1	1		2		2		3	1			2	2	2	1
Corals	Phaceloid				1	1		1	1						1	2		1	1				3	2	3	1	3		2	1	-	1	1+	2+	3	
Corals	Montlivaltiid							1		3	3	1			1				1	1											-		1+	1		
Corals	Isastraeid		1		2	3		2	3			1			1	3		1	1	3							1		2		-		2	3	1+	
Corals	Placosmiliid		1																																	
Corals	Dermosmiliid		1		2	1		1	1				2	2	2			1	1	1		2	2	2	2				1	1	1	1	2	1+	1+	2
Corals	Rhipidogyrid														1	1				1							1		1	1			-	-	-	
Corals	Microsolenid				2	1	3	2	2	3	1	1	3	3	2		1	1	3	2	3	2	2	3	1	1	2		2+	1	3	3	2	1	2	2
Corals	Latomeandrid				2	1	1				1	1			2	1		1	1	2		1		1	1					2	1	1+	1+	1+	1+	
Corals	Haplaraeid														1	1	1	1											1	1			1	1		
Corals	Actinacidid							1			1	1		2	2		1	1		1							1				-	1+	1+	-	-	
Corals	Thamnasteriid														2				1	1							1					1	1	-	-	
Microbialite	Thrombolite		1	1	1+		2	2	1	3	3	1	2	3	2	1	3	2	2+	1	3	1							2	1	1+	3	2	1		
Microbialite	Leiolite																						1	2	1+	2	2	2							2	1
Microbialite	Laminated												1	2														2			-	-				
Microbialite	Columnar			2	2					1	1	0		2	1		1	1	1	2	1	1	1	2		3	1				1	1+	1	-	-	-
Micro-encrusters	Red algae														1	2+									2		2	1		1			-	1+		
Micro-encrusters	Bacinella				1						1				1+	1				3+		2	1+		2+		2	2+	2+	1+		1+	1+	2+	1+	
Micro-encrusters	Lithocodium				1			1			1				1+	1			2	3+			2		3	2	3		3	2	-	1+	1+	2+	2	
Micro-encrusters	Placopsilina				2		1	1						1	2	1		1	1			2		1	1		1		1	1	-	-	1+	-	1	
Micro-encrusters	Nubeculariid				2	1	2	2			1		3	3	1	1	1	2	1	1	1		1	1	1	2	1	1	1		2	2	1+	1	1	1
Micro-encrusters	Tubiphytes				1		1	1	1	1	1			1	2	1	2	2	1		1	1	1	2	2	1	1	1	1		1	2	1+		1+	1
Micro-encrusters	Terebella				1		1	2	1	2	2	1	2	2	1	1	2	1	1	1	3	2	1	2	1		1+		1	1	1+	2+	1+	1	1+	1
Micro-encrusters	Serpulid		1	1			2	1		2	3	1	3	2	2	1	2	2	1+	1+	1		2	2	1		2	1	1	1	2	2	2	1	2	2
Micro-encrusters	"Berenicea"				1		2	1		1	1		2	1	1	1	1	1	1				1	2	1		1	1			1+	1	1	-	1+	
Micro-encrusters	Calcisponge				1		1	1		1	1		1	1	1	1			1								1				1	1	1	-	1	
Bioerosion	**Bioerosion**				2	1	2	2	1	2	2	1	2	2	1	1	2+	2	2+	1	1	2	1	2	1		1		1	1	2	2	2	1	1+	1
Significant Macrofauna	Echinoderms			2	2	2	2	1	2	1	1	1			2	3		2		1			1		1		1			1	1+	-	1+	2	1	
Significant Macrofauna	Bivalves			2+	2	3		2	1	2	1	1	2	1	2	1	2	2+	2	2	2	1	1	1	1		1	1	1+	1	2	2	2	2	1	1
Significant Macrofauna	Gastropods			3	1	1	3	1+	1		1	1	1	1	1+	3	1	1	2	1	1						1	1	1	1	2+	1	1+	1	1	
Significant Macrofauna	Brachiopods				1		1	1	1	1	1				1				1	3											1+	-	1	-		
Significant Macrofauna	C. ag. forams	1	2	3	1		2						1						2												2					
Significant Macrofauna	Large burrows			2																											1+					
Terrigenous input	Quartz	3	3	3	3	2	3	1+	3	2	2	2	2+	2	1+	1+	3	2	2+				3	3					1	1	3	2+	2	1+		
Terrigenous input	Marls	3	1	3			3	1	1	1			3						2	1											3	1	-			
Terrigenous input	Plants	3	2	1						1									1												1+	-				

FIGURE 11—Compilation of diagnostic facies components used for the paleoecological analysis. Relative abundances were assessed on a scale from 0 to 3 (empty boxes=0, 1+ = 1.5). Gray boxes emphasize important components of a given reefal facies. "C. ag. forams" stands for "Complex agglutinated benthic foraminifera" (*Pseudocyclammina*, *Alveosepta*). Coral data of Pertuis and Moutier are placed as indication only, because macrofauna sampling was not as extensive as in the other sections (Moutier samples came from a core and the Pertuis outcrop does not permit extensive macroscopic sampling). Nevertheless, the results from these two sections fit well with those from reefs in comparable environments.

Chateauvieux A and B). However, corals found in the marls may be encrusted by thrombolite to some degree. Alveolar thrombolite is observed in marly and muddy intervals (Hautes-Roches B, Pichoux, Moutier), and important dendritic microbialite development occurs in Chateauvieux B and Tabeillon B, displaying centimeter-size columns. Dendritic microbialite shows a complete lack of associated macro- and microfauna (Tabeil-
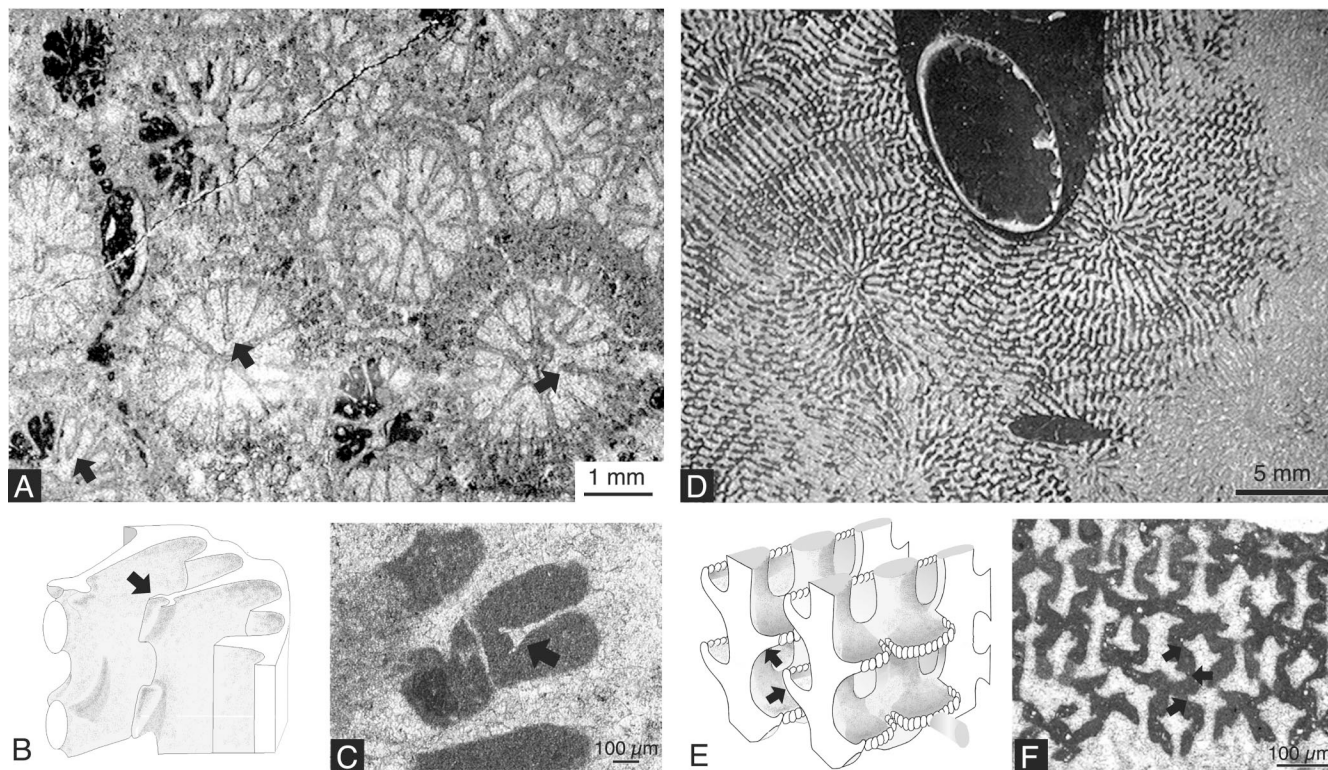
FIGURE 12—Stylinid and microsolenid corals. (A) Transverse section of *Heliocoenia variabilis*, showing auricle structures at the internal edge of the septa (arrows). Thin section, Hautes-Roches section, sample HR85. (B) Three-dimensional reconstruction of a stylinid coral, showing the specific fork-shape structure of the auricles (arrow). Picture modified from Gill (1977). (C) Transverse section of a stylinid coral with auricle (arrow). Thin section, Hautes-Roches section, sample HR235. (D) Transversal section of a microsolenid coral (*Microsolena* sp.) showing the typical perforated septa. Thin section, Hautes-Roches section, sample HR4. (E) Three-dimensional reconstruction of the microsolenid septal structure, showing the characteristic alternated pennulae (arrows). Picture modified from Gill (1967). (F) Longitudinal section of a *Microsolena* sp. with alternated pennulae (arrows). Thin section, Hautes-Roches section, sample HR2.

lon B), with the exception of scarce encrusting foraminifera (*Tubiphytes* and nubeculariids).

Micro-Encrusters: Relation with the Substrate

Micro-encrusters are not distributed randomly in the studied samples. They follow spatial patterns in relation with the substrate. Two layers, representing successive colonization, generally can be distinguished (Fig. 14).

The first layer of micro-encrusters is directly in contact with the substrate (corals or other hard substrates) and generally presents a high diversity of micro-encrusters. These include red algae, organisms having affinity with cyanobacteria (such as cayeuxid algae and *Bacinella irregularis*), foraminifera (such as *Lithocodium aggregatum*, *Placopsilina* sp., and *Bullopora* sp.), serpulid worms, bryozoans from the "*Berenicea*" group, calcisponges, and taxa incertae sedis (such as *Koskinobullina socialis* Cherchi & Schröder).

The second layer overlies the first, partly or completely filling the remaining porosity. It is characterized by micro-encrusters associated with abundant microbialite. Micro-encruster diversity generally is lower than in the first layer, including nubeculariid foraminifera and *Tubiphytes* sp., the annelid *Terebella lapilloides*, and some siliceous sponges. This second layer of micro-encrusters commonly is dominated by *Terebella lapilloides*, or composed exclusively of thrombolite.

Re-colonization of a second layer of micro-encrusters with an association typical of the first layer has never been observed, whereas repetitions of coral growth and first-layer micro-encrusters are found ('sandwich' structure, Fig. 14A).

Micro-Encrusters: General Distribution

Some micro-encrusters, such as terebellid and serpulid worms, "*Berenicea*" group bryozoans, *Tubiphytes*, and nubeculariid foraminifera, are present in almost all reefs, whereas red algae, *Bacinella irregularis*, and *Lithocodium aggregatum* are distributed non-randomly (Fig. 11). Three micro-encruster associations are recognized, according to the distribution of their maxima of relative abundance in the studied reefs.

The first association includes forms typical of the first layer of encrustation: red algae, *Bacinella irregularis*, and the foraminifera *Lithocodium aggregatum* and *Placopsilina* sp. These micro-encrusters only are found in framestone facies and rubble. The maxima of relative abundances occur in pure carbonate settings such as in Tabeillon A and B, Pertuis, Savagnières, and in the pure carbonate rubble of Chateauvieux A.
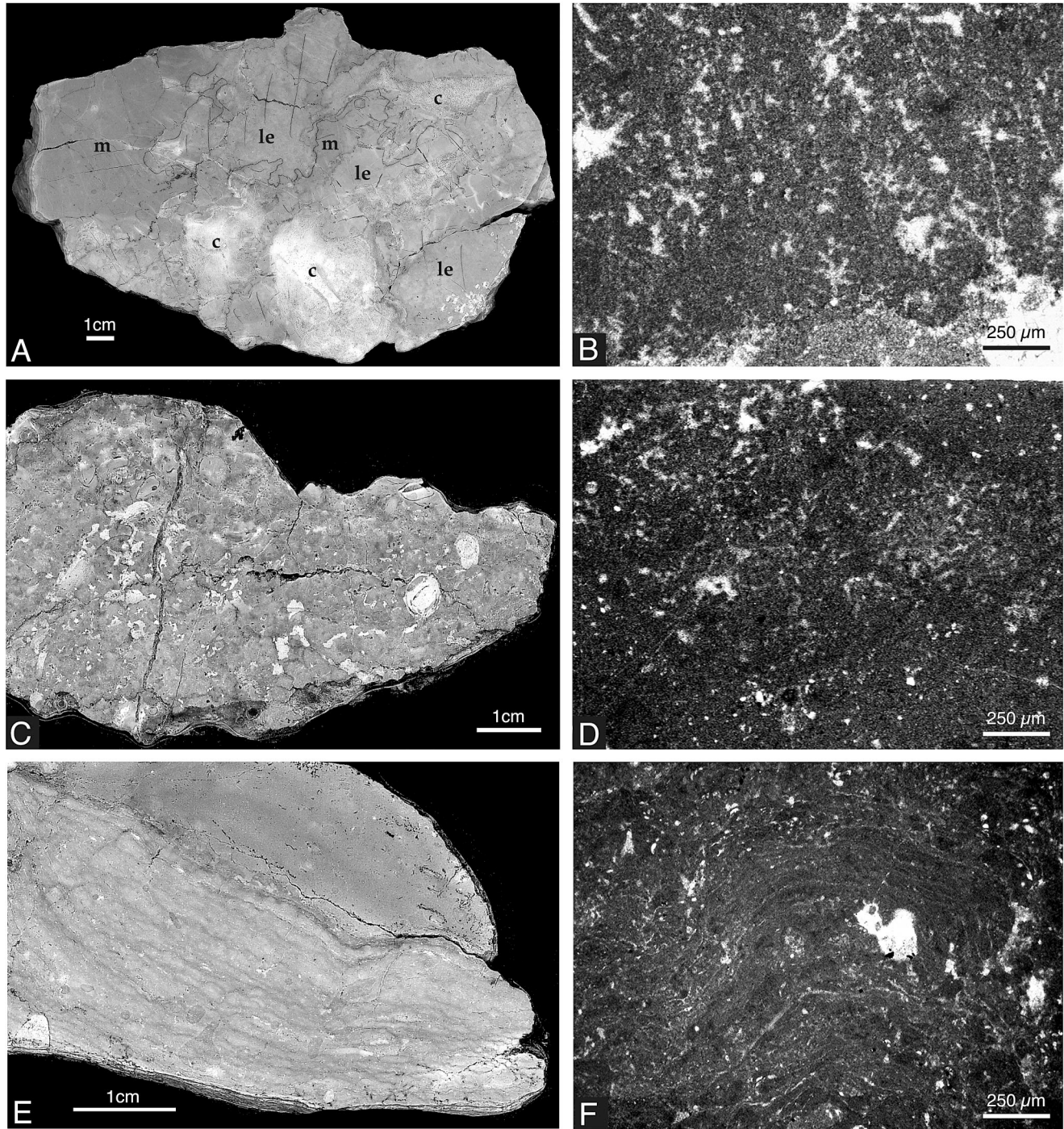
FIGURE 13—Examples of microbialite texture. (A) Very poorly structured thrombolite to leiolite (le), matrix (m), and corals (c). Etched slab, Tabeillon section, sample T118. (B) Micropeloidal to micritic dense microfabric of leiolite. Thin section, Tabeillon section, sample T123. (C) Thrombolitic macrostructure (clotted). Etched slab, Hautes-Roches section, sample HR21. (D) Micropeloidal to micritic dense microfabric of thrombolitic microbialite. Thin section, Pichoux section, sample P65. (E) Stromatolitic macrofabric (laminated). Etched slab, Hautes-Roches section, sample HR101b. (F) Example of stromatolitic microfabric (laminated micropeloidal and dense micrite). The lamination is underlined by the presence of clay minerals (Dupraz, 1999). Thin section, Hautes-Roches section, sample HR142.

The second association involves bryozoans of the "*Berenicea*" group and serpulid worms. These micro-encrusters are found directly in contact with the substrate within the first layer of encrustation. Although they are well distributed in the different reefs, the abundance maximum is observed in the marly facies, where they commonly represent the only forms of micro-encrusters on corals. They are covered locally by a layer of microbialite containing micro-encrusters such as nubeculariid foraminifera, *Tubiphytes*, or *Terebella lapilloides*.
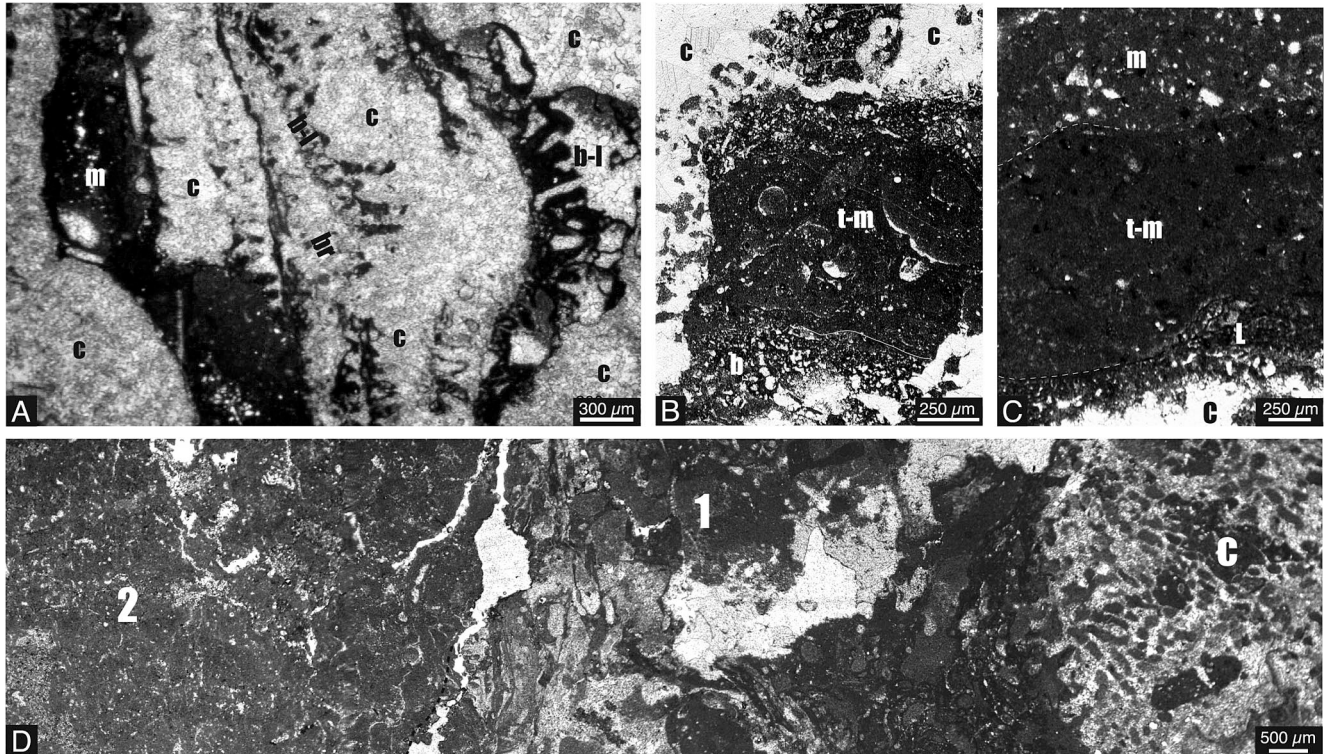
FIGURE 14—Examples of layers of micro-encrusters contained in microbialite. (A) Succession of coral (c) and first layer of encrustation composed of *Bacinella-Lithocodium* (b-l), bryozoan (br), and matrix (m). Hautes-Roches, HR86''. (B) Encrustation displaying two layers. The first one, composed of *Bacinella irregularis* (b) directly encrusts the coral substrate (c). The second one, built of *Terebella* and micropeloidal microbialite (t-m), fills the remaining porosity. Tabeillon, T19. (C) Similar pattern of encrustation as (B), but the second layer (t-m) does not completely fill the porosity, which is topped up finally by matrix (m). Tabeillon reef, sample T12. (D) Encrustation showing progressive transition between two layers: (1) high micro-encruster diversity (*Placopsilina*, ''Serpula'', ''Berenicea'', nubeculariid forams) but without *Lithocodium* and *Bacinella*, (2) poorly-diversified second layer with mainly micropeloidal thrombolite, few *Terebella*, and *Tubiphytes*.

The third association contains organisms typical of the second layer of encrustation. The dominant taxon is the worm *Terebella lapilloides*, which commonly is associated with *Tubiphytes morronensis* and nubeculariid foraminifera. *Terebella lapilloides* is observed in all facies, but its relative abundance is clearly higher in mixed carbonate-siliciclastic settings where it positively correlates with microbialite facies (Fig. 11).

Bioerosion

In the reefs studied, bioerosion is observed in any facies where hard substrate is available. *Gastrochaenolites* (bioerosion by bivalves) is the most abundant ichnogenus. Although lithophagous bivalves generally perforate dead corals, evidence of settlement in living colonies has been found, attested to by motion traces and coral growth reaction (Dupraz, 1999; see also Kleemann, 1994).

Bioerosion is more abundant in the mixed carbonate-siliciclastic environments than in the pure carbonate settings (Fig. 11). In mixed carbonate-siliciclastic settings, bioerosion is commonly more abundant in microbialite facies and in marls than in framestone facies (Fig. 11). Corals found in microbialite-dominated facies are strongly bioeroded. *Gastrochaenolites* (locally with geopetal fillings) commonly is found in pure thrombolite and leiolite deposits, implying early hardening of this encrustation.

The maximum of bioerosion generally occurs just before the maximum of microbialite development (Dupraz and Strasser, 1999). Bioerosion is also more abundant in framestones displaying low coral diversity such as in Pichoux and Rainfo, when compared to high-diversity reefs (Fig. 11).

DISCUSSION

The results presented herein indicate significant differences in micro- and macrofaunal composition within individual reefs and between reefs thriving in different environments. However, similar compositions were found in similar environments within reefs of different ages and positions on the platform (e.g., corals, *Lithocodium*, and *Bacinella* in framestone facies without siliciclastics; lack of heterotrophic macrofauna in pure carbonate settings; microsolenid, thrombolite and *Terebella lapilloides* in clay-influenced environments; poorly encrusted phaceloid corals in pure carbonate mud).

Insight into understanding the compositional differences and similarities of the reefs can be gained by examining how organisms are using food, specifically the trophic structure of the reef. Changes in environmental conditions, such as massive input of terrigenous material, increase in nutrient availability, or increase of carbonate-mud accumulation, can modify the equilibrium between
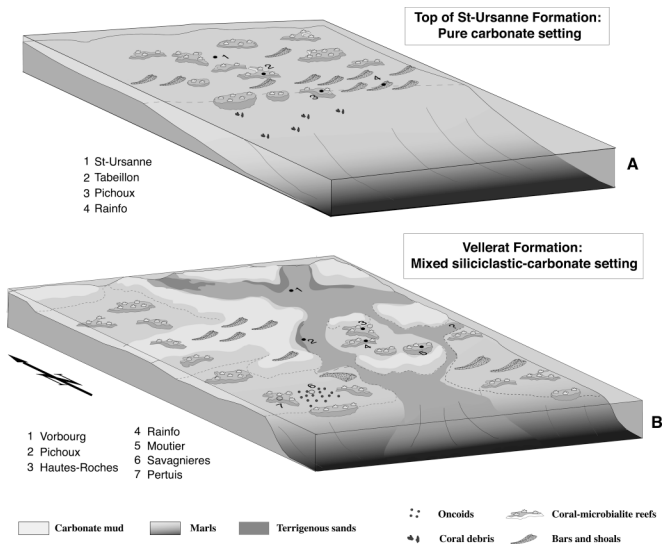
FIGURE 15—Paleogeographical reconstructions of the studied platform during (A) the pure carbonate setting of the St-Ursanne Formation, and (B) during the mixed siliciclastic-carbonate environment of the Vellerat Formation.

different trophic groups. This discussion will focus on the balance between phototrophic (light-dependant) and heterotrophic (obtaining food from organic compounds) modes of life at micro- to macroscale within the reefal build-ups. In this analysis, lithotrophic micro-organisms (obtaining food from inorganic compounds) are grouped with heterotrophic organisms.

The discussion will follow three steps: (1) Reconstruction of the paleogeography of the platform, as the habitat of the different reefs, and identification of the main environmental factors most likely to influence reef settlement, growth, and demise; (2) discussion of the ecological succession in a 'typical' Oxfordian reef; and (3) identification of environmentally sensitive faunal associations based on the spatial and temporal distribution of the trophic structures at the micro- and macroscale. Finally, these interpretations will be synthesized to present a model for the evolution of the trophic structure in these reefs.

Paleogeography and Environmental Factors

Facies and sedimentary structures indicate very shallow water for reefal and non-reefal intervals during the deposition of the St-Ursanne and Vellerat Formations (Strasser et al., 1996; Pittet and Strasser, 1998). Figure 15 presents a paleogeographical reconstruction based on high-resolution sequence-stratigraphic and cyclostratigraphic correlations between the studied sections (Pittet and Strasser, 1998; Dupraz, 1999; Strasser et al., 1999; Pittet et al., 2000). The St-Ursanne Formation represents carbonate environments mainly dominated by lime mud, coral reefs, and oolite shoals. During the deposition of the Vellerat Formation, an interpreted humid climate resulted in increased terrigenous input, and differential subsidence influenced the distribution of the siliciclastics on the platform (Fig. 15). The resulting environmental dichotomy led to pure carbonate deposits in the western part of the platform (e.g., Savanière and Pertuis sections), whereas the eastern part is influenced strongly by terrigenous input (e.g., Hautes-Roches, Rainfo, Moutier, Pichoux sections).

Terrigenous input directly can influence reefs by massive accumulation of clay and quartz, hindering coral settlement (soft substrate) and/or suffocating existing build-ups (e.g., Rainfo, Sous-La-Jean Mattheys, Hautes-Roches B, Chateauvieux A). Terrigenous input also increases the turbidity of the water column, which may induce significant changes in benthic associations. However, although high sedimentation rates generally causes high turbidity, high turbidity does not necessarily imply a significant sediment accumulation, as sediment may bypass the bioconstruction (Woolfe and Larcombe, 1998; Larcombe et al., 2001).

Terrigenous input also may influence reef ecosystems because of the associated nutrients (e.g., Weissert, 1989; Hallock et al., 1993; Föllmi et al., 1994). Freshwater and high nutrient content linked to terrestrial run-off have a direct effect on the carbon budget of coral reef ecosystems (Gattuso et al., 1997; Kawahata et al., 2000). Nutrient availability defines oligotrophic, mesotrophic, and eutrophic conditions (Hallock, 1987; Brasier, 1995a, b). Nutrient increase can result in changes in the trophic structure, characterized by a shift from phototrophic to heterotrophic nutritional modes (Hallock and Schlager, 1986; Föllmi et al., 1994; Caplan et al., 1996). An increase in nutrient levels may lead to massive production of organic matter. Bacterial decomposition of the organic matter then results in oxygen deficiency and, thus, may impact benthic fauna distribution. Siliciclastic components of the terrigenous input contain alkaline metals that increase the overall alkalinity of the ecosystem, thereby enhancing carbonate precipitation related to microbialite formation (Neuweiler et al., 1996; Camoin et al., 1999).

Sea-level fluctuations during the Oxfordian had amplitudes of a few meters only (Pittet, 1996) and, hence, did not strongly influence coral reefs in terms of bathymetry. These fluctuations, however, had indirect effects by changing terrigenous distribution, moving sediment bodies, modifying platform morphology, and closing or opening pathways to the open sea (see also Leinfelder et al., 1993, 1994). The result was a dynamic platform with heterogeneous depositional environments.

Ecological Succession in a 'Typical' Oxfordian Reef

The upward growth of reefs records the superposition or succession of communities that developed on the reef surface and deeper within the build-up. In the reefs studied, this succession can be characterized by examining the spatial distribution of the coral encrustations (micro-encrusters and microbialites). As described above, encrustations typically display two different layers that develop in two different environments: the reef surface and the reef core (Fig. 16). The first layer of encrustation forms in the same (or closely related) environmental conditions as the corals, growing directly on the reef surface or in open cavities. The micro-encrusters of this first layer generally are well diversified. The second layer of encrustation is the result of a moving encrustation front filling the remaining porosity inside the reef, below the living surface. This second zone is poorly diversified and composed mainly of throm-
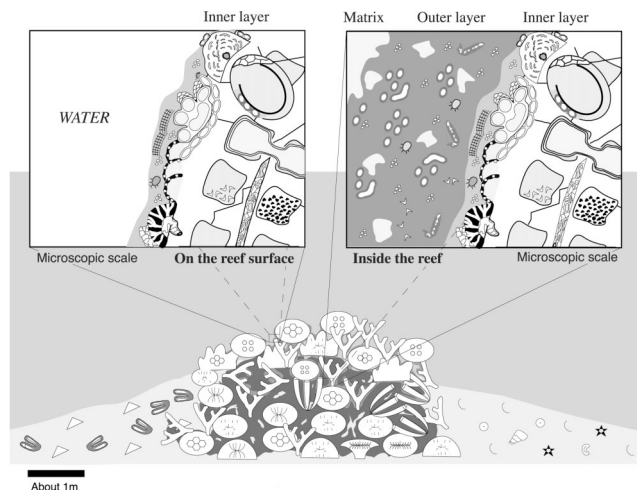
FIGURE 16—Ideal zonation of microbialite and micro-encrusters (for legend see Fig. 3).

bolite. Comparable mechanisms of thrombolitic infilling have been described in Recent reefs (Camoin and Montaggioni, 1994; Laurenti and Montaggioni, 1995; Camoin et al., 1999) and in the Oxfordian reefs of the Paris Basin (Bertling and Insalaco, 1998). Micro-encruster diversity of each layer is controlled by the depositional setting. For example, light zonation in the benthic fauna is well known in Recent reef cavities (e.g., Reitner, 1993) and also in Oxfordian reefs (Helm and Schülke, 1998). At the surface of the reef, micro-encrusters benefit from the same conditions of light and oxygenation as the coral substrate. Even in the shade, micro-encrusters still have enough light to photosynthesize. Inside the reef body, however, light and oxygen become scarce, inducing a decrease in biodiversity. As the reef continues to grow upward, the thrombolite front located inside the reef body migrates in a parallel way, which results in the superposition of the two different encrustation layers.

Accordingly, faunal diversity in the first layer of encrustation can record changes in conditions prevailing in the water column (i.e., general conditions of the lagoon) in the same sense as the macroscopic epifauna and shallow infauna found in the reefs (corals, and other macrofauna). On the other hand, the composition of the second layer of encrustation reflects the internal micro-environmental conditions of the reef core, although these cryptic communities also can be sensitive to general environmental changes producing alkaline and nutrient-rich pore waters (e.g., 'proximal' environments influenced by terrigenous input).

These results suggest that such variations parallel changes observed within the macrofauna (corals, bioerosion, and other heterotrophic macrofauna), which are interpreted to be environmentally driven. Thus, groups of macro- and microfaunal associations interpreted as environmentally sensitive can be defined and used as the basis for paleoecological analysis.

Environmentally Sensitive Fauna

Each key group composing the reefal facies now is examined in relation to its trophic structure and prevailing

environmental conditions. The discussion proceeds from the microscale (microbialites, micro-encrusters) to the macroscale (corals, bioerosion, and other heterotrophic macrofauna).

Microbialite Formation

The origin of microbialites remains a subject of conjecture. Microbialites generally are interpreted to result from carbonate precipitation induced by cyanobacteria (phototrophs) and heterotrophic bacteria that modify the microenvironment by their metabolic activity (e.g., Krumbein and Swart, 1983; Chafetz, 1986; Pentecost and Riding, 1986; Chafetz and Buczynski, 1992; Ehrlich, 1996; Reid et al., 2000). Other research points to organomineralization ("mineral formation in close association with non-living organic substrates"; Trichet and Défarge, 1995, p. 203) related to biofilms rich in extracellular polymeric substance (EPS; e.g., Decho, 1990, 2000; Neuweiler et al., 1999, 2000). A combination of heterotrophic bacterial activities (increasing alkalinity in micro-domains) and EPS-rich biofilm degradation (releasing Ca^{2+}) also has been proposed for carbonate precipitation in microbial mats (Decho, 1990, 2000; Visscher et al., 2000; Dupraz and Reid, 2001).

Thrombolite (the most common form of microbialite found in this study) can be formed by various sciaphile bacteria (preferring shadow) in low hydraulic energy and low allochthonous sedimentation in aerobic and anaerobic microenvironments (Kennard and James, 1986; Laurenti and Montaggioni, 1995; Leinfelder et al., 1996; Camoin et al., 1999). Studies on Recent microbial mats show that oxygen decreases drastically a few millimeters below the surface when oxygenic photosynthesis is not active (e.g., Canfield and DesMarais, 1994; Stal, 1995). Thus, during the night, sulfate-reducing metabolism occurs at the top of the mat (Visscher et al., 1998, 2000). In intertidal microbial mats, sulfate-reducing bacteria are responsible for carbonate precipitation around empty cyanobacterial sheaths (Chafetz and Buczynski, 1992). The micropeloidal structure generally found in the Oxfordian thrombolite may result from carbonate precipitation around clusters of bacteria as observed in recent peloids (Chafetz, 1986). Thus, microbial mats responsible for the micropeloidal structure of the thrombolite inside reef cavities probably formed in oxygen-depleted environments (lack of oxygenic photosynthesis), where anaerobic bacterial respiration, possibly associated with organomineralization, was responsible for carbonate precipitation. Consequently, thrombolite intervals developed on the top of reefs, such as in the sections of Hautes-Roches, Pichoux, and Moutier, are interpreted as having resulted from restricted environmental conditions in the lagoon, where low oxygen, low light, and/or high nutrient content precluded colonization of most organisms other than microbes. The agglutinating worm *Terebella lapilloides* commonly is the only micro-encruster present in these thrombolitic levels, indicating that it probably tolerated low oxygen conditions.

Micro-Encruster Associations

The preserved encrusters can be subdivided into three main associations, each of which is named according to the dominant species: *Bacinella-Lithocodium* association,

"*Berenicea*"-serpulid association, and *Terebella* association (Dupraz and Strasser, 1999). The first two commonly are observed in the first layer or in the transition zone (close to the conditions in which corals lived). The third group mainly is concentrated in the second layer of encrustation, which formed inside the reef body, or on the reef surface under stressed environmental conditions (e.g., mesotrophy, low oxygenation, high turbidity).

The *Bacinella-Lithocodium* group is composed of *Bacinella irregularis*, cayeuxid algae, red algae, and the foraminifer *Lithocodium aggregatum*. This group always is observed in reef parts with good coral diversity and low microbialite content. Its highest relative abundance is observed in reefs having few heterotrophic micro- and macrofauna (Tabeillon, Pertuis, Savagnières; Fig. 17). Although *Bacinella* and *Lithocodium* have been regarded as two growth stages of the same organism (Segonzac and Martin, 1972; Banner et al., 1990), *Lithocodium aggregatum* now is considered as an encrusting foraminifer having symbiotic phototrophic algae in its epidermis (Schmid and Leinfelder, 1996). *Bacinella irregularis* is interpreted as cyanobacterium (e.g., Camoin and Maurin, 1988; Schmid and Leinfelder, 1996). Therefore, the *Lithocodium-Bacinella* group is composed of light-dependant organisms.

The "*Berenicea*"-serpulid group mainly includes these two micro-encrusters, associated with other heterotrophic microfauna such as *Placopsilina* sp. and some calcisponges. Although serpulid worms and to a lesser extent *Berenicea* (bryozoans from the "*Berenicea*" group, see Fig. 3) can be found in many different reefal environments (Figs. 11, 17), they generally are the first micro-encrusters to colonize coral substrates in environments characterized by high sedimentation (clay or carbonate mud). Microsolenid corals found in marls commonly show a lack of any microbial encrustation, but still can be colonized by serpulid worms and "*Berenicea*." These observations indicate an opportunistic behavior for these organisms, even if they can be found living together with other micro-encrusters.

The *Terebella* group is a more complex association. *Terebella lapilloides* is an agglutinating worm preferentially colonizing cavities within coral framestone and borings. *Terebella lapilloides* clearly correlates with the maxima of microbialite (mainly thrombolite) and is interpreted to be a heterotrophic, sciaphile microorganism (Fig. 17). *Terebella lapilloides* also shows a good correlation with terrigenous input (Fig. 17) and preferentially traps clay minerals for building its tube (Dupraz, 1999). *Terebella lapilloides* generally is the only micro-encruster found in thrombolitic intervals, suggesting that it probably tolerated low oxygenation as proposed by Leinfelder et al. (1996). Other heterotrophs are found in association with *Terebella lapilloides*, such as *Tubiphytes morronensis*, nubeculariid foraminifera, and some siliceous sponges (Fig.11). *Tubiphytes morronensis* is interpreted as a foraminifer with a coating of microbial origin (Flügel, 1981; Pratt, 1995; Schmid, 1996). Schmid (1996) proposed a relationship between bathymetry and thickness of this microbial layer, implying a symbiotic relationship with phototrophic algae. This hypothesis has not been confirmed in this study: thick *Tubiphytes* have been found in coral cavities where light was absent. The microbial coating of *Tubiphytes* also could result from a symbiotic association with
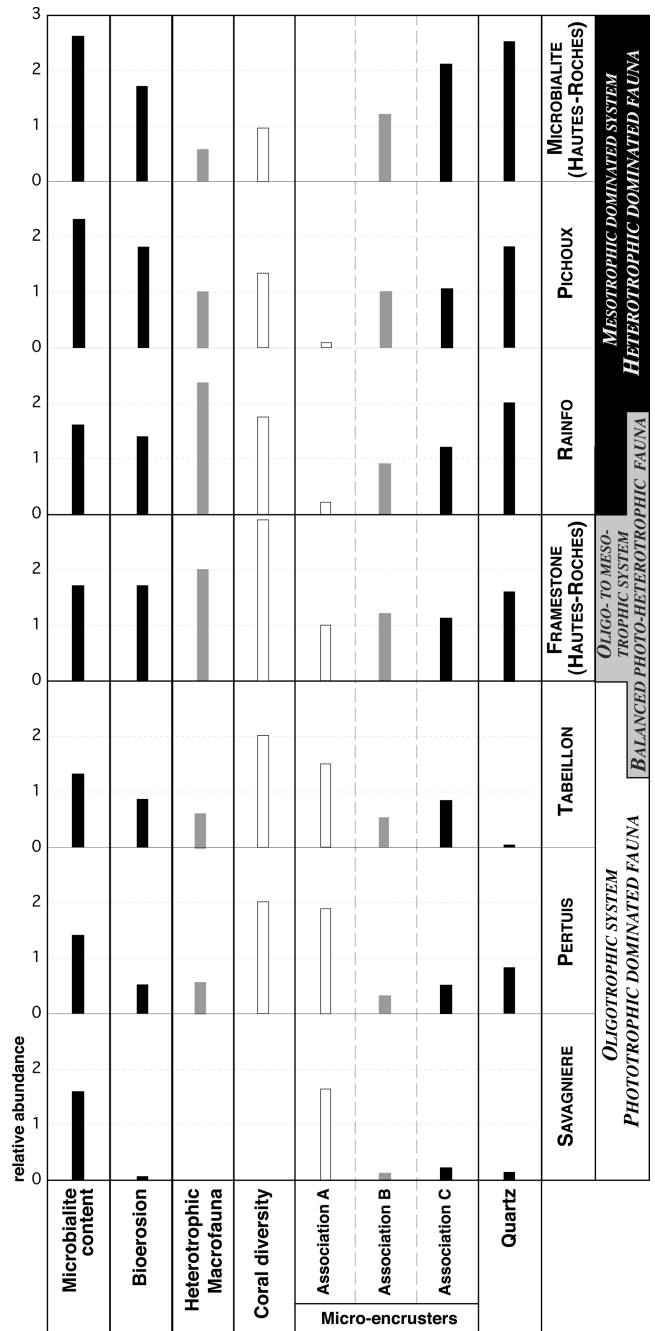

FIGURE 17—Distribution of microbialite, bioerosion, associated heterotrophic macrofauna, coral diversity, micro-encrusters, and quartz in representative sections. Micro-encruster associations: A—*Terebella—Tubiphytes* ('bad-condition' heterotrophic fauna). B—Serpulid worms, "*Berenicea*" group, *Placopsilina*, calcareous sponges (heterotrophic fauna). C—*Bacinella-Lithocodium* (phototrophic fauna). Note the positive correlation between quartz (related to terrigenous input) and microbialite or bioerosion content. Balanced photo-heterotrophic ecosystem offers the best diversity for Oxfordian reefs.

heterotrophic bacteria comparable to bacteria found in Mediterranean sponges and responsible for their lithification (Schumann-Kindel et al., 1996, 1997). This explanation is in better accordance with the microenvironment where *Tubiphytes* is generally found (second layer of encrustation, cryptic environment).

Stylinids versus Microsolenids

A well-developed dichotomy between the distribution of microsolenid (mainly *Microsolena* and *Comoseris*) and stylinid corals has been observed. In this study, stylinid corals are not defined as corresponding directly to the family Stylinidae as introduced by d'Orbigny in 1851 (see Alloiteau, 1952). The term stylinid used here refers to a grouping of genera of several families proposed by Gill (1977). This grouping includes genera having the same morphological specifications (a particular joint between septa and columella, 'auricle' on the septal border) that are easy to recognize under the microscope (Fig. 12). This group includes the genera *Stylina* and *Stylosmilia* (Stylinidae d'Orbigny, 1851), *Heliocoenia* (Agatheliidae Beauvais and Beauvais, 1975), and *Enallhelia* (Euheliidae Vaughan and Wells, 1943). Stylinids represent massive plocoid and fragile phaceloid colonies (corallite diameter around 2 mm), occurring in the higher-diversity intervals of the reefs. They are never present in microbialite and marl intervals, but are frequent in framestones with low terrigenous content. They are associated with framestone and rubble facies with low microbialite content and with micro-encrusters interpreted as having a light-dependent mode of life, such as the foraminifera *Lithocodium aggregatum* and the cyanobacteria *Bacinella irregularis* or *Cayeuxia*. This as well as the poorly developed associated heterotrophic macrofauna (Figs. 11, 17) suggest that stylinid corals thrived in nutrient-poor waters.

On the other hand, microsolenid corals (Fig. 12) are found in a wider range of facies, from coral framestones having low siliciclastic content to marly and microbialite facies. The capability of microsolenid corals to tolerate difficult environments is well documented (e.g., Bertling, 1993b; Fürsich et al., 1994; Lathuilière and Gill, 1995; Insalaco, 1996; Nose and Leinfelder, 1997; Aillud and Dupraz, 1998). They are suspected to have had a complex gastro-vascular system, supported by a dense architecture of perforated septa with pennulae that may have allowed a heterotrophic mode of life comparable to the modern deep-water coral *Leptoseris fragilis* (Schlichter, 1992; Gill and Santantonio, 1995). Other corals, with perforated septa but no pennulae (like *Actinaraea*) do not follow this ecological trend and disappear when environmental conditions deteriorated. Thus, pennulae seem to have an important ecological significance. Microsolenid-rich deposits commonly are interpreted to have formed in deeper water (e.g., Bertling, 1993b; Lathuilière and Gill, 1995; Insalaco, 1996). However, detailed analysis of microfacies and sedimentary structures in the Middle to Upper Oxfordian of the Swiss and French Jura (Gygi and Persoz, 1986; Strasser et al., 1996; Pittet and Strasser, 1998; Dupraz, 1999) indicates that the bathymetry in the study area always remained very shallow and, thus, does not represent a significant light-limiting factor. In accordance with Insalaco (1996), this study proposes that microsolenid-rich intervals are "trophically quite unlike modern coral reefs," and their association with heterotrophic macro- and microfauna implies high nutrient levels. Mesotrophic conditions prevailed in microbialite-microsolenid intervals situated in sectors of the platform strongly influenced by terrigenous input, but the nutrient effect most probably extended beyond the range of active terrigenous sedimentation (e.g.,

Crossland, 1983; Hallock and Schlager, 1986; Birkeland, 1987).

Phaceloid Corals

Phaceloid corals, such as *Stylosmilia* and *Calamophylliopsis*, mainly are found in reef environments rich in carbonate mud. The phaceloid morphology, no longer found in modern reefs, is interpreted to have been especially well adapted to soft substrates and high sedimentation rates in quiet environments. Unlike ramose forms showing budding in the middle of the branch and different corallite orientations, phaceloid corals always grew vertically, keeping the polyps above the sediment, which filled the space between the branches (constratal growth: Insalaco, 1998; see also Chappell, 1980). Changes from massive to phaceloid morphologies within the reefs are interpreted as having resulted from an increase in sediment accumulation.

Special Coral Species: Amphiastraea piriformis

Amphiastraea piriformis meadows were observed in quartz-dominated environments with indeterminate plant fragments, implying very shallow water in a proximal facies (Sous-la-Jean Mattheys). This species displays small massive colonies that lived on soft substrate, with evidence of toppling. *Amphiastrea piriformis* occurs in various environments such as in quiet, shallow water and on soft substrate (Rosendahl, 1985), in shallow and quartz-rich settings (Fürsich et al., 1994), and associated with high turbidity (Fürsich and Werner, 1986). *Amphiastrea piriformis* presents an irregular cerioid organization of corallites very similar to that observed in the Recent coral *Goniastrea retiformis* Lamarck. The environment where *Amphiastrea piriformis* was thriving on the Oxfordian Jura platform possibly can be compared to the proximal, shallow, and highly turbid environment in the Gulf of Papua where *Goniastrea retiformis* occur (Woolfe and Larcombe, 1998). In accordance with Fürsich et al. (1994), this study suggests that *Amphiastrea piriformis* could remove sediment from corallite surfaces with a cleaning mechanism similar to that of some modern corals (Loya, 1976). In addition, *Amphiastrea piriformis* also was able to tolerate high nutrient levels associated with terrigenous input.

Bioerosion and Other Heterotrophic Macrofauna

Bioerosion plays a major role in the control of reef growth. The balance between coral growth and bioerosion determines whether a reef will grow, remain in steady state, or be eroded. In contrast to Recent reefs where sponges are the dominant reef borer (e.g., Perry and Bertling, 2000), the main bioeroding agents in Oxfordian reefs are bivalves. These organisms are heterotrophic filter-feeders, and their activity can be related to nutrient availability (Hallock, 1988). Increase in nutrients through terrigenous input can shift the equilibrium of the reef toward erosion, as illustrated in Figure 17. In such settings, bioerosion is higher in the microbialite (quartz-rich intervals) than in the framestone facies of Hautes-Roches, Moutier, and Rainfo patch reefs. In Hautes-Roches, bioerosion increases drastically at the top of the framestone facies just below microbialite-dominated intervals, thus suggesting

an increase in nutrient availability (Dupraz and Strasser, 1999). However, bioeroding organisms cannot cope with significant accumulations of clay such as found in Sous-La-Jean Matthey or Hautes-Roches B.

Heterotrophic macrofauna other than corals are used in this study as paleoecological indicators in two ways: (1) abundance and diversity, and (2) relation to the sediment matrix. Pure carbonate environments preserve few heterotrophic macrofauna (Fig. 17), which indicates, together with high phototrophic and low heterotrophic micro-encrusters content and moderate coral diversity (Fig. 17), that these reefs where thriving in nutrient-poor waters. Heterotrophic faunas are well represented in high-diversity framestones moderately influenced by siliciclastics, such as in Moutier and Hautes-Roches A (Figs. 11, 17). Thus, in contrast to pure carbonate settings, these higher-diversity reefs grew in water moderately charged in nutrients (mesotrophic environment). Heterotrophic infauna within clayey sediment (e.g., Hautes-Roches B) or absence of infauna (e.g., Rainfo) suggest oxygenated or oxygen-deficient sediment, respectively. In addition, population explosions of grazing gastropods (Rainfo, Hautes-Roches B) may indicate a massive increase of primary production in the form of fleshy algae.

SYNTHESIS: EVOLUTION OF TROPHIC STRUCTURE IN OXFORDIAN REEFS

The high-resolution analysis of ecologically sensitive micro- and macrofaunal associations presented in this paper indicates that the studied Oxfordian patch reefs represent three main trophic structures: phototrophic-dominated, balanced phototrophic-heterotrophic, and heterotrophic dominated (Figs. 18, 19). Figure 18 depicts possible theoretical pathways of development of a high-diversity coral reef as a function of environmental factors. The flowchart in Figure 19 (in association with Fig. 20) presents a compilation of possible scenarios for the development of the Oxfordian reefs documented in this study. Changes from one trophic structure to another are interpreted mainly to be driven by the distribution of terrigenous input on the platform, by sediment accumulation, and by nutrient availability. In the absence of terrigenous input, sedimentation of carbonate mud and the migration of sediment bodies are considered to be responsible for major changes in reefal trophic structure, as summarized below.

Reefs with Phototrophic-Dominated Fauna

These reefs developed in environments characterized by an absence of siliciclastic input. Nutrient-poor water led to a phototrophic-dominated mode of life. However, this environment was not ideal for Oxfordian reef growth because coral diversity was moderate and the associated heterotrophic fauna scarce (Figs. 17, 18A). Stylinid corals prevailed and micro-encrusters were dominated by light-dependant *Lithocodium-Bacinella* associations (Fig. 17); serpulid worms were the only heterotrophs well adapted to this environment. Bioerosion by bivalves was low. Microbialite formed inside the reef where heterotrophic bacterial metabolism was fueled with organic matter produced by phototrophs. The leiolitic front inside the reef mi-

grated at the same speed as the reef growth and never reached the surface of the build-up. A modification of the reef structure could occur due to an increase of *in situ* carbonate sediment production (Figs. 18, 19B), or when the bioherm was influenced by migrating carbonate sand bodies (ooids or mud; Figs. 18, 19C). With a moderate increase in sediment accumulation, stylinids slowly disappeared, but actinastraeids were still common (Fig. 18). Phaceloid, ramose, and flabellate forms increased. A drastic increase in sedimentation rate led to a phaceloid-dominated fauna characterized by *Calamophylliopsis* and *Stylosmilia* (Fig. 18). Increase in water energy generally resulted in rubble deposits. In these reefs, this facies is dominated by isastraeid corals. *Isastraea* and *Complexastraea*, which are found associated with grainstone and rudstone facies, have a sturdy structure and dense endothecal dissepiments, which may have helped these taxa to cope with high-energy events. Although much of the rubble is allochthonous, some large coral colonies just toppled.

Reefs with Balanced Phototrophic-Heterotrophic Fauna

These reefs were thriving in environments moderately influenced by terrigenous input. No important siliciclastic deposit occurred, but quartz grains are encountered throughout the structures. Moderate nutrient content permitted a well-diversified reef structure, displaying an equilibrium between phototrophic and heterotrophic micro- and macrofauna (Figs. 17, 19D). In accordance with Leinfelder et al. (1996), the data presented herein suggest that such a balanced nutrient system was the ideal environment for reef growth during the Oxfordian. Stylinid corals were still present, but other genera dominated in the construction of the reef (Fig. 18), and microsolenid corals also are encountered. The associated heterotrophic macrofauna was relatively diversified (bivalves, echinoids, gastropods), and bioerosion by bivalves was well developed (Fig. 17). Micro-encrusters at the reef surface (first layer of encrustation) show a high diversity and mirror equilibrium between phototrophs and heterotrophs, paralleling that observed in the macrofauna (Fig. 17). The *Terebella* association was found inside the reef cavities together with abundant microbialite. Terrigenous material rich in alkali metals increased water alkalinity (Blackburn, 1983; Krumbein and Swart, 1983; Neuweiler et al., 1996; Camoin et al., 1999). This, together with nutrients and organic matter fueling heterotrophic metabolism, enhanced microbially-mediated carbonate precipitation. Thus, the general amount of microbialite increased noticeably compared to the phototrophic environment. The front of microbialite growing inside the reef was still in equilibrium with coral growth and did not reach the reef surface.

Reefs with Heterotrophic-Dominated Fauna

Coral reef ecosystems characterized by a heterotrophic-dominated fauna exhibited a wide range of micro- and macrofaunal distributions that were driven by two main environmental factors.

The first factor was a high rate of siliciclastic accumulation (mainly clay), that progressively killed the reef (Fig. 19I-J-K). Microsolenid corals could survive for some time in this environment, forming meadows of flat to mush-
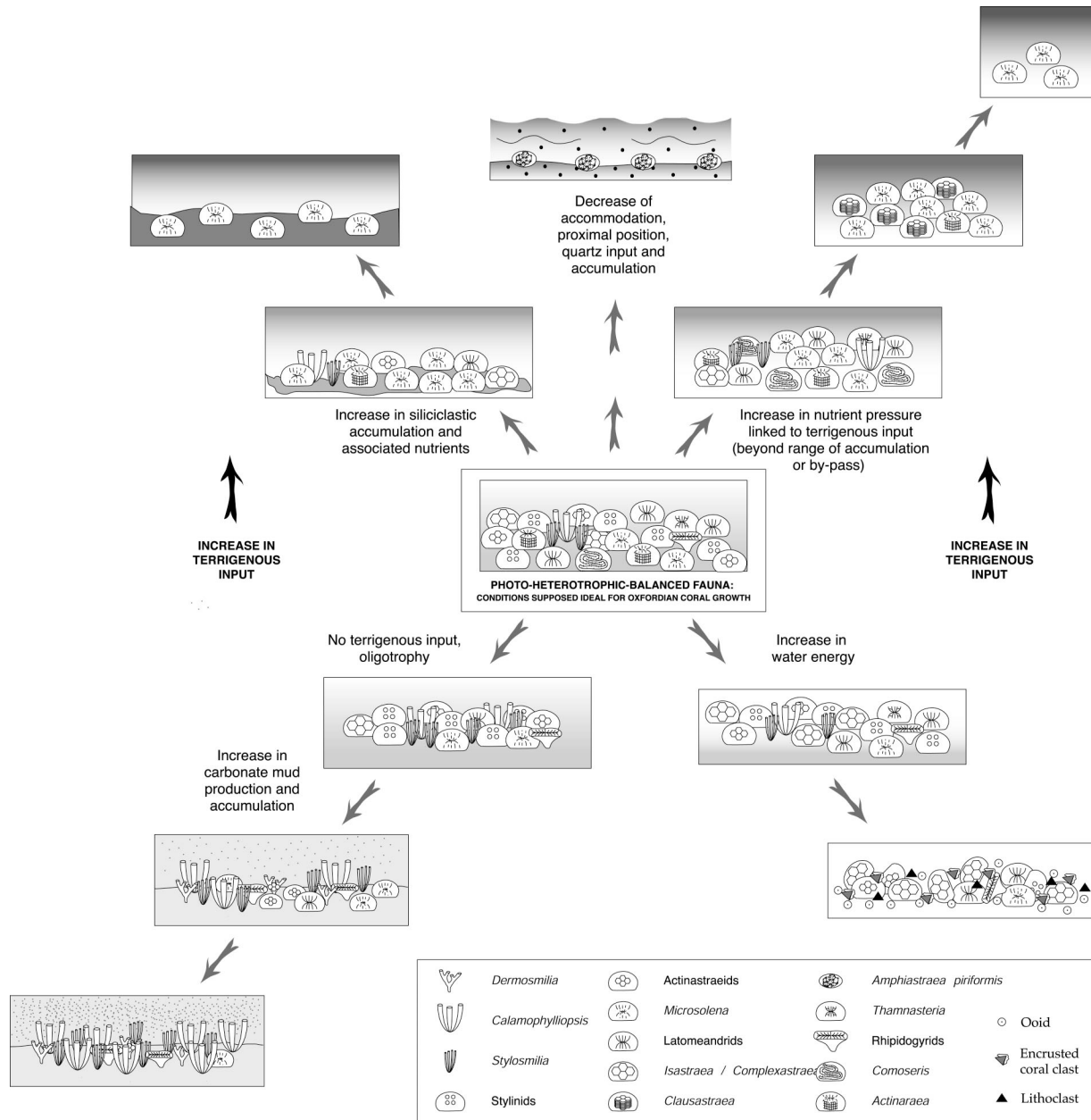
FIGURE 18—Development of coral composition in a model reef (legend in Fig. 3). For discussion, refer to text.

room-shaped colonies. Once established (generally on bioclasts), they could develop convex bases and fan-like morphologies to outpace sediment accumulation (e.g., Bertling, 1993a), or to compensate for sinking into the mud due to increased weight. Heterotrophic epifauna (e.g., the big gastropod *Bourguetia saemanni*, echinoids) and endofauna (e.g., large and coarse terebellid worms, *Thalassinoides*, *Pholadomya* sp.) colonized this substrate (Fig. 19I). Phototrophic microfauna (*Lithocodium*, *Bacinella*, *Cayeuxia*) was absent, and the micro-encrusters were characterized by serpulid worms, *Terebella lapilloides*, siliceous sponges, and *Tubiphytes morronensis*. A rapid increase of clay input may have led to anoxic sediment without endofauna (Fig. 19J), and, finally, to more or less sterile marls (Fig. 19K).

The second factor was an increase of nutrient pressure linked to terrigenous input, but without significant sediment accumulation (Fig. 19 D-E-F-G). This can be explained by sediment by-passing around the bioherm, or by the extent of the nutrient effect beyond the range of terrigenous accumulation. The trophic structure of the reef at micro- and macroscale progressively shifted from phototrophic to heterotrophic. Coral diversity rapidly decreased; the stylinids disappeared first, followed by other phototrophic taxa (Fig. 18). The substrate was colonized by microsolenid corals that thrived as nutrient pressure

FIGURE 19—Development of a model reef as a function of sedimentation rate (siliciclastics and carbonate), turbidity, nutrient availability, oxygenation, water depth, and position on platform (proximality; for legend see Fig. 3).

increased. This shift in environmental conditions also was monitored by the micro-encrusters, as phototrophic forms (*Cayeuxia*, *Bacinella*, *Lithocodium*) disappeared from the first layer of encrustation (Fig. 17). A similar reaction has been observed for recent foraminifera in Caribbean reefs (Edinger and Risk, 1994). Heterotrophs such as calcareous sponges, serpulids, nubeculariid foraminifera, and *Placopsilina* (agglutinated foraminifera) were still present in the first layer. Bioerosion by bivalves increased drastically, which also may be indicative of an increase in nutrient pressure (e.g., Hallock, 1988). The front of thrombolite continued to form in the reef core. If nutrient availability and associated turbidity (suspended clay and/or phytoplankton blooms) increased, even microsolenids and heterotrophic macrofauna could not have coped with the deteriorating environmental conditions any longer (Fig. 19F). Bioerosion was more active than reef growth, leading to a hiatus in the reef growth. Thus, the thrombolitic front reached the top of the build-up and, eventually, covered it (Fig. 19G). Therefore, the microbialite covering the top of the reefs was not the cause of coral reef demise, but the consequence.

CONCLUSIONS

The detailed study of Oxfordian patch reefs and their sedimentological context on the shallow Swiss Jura plat-

form allows the identification of various environmental parameters responsible for reef growth and reef demise. Semi-quantitative analyses of the distribution of corals, microbialites, and micro-encrusters within the bioherms, as well as of the fauna and the sediment surrounding the reefs, were carried out. The changes through time of the various faunal associations were traced. Shifts in dominant nutritional modes within and between reefal ecosystems correspond to changes in environmental conditions. The general changes of ecologically sensitive macro- and micro-faunal associations from phototrophic- to heterotrophic-dominated modes are interpreted as having been controlled mainly by terrigenous input and associated nutrients. These shifts are observed in time (stratigraphic succession) as well as in space (position on the platform).

The true trophic structure of Oxfordian reefs is impossible to assess because many of the players are not fossilized. Nonetheless, detailed analysis of the organisms left in the sedimentary record and the evaluation of their interactions and successions permits a comprehensive paleoecological interpretation. The major obstacles for any direct comparison between Recent and fossil ecosystems include the low time resolution in the stratigraphic record and incomplete fossilization of the community members. Some causes responsible for recent coral reef crises, such as bleaching (Brown, 1997; Baird and Marshall, 1998) or

Major Evolutions and Stages		Dominating nutrition mode	Corals	Microbialite	Bioerosion	Macrofauna	Matrix	Reef examples	Links to other stages
				Micro-encrusters					
Evolution A→C Pure carbonate Accumulation increase	A	Phototrophic dominated	Moderate diversity (Stylinid-dominated)	Moderate - 2 layers (leiolite) / Phototrophic-dominated *Bacinella-Lithocodium*	Low	Very poor (rare rhynchonellids)	Mudstone to wackestone	Tabeillon A-B - Pertuis	B-C
	B	Phototrophic - dominated	Dominated by branching mophologies	Absence, thin layer or dendroid forms / Opportunism Serpulids-bryozoans	Low	Very poor (rare rhynchonellids)	Mudstone	Tabeillon A-B	A-C
	C	Phototrophic - dominated	Debris reef (more Isastreids)	- / Serpulids-bryozoans-*Lithocodium* ass.	Low	Inocerams, echinoderms and other clasts	Grainstone (ooids-bioclasts)	Tabeillon A-B - Pertuis	A-B
Evolution D→G Siliciclastic influence Without significant accumulation	D	Balanced hetero-phototrophic	High diversity (Presence of stylinids)	Moderate - 2 layers (thrombolite) / Heterotrophic-dominated	Moderate	Abundant Mainly epifauna, shal-low infauna, cryptic (molusks, echinoids)	Mudstone to packstone	Haute-Roches A (Framestone) - Moutier	E-I-N
	E	Heterotrophic-dominated	Moderate diversity (microsolenid-dominated)	Moderate - 2 layers (thrombolite) / Heterotrophic-dominated	Moderate to high	Abundant Mainly epifauna, shal-low infauna, cryptic (Moluks, echinoids)	Mudstone to packstone	Pichoux - Chateauvieux B	D-F-J-N
	F	Heterotrophic-dominated	Low diversity (microsolenid)	Moderate - 2 layers (thrombolite) / Heterotrophic-dominated	Very high	Epifauna (brachiopods, oysters)	Mudstone to packstone	Pichoux - Hautes-Roches A (Microbialite) - Chateauvieux B	E-G-K
	G	Heterotrophic-dominated	Dead	High - 1 layer (thrombolite - rare stromatolite) / *Terebella lapilloides*	Low	-	Mudstone	Pichoux - Hautes-Roches A (Microbialite)	F-H
	H	Anaerobic bacteria	Dead	Nutrients and clays inhibiting carbonate precipitation	-	-	Clays - marls	Pichoux - Hautes-Roches (marls)	G
Evolution H→J Siliciclastic influence significant accumulation	I	Heterotrophic-dominated	Low diversity (microsolenids)	Low - 1 layer (contrasted thrombolite) / Opportunistic serpulids & bryozoans	Moderate	Epi- and endofauna (gastropods, oysters, agglutinated forams)	Marls	Hautes-Roches B - Beginning of Hautes-Roches A	D-J
	J	Heterotrophic-dominated	Low diversity (microsolenids)	Low - 1 layer (contrasted thrombolite) / Opportunistic serpulids & bryozoans	Moderate	Epifauna (gastropods, ag-glutinated forams)	Marls	Rainfo	I-E-K
	K	Anaerobic bacteria	Dead	-	-	-	Marls-clays	Rainfo - Hautes-Roches A-B	J
Evolution K→L Proximality, siliclastic infl.	L	Hetero-phototrophic (more or less) balanced	Monospecific (*Amphiastrea piriformis*)	Low to absent (thrombolite) / Rare *Lithocodium-Bacinella*	-	-	Floatstone to packstone with quartz, plant fragments	Sous-la-Jean Matthey	M
	M	Heterotrophic -dominated	Dead	-	-	-	Marls-Clays quartz-plants	Sous-la-Jean Matthey	L
Ev. M Depth increase	N	Heterotrophic -dominated	Low diversity (Microsolenids)	High (thrombolite) / Heterotrophic-dominated	High	Mainly epifauna and cryptic, shallow in-fauna, (brachiopods, sponges, oysters, forams)	Mudstone to wackestone with quartz	Chateauvieux A	D-E

FIGURE 20—Dominant components involved in each stage of the flowchart presented in Fig. 19, and examples of reefs describing the corresponding stages (Dupraz, 1999; Dupraz and Strasser, 1999; this paper). The major observed development trends are A→C, D→G, H→J, K→L, and M, but also links to other stages may occur.

coral diseases, presently are impossible to assess or recognize in the fossil record. However, the potential effects of other factors, such as nutrient excess and smothering by sediment, can be placed in perspective by the present study of Oxfordian reefs.

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