

General Palaeontology (Palaeoecology)

High-frequency palaeoenvironmental fluctuations recorded in Jurassic coral- and sponge-microbialite bioconstructions

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Abstract

During the Jurassic, coral and sponge reefs were particularly widespread along the northwestern Tethys. These bioconstructions occurred from shallow- to deep-shelf settings, in pure carbonate, carbonate-dominated or clay-rich mixed carbonate-siliciclastic sedimentary contexts. According to the depositional environment, the amount of microbialites strongly fluctuates, to form up to 70% of the reef volume. This study focuses on bioconstructions where microbialites constitute at least 15% of the reef volume. Analysis of the close relationships between the reef structures and the stacking pattern of laterally-deposited sediments reveals analogous architectures and growth modes between coral- and sponge-microbialite bioconstructions. Firstly, corals or sponges erected a primary framework more or less projected above the sea floor (constratal or superstratal growth fabrics). Contemporaneously, a thin microbialite layer encrusted the local dead parts of corals or sponges. In a second stage, microbialites largely developed and entirely covered the reef surface, becoming the main reef builders. The whole development of coral- and sponge-microbialite reefs corresponds to a 'low-frequency reef-growth phase'. These bioconstructions also display surfaces of reef growth interruption delimiting 'medium-frequency reef-growth phases'. They include several 'high-frequency reef-growth phases' (or elementary units) corresponding to coral or sponge frameworks plus microbialite crusts. At the scale of the elementary unit, microbialites are interpreted to reflect nutrient-richer conditions and developed to the detriment of phototrophic-, mixed- or heterotrophic-dominated assemblages of corals or sponges. The development of Jurassic coral and sponge bioconstructions was punctuated by high-frequency (millennial time-scale) ecological crises during which microbialites occurred at the reef surface. Such ecological shifts from skeletal reef metazoans (i.e. corals or sponges) to microbialite crusts were recorded whatever the palaeogeographical position (shallow-proximal platform or deep-distal shelf) along the northwestern Tethys margin. Three main orders of climatic oscillations, correlated to the 'high-, medium- and low-frequency reef-growth phases', could have directly regulated the amount of terrigenous materials and nutrients delivered to the ocean, which in turn controlled platform carbonate production and accumulation, as well as reef development. *To cite this article: N. Olivier et al., C. R. Palevol 6 (2007).*

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Résumé

Fluctuations paléoenvironnementales à hautes fréquences enregistrées dans les récifs jurassiques à coraux ou à spongiaires riches en microbialites. Au Jurassique supérieur, la marge nord-téthysienne présentait une large extension des plates-formes carbonatées et mixtes, carbonatées-silicoclastiques. Des plates-formes proximales aux bassins épicontinentaux, les écosystèmes récifaux à coraux et à spongiaires étaient abondants. En fonction du milieu de dépôt, ces récifs peuvent être largement constitués de microbialites (jusqu'à 70% du volume récifal). Cette étude a été effectuée sur des bioconstructions composées au minimum de

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15% de microbialites. Les relations géométriques entre les structures bioconstruites et l'agencement des dépôts latéraux révèlent une architecture et un mode de développement analogues entre les récifs corallo- et spongio-microbialitiques. Les coraux ou les éponges édifient une structure primaire, plus ou moins élevée, au-dessus du fond marin (trame récifale constratale ou superstratale). Dans le même temps, une première couche microbialitique s'installe sur les parties nécrosées des madréporaires ou des spongiaires. Ensuite, les microbialites recouvrent largement l'intégralité de la structure bioconstruite. Les microbialites jouent alors un rôle édificateur majeur. La totalité de la bioconstruction est assimilée à une « phase de croissance récifale de basse fréquence ». Des surfaces majeures d'interruption de croissance délimitent des « phases de croissance récifale de moyenne fréquence ». Ces dernières sont composées de plusieurs « phases de croissance de haute fréquence » (ou unités élémentaires), correspondant à la succession entre une trame squelettique primaire (corallienne ou à éponges) et un encroûtement microbialitique. À l'échelle d'une unité élémentaire, le développement des microbialites, qui s'effectue au détriment des assemblages phototrophes, mixtes ou hétérotrophes de coraux ou d'éponges, est interprété comme reflétant une augmentation de la teneur en nutriments. Les récifs à coraux et à spongiaires riches en microbialites ont enregistré des crises écologiques à haute fréquence (à l'échelle de quelques milliers d'années), pendant lesquelles les microbialites se formaient à la surface de bioconstructions situées sur les plates-formes proximales, comme dans les bassins épicontinentaux. Trois principaux ordres d'oscillations climatiques, corrélés aux « phases de croissance récifale de basse, moyenne et haute fréquences », contrôlaient probablement la quantité de matériel terrigène et de nutriments déversés dans les océans, et du même coup le développement des récifs. **Pour citer cet article : N. Olivier et al., C. R. Palevol 6 (2007).**

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Keywords: Coral and sponge reefs; Microbialites; Nutrients; Accumulation rate; Palaeoenvironments; Jurassic

Mots clés : Récifs à coraux et à éponges ; Microbialites ; Nutriments ; Taux d'accumulation ; Paléoenvironnements ; Jurassique

1. Introduction

In the Recent, the presence of coral reefs reflects peculiar environmental conditions of marine waters (e.g., nutrient content, turbidity, light, water depth, temperature, and salinity; [22]). Modern coral reefs are very sensitive ecosystems with respect to environmental disturbances, notably pointing to a complex relationship between corals and algal–cyanobacterial benthic communities [40]. Since a decade or more, an increase of algae in coral ecosystems is evidenced, due to various natural and/or anthropogenic disturbances such as major storms, deforestation, or overfishing [21,24]. However, if carbonate precipitation of microbial mats frequently lead to the formation of microbialites in some Pleistocene and Holocene coral reefs [4,6], microbialites are only locally observed at the surface of modern coral bioconstructions [63]. Environmental changes and their frequency of occurrence, which could durably affect modern reef ecosystems and favour microbialite formation, are difficult to constrain at the scale of human observations. In this context, ancient reef systems are of first interest for understanding the behaviour of reef organisms in response to major environmental fluctuations.

In Late Jurassic oceans, coral and sponge bioconstructions were particularly abundant, forming a discontinuous reef belt over 7000 km along the northern Tethys and central Atlantic margins [39]. Late Jurassic times were also a period favourable to the formation of microbialites [58,67]. Coral reefs developed in relatively shallow and proximal settings, whereas sponge

bioherms occurred in deeper environments [10,37]. Various proportions of microbialites commonly contributed to coral and sponge reefs, up to form pure microbial reefs [11,23,35,36]. The presence of surfaces of reef growth interruption shows that the development of Jurassic coral- and sponge-microbialite reefs was not continuous and probably recorded palaeoenvironmental fluctuations. Moreover, the two main reef components, skeletal metazoans (i.e. corals and sponges) and benthic microbial communities do not necessarily reflect the same palaeoenvironmental conditions. If the internal structure of sponge-microbialite bioherms has been intensively studied [16,17,48,51], detailed analysis of coral-microbialite reefs are only supported by rare studies [46,49,60] and comparative works on the architecture of these two types of bioconstructions is still lacking. Moreover, the understanding of the respective role of physical-chemical parameters that controlled Jurassic microbialite-rich reefs is still debated.

Based on a detailed analysis of Jurassic coral- and sponge-microbialite reefs from various depositional setting of France and Germany, this work (i) synthesizes and compares the growth modes of these two types of bioconstructions, and (ii) discusses the main palaeoenvironmental factors controlling reef development at the scale of the shelf.

2. Material

The analyzed bioconstructions correspond to Middle (Bajocian) and Upper (Oxfordian, Kimmeridgian) Juras-

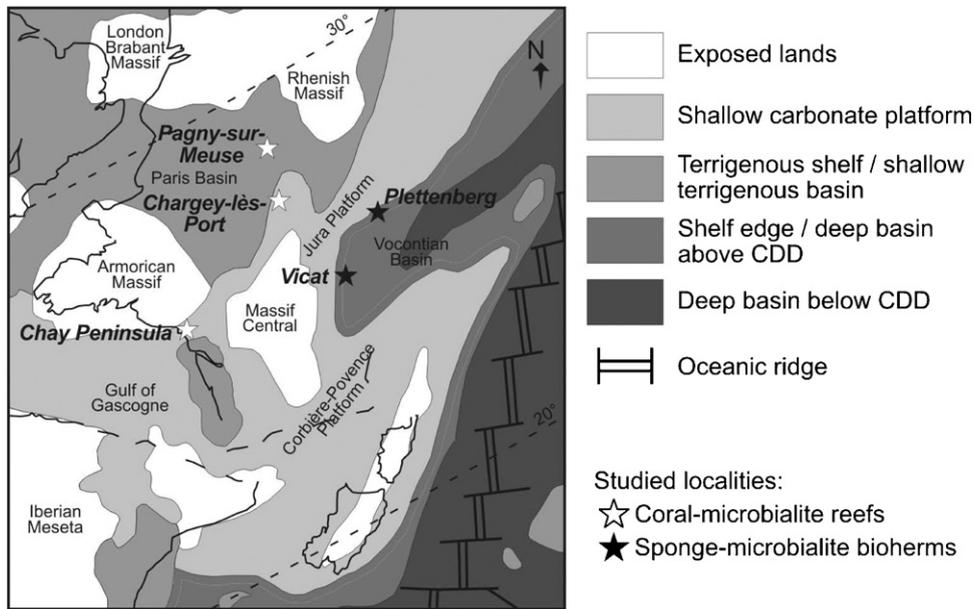


Fig. 1. Location of studied coral- and sponge-microbialite reefs on a palaeogeographic map during the Upper Jurassic (Early Kimmeridgian; after [7]).

Fig. 1. Position des récifs corallo- et spongio-microbialitiques étudiés sur une carte paléogéographique du Jurassique supérieur (Kimmeridgien inférieur; d'après [7]).

sic coral- and sponge-microbialite reefs. It is not in the scope of the present study to give the whole characteristics of the analyzed bioconstructions. The reader can refer to Olivier et al. [46,47,49] for coral-microbialite reefs of the Chay Peninsula, Pagny-sur-Meuse, and Chargey-lès-Port, respectively; and to Olivier et al. [48] and Gaillard [17] for sponge-microbialite bioherms of Plettenberg and the French Jura, respectively. Only a brief description of studied localities is given here (Fig. 1):

- (i) the Chargey-lès-Port quarry, near Vesoul (north-eastern France). A 16-m-thick section exhibits seven reef levels of Lower Bajocian age. These coral-microbialite reefs developed on the ‘Haute-Saône’ plateau at the transition between the Paris Basin and the northern Jura Platform [64];
- (ii) the Pagny-sur-Meuse quarry, about 33 km west of Nancy (northeastern France). A 95-m-thick section of Middle-Upper Oxfordian age displays four coral-microbialite reef levels. These bioconstructions developed on the Lorraine platform on the eastern margin of the Paris Basin;
- (iii) the Chay Peninsula, about 10 km south of La Rochelle (western France). Three successive reef levels are visible in the 16-m-thick composite section of the Lower Kimmeridgian. These coral-microbialite reefs developed on La

Rochelle–Angoulême platform, opened to the southwest onto the Aquitaine Basin;

- (iv) the Plettenberg quarry, in the western part of Swabian Alb (southern Germany). Numerous sponge-microbialite reef levels of Late Oxfordian to Early Kimmeridgian developed in a deep-shelf setting, located about 50 km to the east of the Jura Platform [41];
- (v) the Vicat quarry and the Pontet section in the southern French Jura Mountains (eastern France). These two localities display numerous levels of sponge-microbialite bioherms of Middle to Upper Oxfordian age. These bioconstructions are palaeogeographically located on the external part of the Jura platform, in an intermediate position between more proximal coral facies and deeper deposits of the Dauphinois Basin [18].

3. Depositional context and general reef composition

Coral- and sponge-microbialite reefs developed in different sedimentary environments; either in term of bathymetry (shallow platform vs. deep shelf/epicontinental basin) or in term of terrigenous influence. Three main contexts are here defined according to the relative abundance of terrigenous material in the environments: (a) pure-carbonate contexts; mixed

carbonate-siliciclastic contexts that can be either (b) carbonate- or (c) clay-rich.

3.1. Coral-microbialite reefs of pure carbonate context

They are observed in the locality of Pagny-sur-Meuse. In this lagoonal setting, bioconstructions are up to 15 m high and at least 100 m wide, with an overall convex upper surface. Corals are relatively diversified with 15 genera and form 61% of the reef volume. Stylinids (i.e. the phaceloid *Stylosmilia* and the plocoid *Stylina* according to Gill [19]) are the dominant forms. Giant coral colonies are common, such as 5–10-m-height phaceloid *Aplosmilia* or 1.3-m-diameter massive *Stylina*. Microbialites grew as thin crusts (<5 cm thick) and do not exceed 16% of the reef volume. These crusts correspond to centimetre-scale columns of thrombolitic fabric, nearly exclusively made of clotted micrite, almost devoid of microencrusters and bioeroders. Microencrusters, mainly represented by *Bacinella* and *Lithocodium*, are commonly observed, but directly on the coral surfaces, below microbialite crusts. Intra-reef sediments form 11% of the reef volume.

3.2. Bioconstructions of mixed carbonate-rich context

They correspond to some coral-microbialite reef levels of the Chay Peninsula and Chargey-lès-Port, and sponge-microbialite bioherms of French Jura (Vicat quarry).

At the Chay Peninsula, coral-microbialite reefs display moderate dimensions (up to 50 m long and 6 m thick). The coral fauna represents 23% to 37% of the reef volume. Coral diversity differs according to the reef level considered (9 to 12 genera). Stylinids, microsolenids and thamnasterids are the dominant forms (about 20–40% each). Microbialites constitute between 57% and 69% of the reef volume. Microencrusters (mainly nubecularids, *Tubiphytes*, bryozoans, *Koskinobullina*, calcareous sponges, and oysters) observed in the encrusting succession are common to frequent. *Bacinella* and *Lithocodium* are also locally observed. Intra-reef sediments constitute between 3% and 7% of the reef volume.

The Bajocian bioconstructions of Chargey-lès-Port are significantly different according to the reef level considered. Coral-microbialite bioherms have metre-scale dimensions and are characterized by a low coral diversity, with only eight identified genera. However, corals represent the main constituent of the bioherm (around 60% of the reef volume). Microbialites and intra-reef

sediments represent up to 14% and 26% of the reef volume, respectively. The coral fauna is dominantly made of massive *Isastrea*, and to a lesser extent of lamellar *Thamnasteria* and *Periseris*, whereas branching ramose forms (*Dendraranea*) are only locally observed. One biostrome level appears as an exception, almost exclusively constituted by the phaceloid *Cladophyllia*. In this relatively thin bioconstruction (up to 90 cm thick), microbialites form up to 70% of the reef volume.

Sponge-microbialite bioherms of French Jura are made of three main components: siliceous sponges, microbialites, and sediments, which form around 18%, 46%, and 35% of the reef volume, respectively. Other reef components, constituting less than 2% of the reef volume, are mainly bryozoans and serpulids, associated with brachiopods, calcareous sponges, oysters and other bivalves. Sponges are composed of about 89% hexactinellids and 11% lithistids. In this sedimentary context, siliceous sponges display large sizes, and tube- and dish-shaped specimens frequently exceed 50 cm in diameter, respectively. Microbialites are represented by very thick crusts (up to 15 cm) with a columnar morphology.

3.3. Bioconstructions of mixed, clay-rich contexts

They correspond to some coral-microbialite reef levels of Pagny-sur-Meuse and the Chay Peninsula, as well as sponge-microbialite reef levels of Plettenberg and the French Jura (Le Pontet section).

At Pagny-sur-Meuse and the Chay Peninsula, bioconstructions correspond to metre-scale patch reefs. Coral diversity strongly differs according to the reef level considered (6 to 16 genera). Corals form up to 56% of the reef volume, and are mainly microsolenids, thamnasterids, and *Calamophylliopsis*. Microbialites are abundant, but do not exceed 55% of the reef volume. Microbialite crusts generally display a massive aspect. They frequently show numerous growth interruptions, marked by millimetre- to centimetre-scale horizons of dark colour, strongly bored by bivalves (*Gastrochaenolites*) and encrusted by abundant oysters. In that case, microbialites are associated with abundant and diversified microencrusters (mainly nubecularids, *Tubiphytes*, bryozoans, *Koskinobullina*, calcareous sponges, and oysters). Locally, microbialites also display a columnar morphology. In that case, microencrusters are less frequent and are mainly represented by *Tubiphytes* and *Terebella*. Intra-reef sediments do not exceed 5% of the reef volume.

At Plettenberg and the French Jura, sponge-microbialite bioherms have small metre-scale dimensions. Siliceous sponges, microbialites, and sediments

form around 23–37%, 28–58%, and 17–31% of the reef volume, respectively. Other reef components (mainly serpulids and bryozoans) constitute around 1–4% of the reef volume. Sponges are composed of about 67–89% hexactinellids and 11–33% lithistids. Sponges have generally small dimensions (few decimetres). Microbialite crusts are relatively massive and thin (less than 5 cm thick) with planar or domal shapes.

4. Coral- and sponge-microbialite reef architecture

Most of studied coral- and sponge-microbialite bioconstructions display a lenticular shape (Fig. 2). This type of morphology translates a first phase of lateral and vertical reef expansion, and a second phase of reef reduction, until a final reef collapse. Such an evolution reflects a ‘low-frequency reef-growth phase’. Only some coral-microbialite bioconstructions of the Chay Peninsula and Chargey-lès-Port present a flat upper surface. All studied bioconstructions show major surfaces of reef growth interruption delimiting ‘medium-frequency reef-growth phases’. These latter include several elementary units,

here defined as ‘high-frequency reef-growth phases’. These units are made of two main sub-units: first, a coral or sponge framework and second, an encrusting succession made of microbialites and various encrusters. Whatever the depositional context, surfaces delimiting elementary units are more or less difficult to follow through the bioconstructions and within the lateral deposits. A good correlation between different reef-growth phases and lateral deposits is facilitated when sediments are well bedded. Generally, ‘medium- and high-frequency reef-growth phases’ can be correlated to units of several limestone beds. In mixed clay- and carbonate-rich contexts, these major reef-growth interruptions laterally correspond to more or less thick marly levels (Fig. 2B and C).

At the scale of an elementary unit, when the coral framework is well-projected above the sea-floor sediment (superstratal growth fabric *sensu* Insalaco [25]), very diversified microbialite morphostructures can develop such as mammilated microbialites at the underside and on the flanks of the coral framework, and pseudostalactitic microbialites at the roof of intra-reef cavities [46] (Fig. 3A). On the other hand, a reduced relief above the sea floor (constratal growth fabric

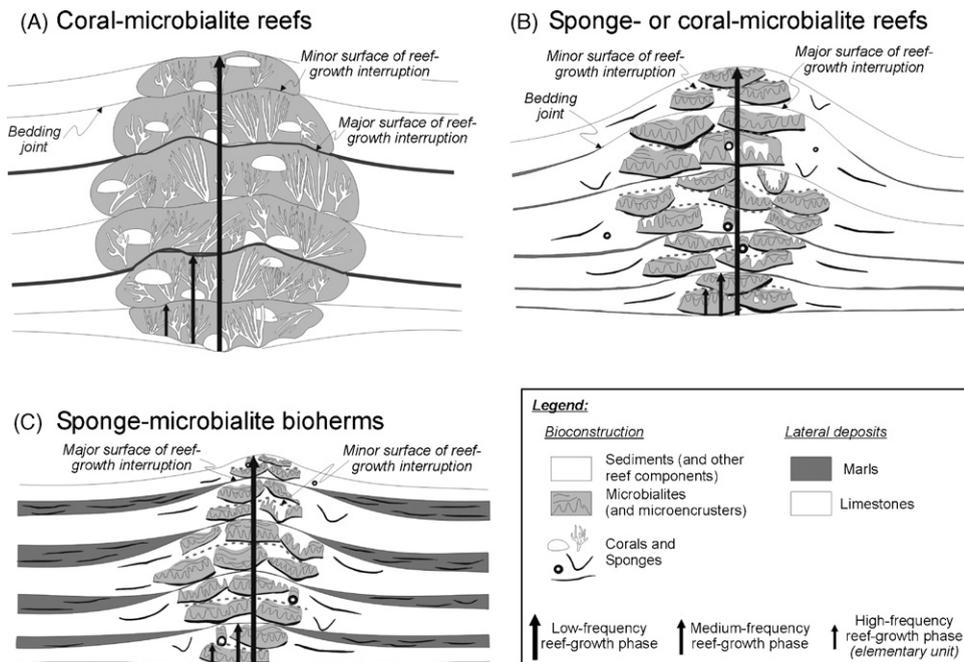


Fig. 2. Schematic representations of sponge- and coral-microbialite reef architectures according to the lithology of lateral deposits. The reef development can be subdivided in ‘high-, medium- and low-frequency reef-growth phases’. (A) Coral-microbialite reef in a pure carbonate context; (B) Coral- or sponge-microbialite reef in a mixed, carbonate-rich context; (C) Sponge-microbialite reef in a mixed, clay-rich context. See text for more explanations.

Fig. 2. Représentations schématiques des architectures des récifs corallo- et spongio-microbialitiques par rapport à l’agencement des dépôts latéraux. Le développement récifal peut être subdivisé en « phases de croissance de haute, moyenne et basse fréquences ». (A) Récif corallo-microbialitique dans un système sédimentaire purement carbonaté ; (B) Récifs corallo- et spongio-microbialitiques dans un système mixte carbonaté-silicoclastique, à dominante carbonatée ; (C) récif spongio-microbialitique dans un système mixte, riche en argiles. Se reporter au texte pour plus d’informations.

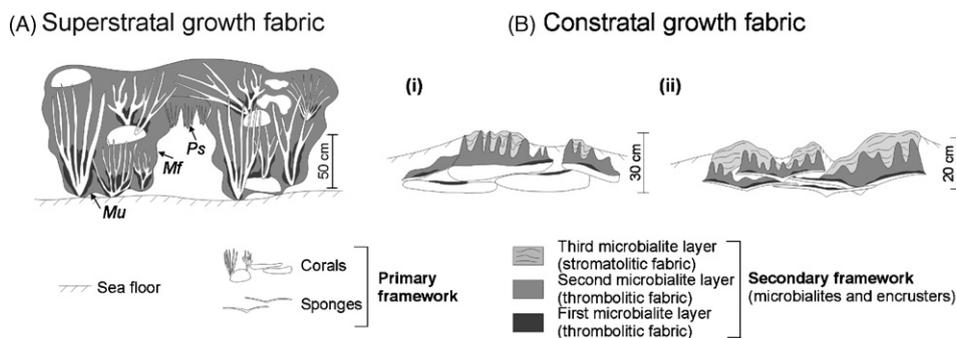


Fig. 3. Growth fabrics of the studied coral- and sponge-microbialite bioconstructions (*sensu* Insalaco [25]). (A) Superstratal growth fabric. Such architecture was only observed in coral-microbialite reefs. The framework is well projected above the sea floor and provides numerous intra-reef cavities where various microbialite morphostructures developed. The microbialite succession is two-layered. Ps, Pseudostalactite microbialites; Mf, mammilated microbialites of bioherm flanks; Mu, mammilated microbialites of bioherm underside. (B) Constratal growth fabric. Such architecture was observed in both some coral- (i) and sponge- (ii) microbialite reefs. These bioconstructions display a three-layered microbialite succession, only observed on the upper surface of primary coral or sponge frameworks.

Fig. 3. Trames récifales (*sensu* Insalaco [25]) des récifs corallo- et spongio-microbialitiques étudiés. (A) Trame récifale superstratale. Cette architecture récifale est uniquement observée dans les récifs corallo-microbialitiques. La trame récifale développe un fort relief au-dessus du fond marin. Cela entraîne la formation de nombreuses cavités intra-récifales, ainsi que des morphologies microbialitiques variées. Les microbialites sont composées de deux couches. Ps, Microbialites pseudostalactitiques ; Mf, microbialites mamelonnées de flanc de bioherme ; Mu, microbialites mamelonnées de base de bioherme. (B) Trame récifale constratale. Ce type de trame récifale est observé dans des récifs (i) corallo- et (ii) spongio-microbialitiques. Les microbialites sont formées de trois couches.

sensu Insalaco [25]) characterizes sponge-microbialite bioherms and other coral-microbialite bioconstructions (Fig. 3B). When coral or sponge frameworks display a constratal growth fabric, microbial crusts have planar, domal or columnar shapes, and always show an upward growth direction on the upper surface of the skeletal framework.

Microbialite crusts are composed of two layers of different fabrics and structures in coral reefs of superstratal growth fabric, whereas they are three layered in coral reefs and sponge bioherms of constratal growth fabric (Fig. 3). The first microbialite layer is directly observed on corals or sponges. It is relatively thin (millimetre- to centimetre-thick), laterally discontinuous, and presents a flat or slightly wavy upper surface. Microscopically, this layer is dominantly made of dense micrite, but can also be partially formed by clotted micrite. Its mesofabric is generally clotted, and thus corresponds to thrombolites, but can also locally be structureless (leiolitic). Just above the first microbialite layer, and/or directly on the sponge or coral surfaces, is a second centimetre-thick (up to 8 cm) layer that generally displays domal or columnar shapes. At the mesoscopic scale, this layer is most commonly thrombolitic, although a more or less marked lamination or a structureless fabric can locally occur. Microscopically, it is generally made of peloidal to clotted micrites, locally associated with dense micrite. The whole surface of sponge or coral frameworks is generally covered by the second microbialite layer. A third microbialite layer covers the upper part of the second layer in bioconstruc-

tions of constratal growth fabric (Fig. 3B). It is usually of lighter colour than the two first microbialite layers, making its distinction difficult with non-microbial carbonate mud. Depending on the density of the lamination, the third layer is either a stromatolite or a laminated thrombolite. When lamination is relatively sparse, the third layer tends to be leiolitic. At the microscopic scale, the lamination is marked by thin, micritic horizons, which can be traced laterally on several centimetres. These micritic horizons can cover layers of either dense and peloidal micrites or sparitic cement. The third microbialite layer is generally covered by allomicrite, but can also be directly overlain by a new generation of sponges or corals.

5. Discussion

5.1. Reef architecture and growth

5.1.1. Reef development

Whatever the depositional environment and the main skeletal metazoans, the studied coral- and sponge-microbialite reefs show very similar architectures and growth modes. Bioconstructions are all made up of elementary units (or 'high-frequency reef-growth phase'). The first stage of development of these elementary units corresponds to the edification of a primary coral or sponge bioconstruction (Fig. 4). This primary growth fabric is constratal in sponge bioherms, whereas it is either superstratal or constratal in coral reefs. A first and

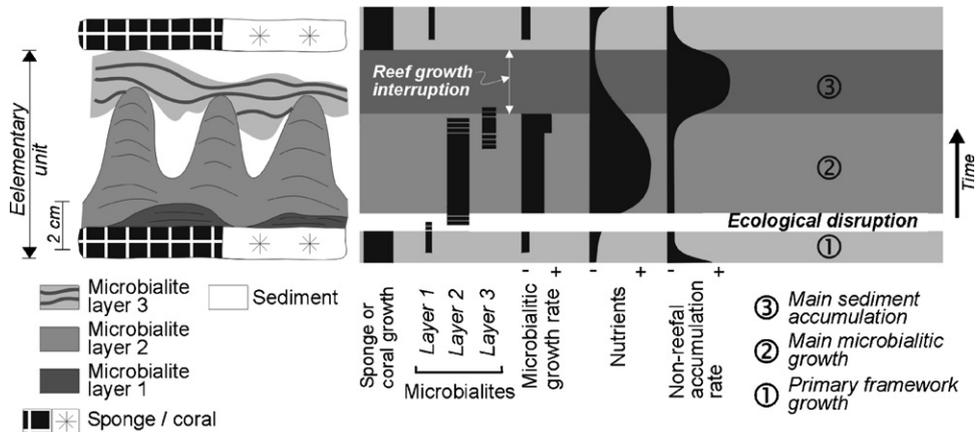


Fig. 4. Growth model of an elementary unit ('high-frequency reef-growth phase') occurring in coral- or sponge-microbialite bioconstructions of constrictal growth fabric. See text for more explanations.

Fig. 4. Modèle de croissance d'une unité élémentaire (« phase de croissance récifale de haute fréquence ») dans des récifs corallo- ou spongio-microbialitiques possédant une trame récifale constratral. Voir le texte pour plus d'informations.

thin (millimetre-scale) microbialite layer developed on the local dead part of corals and sponges. This layer is considered as contemporaneous of the coral or sponge growth [11,12,47,48]. The first microbialite layer does not necessarily represent the first stage of the encrustation. Some microencrusters, such as *Bacinella* and *Lithocodium*, are directly observed on the coral surface, below the first microbialite layer. Both in coral- and sponge-microbialite bioconstructions, the second centimetre-thick microbialite layer entirely covers the coral- or sponge-reef surface, playing an important binding role and becoming the main reef builder. The succession between a first skeletal reef component (i.e. corals or sponges) and an important volume of microbialites at the reef front suggests an ecological disruption (Fig. 4). More or less abundant and diverse microencrusters can be associated with both the first and second microbialite layers. The third microbialite layer is observed only within coral or sponge bioconstructions of constrictal growth fabric. This microbial crust of stromatolitic fabric overlapped the previous reef components, playing probably an important binding role before being covered by sediments. Only sparse microencrusters (*Terebella*) are observed within the third microbialite layer. Commonly, sediments overlay coral- or sponge-microbialite elementary units, pointing to a reef growth interruption. In some cases, notably in most of coral reefs of superstratal growth fabric, sediments are lacking between two successive elementary units, emphasizing a relief formation.

The reef development is marked by major reef-growth interruptions that delimit 'medium-frequency reef-growth phases' constituted of several elementary units. In mixed, clay-rich contexts, these periods of reef-

growth interruption are particularly well marked and correspond to centimetre-thick marly levels (Fig. 2C). In pure carbonate or mixed carbonate-rich contexts, these periods of reef growth interruption seem shorter and are laterally correlated to a thin (millimetre-scale) marly interval or to a bed joint (Fig. 2A and B).

Sponge- and coral-microbialite reefs always initiated laterally to limestones. Their 'low-frequency reef-growth phase' final demise can follow different pathways. In pure carbonate contexts of Pagny-sur-Meuse, coral-microbialite bioherms were definitively covered by limestone beds. In mixed carbonate-rich contexts, the final demise of coral-microbialite reefs of the Chay Peninsula is marked by an erosional surface, leading to a final flat-topped bioconstruction. At the Chay Peninsula, coral-microbialite reefs of mixed carbonate-rich contexts are definitively covered by marly levels. If sponge-microbialite bioherms can be definitively covered by a limestone bed in mixed carbonate-rich contexts, they are covered by either a marly level or a limestone bed in mixed clay-rich contexts.

5.1.2. Growth rates

Using a cyclostratigraphic approach in Swabian deep-shelf deposits, where developed sponge-microbialite bioherms, a marl-limestone couplet can be assimilated to the 20-kyr precession cycle [48,53]. Such a marl-limestone couplet is laterally correlated to a 'medium-frequency reef-growth phase' that can be subdivided into 3 to 10 elementary units. Thus, the formation of an elementary unit (i.e. the succession between a primary coral or sponge framework and a microbialite crust) can be at least reasonably estimated to occur at a millennial

timescale. Such duration is compatible with an estimation of the approximated time necessary for a coral- or sponge-microbialite elementary unit to develop. Following the banding structure observed in fossil corals that is assumed to represent annual growth increments [2], the mean growth rate of Jurassic corals is estimated to be in the order of 1 mm yr^{-1} (e.g., [32,33,44]). Estimation of Upper Jurassic sponge growth rate is more difficult. Based on modern sponge reefs of the west coast of Canada (British Columbia), although quite uncertain, a cm yr^{-1} growth rate for Upper Jurassic siliceous sponges can be assumed [30,68]. Thus, a centennial to millennial duration can be considered for coral and sponge primary frameworks edification within an elementary unit.

Due to the lack of modern equivalent, the evaluation of the microbialite growth rates is more difficult. Microbialite crusts observed in some modern coral reefs have an extremely low growth rate, of about 0.005 mm yr^{-1} [55]. On the other hand, thrombolites from some Pleistocene coral reefs were interpreted to present a very high growth rate, estimated to be equal to the reef accretion, which is comprised between 1.1 and 2.6 cm yr^{-1} [5]. Following the working hypothesis of a millennial time scale for an elementary unit to form, a microbialite growth rate $\leq 1 \text{ mm yr}^{-1}$ is suggested. Higher growth rate would lead to consider long periods of reef growth interruptions that are not corroborated by field observations such as heavily bored surfaces. Considering a microbialite growth rate of about 1 mm yr^{-1} , thicker microbialite crusts (up to 15 cm) will form in one or two centuries, corroborating a millennial timescale for the formation of one elementary unit.

Although a more precise estimation of the microbialite growth rate would be speculative, their petrographical characteristics support substantial variations in studied coral and sponge reefs. During the second microbialite layer development, differences in microfabrics and microencruster abundances can be interpreted in terms of variations in the microbialite growth rate. In sponge and coral reefs of pure carbonate or mixed carbonate-rich contexts, the second microbialite layer is generally made up of clotted or peloidal micrites that developed columnar shapes. In that case, microencrusters associated to this second layer are very sparse, suggesting a relatively continuous and high microbialite growth rate [47]. In mixed clay-rich contexts, the second microbialite layer is made of dense or clotted micrites with a domal shape or a wavy upper surface. In that case, numerous microencrusters alternate with this second microbialite layer. Thin (up to 1-cm-thick) and dark horizons of massive microbialites, underlined by numerous boring bivalves and oysters, are also commonly

observed and can be compared with the basal crusts described by Schmid [60] or with modern crusts covering hardgrounds [57]. Such horizons emphasize particularly long microbialite growth interruption events. Thus, the presence of abundant encrusters associated with a dense to clotted micrite emphasizes a lower and more irregular microbialite growth rate in siliciclastic-rich environments compared to pure or carbonate-rich contexts, where microbialites are commonly made of peloidal micrite with rare encrusters [47].

5.2. Controlling factors

In the recent literature, numerous factors such as nutrients, oxygenation, pH level, alkalinity, sedimentation, temperature, and sea-level changes (which in turn influenced water energy, depth, and light) are invoked to have controlled reef, coral, sponge, and microbialite development (e.g., [11,12,26,35,36,50,56,60,61,67]). The different factors controlling the reef development can result from either auto- or allocyclic processes, making their identification difficult. With relatively similar architectures and growth modes, studied coral and sponge reefs are characterized by the presence of microbialites at their surface. Thus, it can be assumed that the succession between a primary coral or sponge framework and the microbialite encrusting is predominantly driven by allocyclic factors. The possible interaction between several controlling factors can also make difficult the determination of a causal mechanism of an observable resulting effect. However, a recent study of Upper Jurassic sponge-microbialite bioherms shows that only few dominant factors, such as the trophic conditions and/or the accumulation rate, affecting durably the depositional environment, were predominantly recorded by fossil bioconstructions [48].

5.2.1. Clay content and associated nutrients

The amount of nutrients in the water column defines oligo-, meso-, and eutrophic conditions, which control the trophic structure and the feeding modes in modern reef systems [20]. Numerous studies emphasize an important role played by nutrients in controlling the formation of Jurassic microbialite-rich coral or sponge build-ups (e.g., [11,29,36,38,60]). Unfortunately, modern equivalent of Upper Jurassic coral- and sponge-microbialite reefs are unknown, making difficult an actualistic approach. In modern siliceous sponge reefs on the western coast of British Columbia, the presence of microbial deposits is not proven [9,68]. If microbialites are commonly observed in modern coral reefs, these crusts are generally confined in the internal

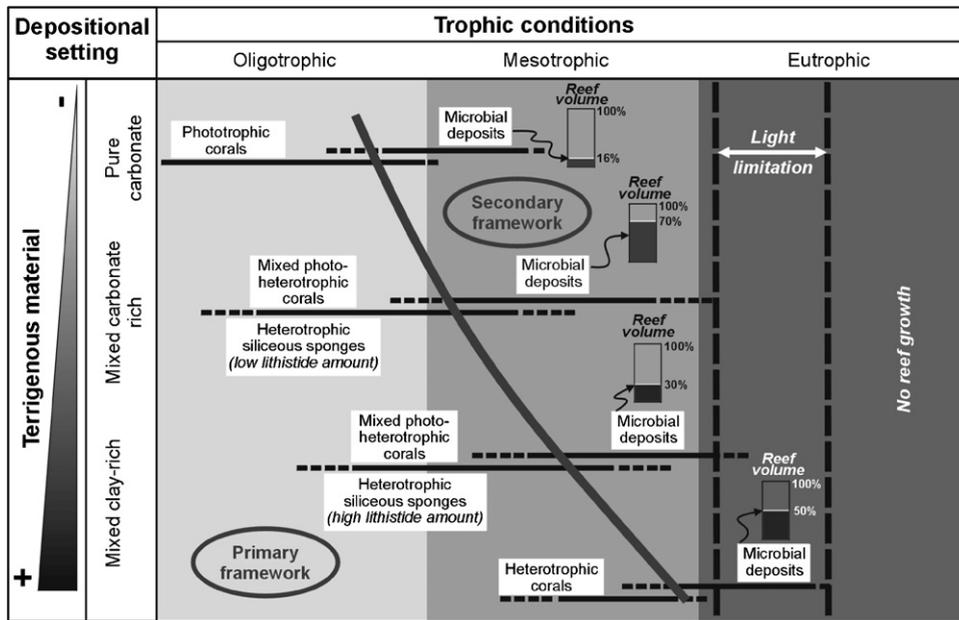


Fig. 5. Nutrient gradient relative to the depositional settings of Jurassic coral- and sponge-microbialite bioconstructions. Coral- or sponge-microbialite shifts occurred under different trophic conditions. In oligotrophic waters, a low amount of microbialites developed on a phototrophic coral assemblage. In low- to mesotrophic conditions, mixed photo-heterotrophic corals and heterotrophic siliceous sponges support a particularly voluminous microbialite development. In high-mesotrophic conditions, a light limitation led to a reduced microbialite development on a heterotrophic coral primary framework. The microbialite amounts are given with regard to coral reefs. See text for more explanations.

Fig. 5. Relations entre les conditions trophiques, l'environnement de dépôt et la composition des récifs corallo- et spongio-microbialitiques. Dans des conditions oligotrophes, une faune corallienne phototrophe sert de support à un encroûtement microbialitique réduit. Des assemblages coralliens mixtes photo-hétérotrophes ou des spongiaires siliceux hétérotrophes, associés à un important volume microbialitique, caractérisent des conditions faiblement mésotrophes. Sous des conditions fortement mésotrophes, une action limitante de la lumière tend à réduire le développement des microbialites sur un support corallien hétérotrophe. La quantité donnée de microbialites concerne les récifs coralliens. Voir le texte pour plus d'informations.

parts of the bioconstructions (e.g., [55,69]). Nevertheless, some modern coral reefs of French Polynesia reveal a microbialitic formation at the reef surface, following an increase in the nutrient availability [63]. Microbialite formation induced by temporal pulses of nutrient release has been mentioned within some Pleisto-Holocene coral reefs [4,6]. Similarly, Dupraz and Strasser [11,12] have explained the development of large amounts of microbialites at the surface of some Upper Jurassic coral reefs by an increase of the nutrient content linked to terrigenous inputs.

The causal mechanism responsible for the nutrient content fluctuations in the water column can strongly differ according to the bioconstruction considered and its depositional setting. The presence of upwellings can bring nutrient-rich waters in shallow platforms [38]. However, neither sedimentary nor palaeontological field arguments confirm such hypothesis in the studied cases. Nutrients can also be released from sediments after, for example, a storm event in pure carbonate contexts of Pagny-sur-Meuse [47]. In mixed clay- or carbonate-

rich contexts, it is assumed that nutrients mainly derived from terrigenous inputs, probably triggered by climatic oscillations. According to the amount of clay content in the system, studied sponge- and coral-microbialite reefs show significantly different compositions and dimensions (Fig. 5).

In mixed clay-rich contexts, coral- and sponge-microbialite bioherms are small, with lateral extents that do not exceed 15–20 m. Skeletal metazoans also display reduced sizes. In sponge bioherms, dish-shaped and lamellar sponges generally rarely exceed 10 cm in diameter. Similarly, sizes of branching and domal corals generally remain below few tens of centimetres in height and in diameter, respectively. Nutrient-rich waters are also emphasized by sponge or coral assemblages. Sponge bioherms are made of a relatively important amount of lithistids (up to 33% of the sponge assemblage) and microbialites (up to 58% of the reef volume). Such an amount of lithistids, considered as active filter feeding organisms [38], suggests relatively high-trophic conditions. In coral reefs, the amount of terrigenous material

and nutrients deduced from the coral assemblages seems also correlated with the microbialite content. In mixed clay-rich contexts of Pagny-sur-Meuse, microbialites represent 16–30% of the reef volume when the coral assemblage (mainly *Thamnasteria*, *Microsolena*, and stylinids) is mixed photo-heterotrophic, and up to 50% with a heterotrophic association (mainly *Microsolena*, *Calamophylliopsis*, and *Thecosmilia*). In this later case, microbialites show numerous surfaces of growth interruption, which are marked by abundant heterotrophic encrusters (e.g., oysters and bryozoans) and an intense bioerosion, enhancing a high nutrient level (Fig. 5).

In pure carbonate context of Pagny-sur-Meuse, reef composition and dimension emphasize oligo- to low-mesotrophic waters. These coral-microbialite bioconstructions display very large dimensions, up to 15–20-m-thick and more than 100 m of lateral extent. Corals are diversified and commonly display metre-scale dimensions. The coral assemblage (i.e. mainly *Aplosmilia* and stylinids) and the microencruster association (*Bacinella* and *Lithocodium*) are characteristic of oligotrophic conditions [11,36]. Microbialites are not abundant and their contribution to the reef volume does not exceed 16%. However, they can locally form a relatively thick crust (up to 5 cm), made of thrombolitic columns. Considering a nutrient release from sediments after a storm event, the time interval during which waters are nutrient-rich is relatively short. Even so, the coral reef damage, coupled with a possible biofilm capacity to prevent or limit the coral recovery and settlement, allowed rapid but reduced microbial development. Relatively fast and continuous microbialite growth is indeed suggested by rare microencrusters and no significant boring activity.

In mixed carbonate-rich contexts, intermediate reef patterns characterized sponge- and coral-microbialite bioconstructions. Reef composition and dimension emphasize low- to high-mesotrophic conditions. Bioconstructions show relatively high dimensions, up to 10 m thick and 50 m of lateral extent. Dish-shape hexactinellids commonly exceed 1 m in diameter. Some branching coral colonies (e.g., *Calamophylliopsis*) also exceed 1 m in diameter and height. The coral reefs are represented by a mixed photo-heterotrophic coral assemblage. Heterotrophic microencrusters are common, whereas *Bacinella* and *Lithocodium* are only locally observed in some coral bioherms (e.g., Chay Peninsula). Mixed carbonate-rich contexts seem to be the more favourable environment for microbialite development in coral reef (up to 70% of the reef volume; Fig. 5). In sponge bioherms, the high amount of microbialites (46% of the reef volume), their thickness (up to 15 cm),

and their columnar shape also suggest very favourable conditions to a rapid development.

The nutrient content controlled the general reef composition, but its fluctuations have also an impact on the reef development. In the model of Fig. 4 that illustrates the main factors controlling the formation of an elementary unit, the microbialite development at the front of coral and sponge reefs is mainly explained by an increase in the nutrient content. Independently of trophic conditions that occurred during coral or sponge growth, this model emphasizes the rapidity of the shift towards relative more nutrient-rich conditions that favoured the bloom of benthic microbial communities and the formation of the second microbialite layer at the reef surface. Olivier et al. [48] demonstrated that fluctuations of the nutrient content controlled sponge-microbialite reef growth in a mixed clay-rich context (Fig. 6). The bioherm development (i.e. ‘low-frequency reef-growth phase’) can be included in a low frequency fluctuation of the nutrient content. Considering calcareous microfossils, marly levels that surround the sponge-microbialite bioherms are characterized by the highest occurrence of small ‘eutrophic species’. In the middle part of bioherms, corresponding to their maximal lateral extent, lateral deposits display higher carbonate content and more oligotrophic nannofossils. By analogy, ovoid-shaped coral-microbialite reefs of mixed clay-rich contexts, which are stratigraphically surrounded by marly levels, may also reflect similar continuum in the trophic conditions. The coral-microbialite reef growth only occurred laterally to limestone deposits (mesotrophic conditions), whereas it finally demised under eutrophic conditions during the deposition of marly levels. Although less visible in the lithology, similar continuum in the trophic conditions can be applied to sponge- and coral-microbialite bioherms of mixed carbonate-rich or pure carbonate contexts. In both cases, maximum lateral extents of bioconstructions occurred under a relatively low nutrient content (oligo- to mesotrophic conditions), and the reef development reduction probably reflects more nutrient-rich waters. Nannofossil assemblages analyzed laterally to sponge-microbialite bioherms of Plettenberg also display significant differences at the scale of the ‘medium-frequency reef-growth phases’. In this mixed clay-rich context, the limestone beds, which are laterally correlated to the sponge-microbialite bioherm development (i.e. ‘medium-frequency reef-growth phase’), are characterized by a predominance of oligotrophic nannofossil assemblages [48]. In marly levels, during reef growth interruptions, meso- to eutrophic assemblages of nannofossils predominated. Less abundant sponges, and reduced microbialite

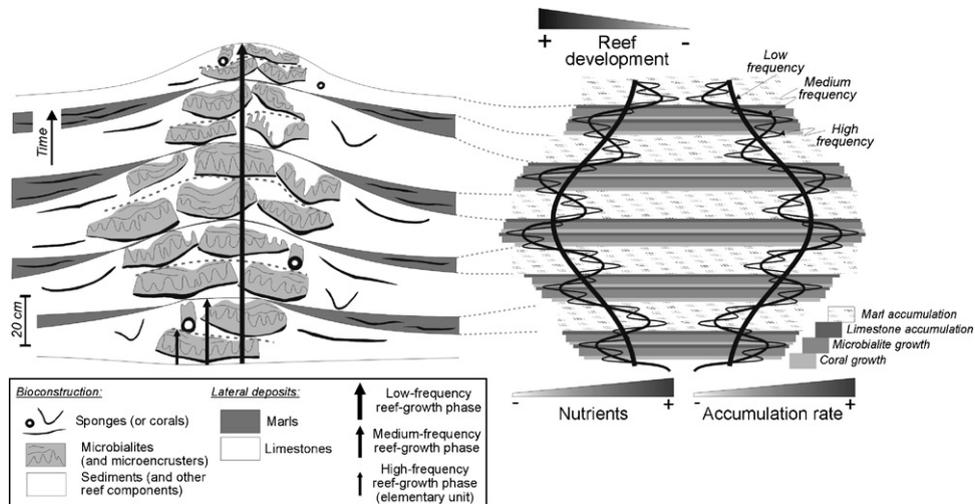


Fig. 6. Growth model of studied Jurassic coral- and sponge-microbialite reefs mainly driven by trophic level and carbonate accumulation. The illustrated case corresponds to a sponge-microbialite bioherm of mixed, clay-rich context. Each 'medium reef-growth phase' is theoretically composed of two elementary units. The reef development is controlled by three orders of nutrient content and accumulation rate fluctuations. Equivalent models could be invoked for other coral- or sponge-microbialite reefs of pure carbonate and mixed, carbonate-rich contexts. See text for more explanations.

Fig. 6. Model de croissance des récifs corallo- et spongio-microbialitiques. Le développement de ces bioconstructions est principalement contrôlé par la teneur en nutriments et le taux d'accumulation. Le cas illustré correspond à un bioherme spongio-microbialitique dans un contexte sédimentaire mixte, riche en argiles. Chaque « phase de croissance récifale de moyenne fréquence » est théoriquement composée de deux unités élémentaires. Trois ordres de fluctuation de la teneur en nutriments et du taux d'accumulation contrôlent le développement récifal. Des modèles équivalents peuvent être appliqués aux récifs corallo- et spongio-microbialitiques des contextes sédimentologiques mixtes, riches en carbonates. Voir le texte pour plus d'informations.

development in marly intervals, led to the loss of a real reef-framework when high nutrient content (eutrophic conditions) might have occurred (Fig. 6).

5.2.2. Accumulation rate of sediments

A very low accumulation rate of sediments is necessary for the installation of coral or sponge larvae. For coral reefs of superstratal growth fabric, the accumulation rate should remain relatively low to null during the entire primary coral framework edification, as suggested by mammilated microbialites with a downward growth direction at the underside of coral colonies (Fig. 3A). This leads us to consider with cautions the usual and perhaps too much easily admitted interpretation of high-branching corals as a witness of oversedimentation. In bioconstructions of constratal growth fabrics, the presence of some encrusters such as bryozoans, serpulids, and thecideid brachiopods on the lower surface of dish-shaped siliceous sponges and lamellar or massive corals also implies a low accumulation rate during the formation of the primary skeletal framework (cf. [17,31]; Fig. 4).

Although the formation of ancient microbialites is generally considered as reflecting a sedimentation rate close to zero, because biofilms are not able to survive

high sediment input [36], the successive microbialite layers observed within elementary units highlight accumulation rate variations. Both in coral and sponge reefs, the first microbialite layer development is contemporaneous with corals or sponges, and thus developed under a low-to-null accumulation rate. The second microbialite layer, with a domal or columnar shape, may reflect disturbing influence of sediment particles on the biofilm surface [13,55]. However, a columnar growth form of microbialites can also be considered as of biological origin and dependent on a sufficient accommodation space [3,65]. Thus, sediment accumulation could also remain strongly reduced during the second microbialite layer formation. In that case, columnar thrombolites more probably reflect rapid microbialite growth rather than a direct reaction against burial (Fig. 4). The downward growth direction characteristic of columnar mammilated microbialites of bioherm underside supports such interpretation. Sponge-microbialite bioherms are always characterized by the presence of a third stromatolitic layer that ends the microbialite encrustation [10,17,48]. This third layer was also observed in some Bajocian coral-microbialite bioherms of constratal growth fabric [49]. Such upward succession from a thrombolitic (microbialite layer 2) to

a stromatolitic (microbialite layer 3) fabric is commonly observed in the fossil record [1,14,28,42] and in modern settings [15], and can be interpreted as the result of an increase of the accumulation rate [10,17,48,51,62]. Thus, at the scale of an elementary unit of constrictal growth fabric, the fluctuation of the accumulation rate tends to be irregular and progressively increases during the formation of the third microbialite layer. Only a decrease of the accumulation rate permits the installation of a new generation of sponges or corals. The third stromatolitic layer is absent in coral-microbialite reefs of superstratal growth fabric. In these bioconstructions, sediments directly covered the second microbial crust, suggesting a too rapid increase of the accumulation rate that did not allow the formation of a stromatolite layer. Such a scenario seems to have occurred in pure carbonate contexts, where microencrusts are lacking at the second microbialite layer surface. In mixed clay-rich contexts, microbialites are generally heavily encrusted and bored, suggesting a longer period before being definitively covered by sediments. Whatever the depositional context and the reef-growth fabric considered, the increase of the accumulation rate progressively tends to surpass the microbialite growth rate, leading to the end of the elementary unit development (Fig. 4). Phases of sediment accumulation mainly occurred during periods of reef-growth interruption. The presence of limestone beds at the top of some coral- or sponge-microbialite reefs also suggest that final demise of some bioconstructions (i.e. at a ‘low-frequency reef-growth phase’) can be due to an increase of the accumulation rate.

5.2.3. Sea-level fluctuations

Reef growth and environmental parameters can be considerably affected by sea-level fluctuations [38]. Water-depth estimations corresponding to deep ramp or epicontinental basin settings are generally assumed for sponge-microbialite bioherms [17,34, 41]. In recent studies on Upper Jurassic sponge-microbialite bioherms of southwestern Germany, an important control of sea-level fluctuations during the reef development was suggested [51,59]. These authors explained the transition between the second thrombolitic layer and the third stromatolitic layer by a depth decrease. Furthermore, they consider that elementary units initiated on an erosional surface, which probably resulted from a storm event. In studied Plettenberg and French Jura sponge-microbialite bioherms, such erosional surfaces have not been observed, and as described by Gaillard [17], elementary units are frequently delimited by stylolitic structures. Abundant ammonites, few solitary corals, as well as the absence of hummocky cross-stratifications and

calcareous algae, suggest a depth probably below the storm-wave base [48,53]. The presence of strong deep currents, such as it is observed in modern sponge reefs on the western Canadian continental shelf [68], may be sufficient to explain the numerous tuberoids in the lateral deposits of the bioconstructions. A water depth in the range of 60–100 m is assumed for the studied sponge-microbialite bioherms. Thus, low amplitudes (a few metres) of bathymetric changes in the Upper Jurassic [52] cannot have a direct influence on ‘high-, medium- or low-frequency reef-growth phases’. On the other hand, such sea-level changes directly controlled the carbonate production on the Jura shallow platform, and the amount of carbonate exported to epicontinental basins [54]. Thus, sea-level changes indirectly controlled sponge-microbialite development via the accumulation rate. Concerning coral-microbialite reefs, changes in water depth may be particularly important and directly controlled their development. An effect of sea-level fluctuations is well visible at the scale of the ‘low-frequency reef-growth phase’ in the Chay Peninsula, where the bioconstructions of two reef levels are flat-topped, probably because they caught-up the sea level. Although more difficult to highlight, a similar direct depth-water stress cannot be excluded at the scale of ‘high-frequency reef-growth phase’, leading to the end of the sediment accumulation phase.

5.2.4. Oxygenation

The existence of dysoxic to anoxic waters is one of the most cited factors of the literature explaining the formation of pure thrombolitic bioherms in the deep part of Jurassic epicontinental basins [35,38,59,60]. Authors considered that seawaters were oxygen depleted, as suggested by the presence of glauconite and the bivalve *Aulacomyella* in sediments. The predominance of microbial deposits associated with the *Terebella–Tubiphytes* association, coupled with rare metazoans, is also interpreted as being significant of oxygen-poor waters in the deeper part of epicontinental seas [60]. Such arguments are also applied to platform settings, in order to explain the transition between coral- or sponge-dominated levels and pure thrombolite-dominated levels [36]. Oxygen-depleted and nutrient-rich waters have been invoked in the formation of microbialite-rich coral reefs of the Chay Peninsula [35]. In studied sponge- and coral-microbialite reefs, the main microbialitic crusts (i.e. second and third microbialite layers) are posterior to the primary coral or sponge framework. Thus, the formation of microbialites could reflect dysoxic waters. The existence of oxygen-depleted waters during the formation of microbialites has been tested using rare-earth elements (REE; [45]).

The specific behaviour of the cerium (Ce) in the lanthanide group gives information on the oxygenation state of ancient seawaters. In pure carbonate lagoon setting of Pagny-sur-Meuse, seawater-like REE patterns, highlighted by strong negative Ce anomalies measured on microbialite samples, suggest a well-oxygenated water column. Moderate negative Ce anomalies, reported in microbialites of carbonate-dominated sponge bioherms (Plettenberg), evoke relatively well-oxygenated seawaters. In mixed carbonate- and clay-rich contexts of the Chay Peninsula and Pagny-sur-Meuse, high amounts of siliciclastics masked the seawater signature, and do not allow us to define the redox conditions. Therefore, in the studied Upper Jurassic coral and sponge reefs, the oxygenation state has not played a major role in the formation of microbialites.

5.2.5. Terrigenous inputs

Terrigenous inputs can also increase the alkalinity of seawater, enhancing the carbonate precipitation related to microbialite formation [27,43,55]. However, the absence of positive Ce anomalies, as well as strongly enriched Heavy REE patterns in the studied microbialites, suggest that ambient seawaters were characterized neither by a high alkalinity nor by a higher pH than that of modern seawaters [45].

Terrigenous inputs can increase the turbidity of the water column, influencing photophilic reef communities. The presence of light-dependent microencrusters such as *Bacinella* and *Lithocodium* in some coral reefs suggests well-illuminated waters [36]. A light dependence of microbialites in coral or sponge bioconstructions is highlighted by their upward growth direction, whereas sciaphilic organisms encrusted the downward facing surface of substrates [17,46]. Such an observation is compatible with the fact that 1 to 10% of the surface light intensity reaches depths of 60–100 m [66]. Periods of reduced light intensity in the water column probably occurred in mixed clay-rich contexts, due to higher amounts of terrigenous material (Fig. 5). During such periods of low light intensity, microbialites could stop their growth, allowing the formation of intensively bioeroded and encrusted surfaces.

5.2.6. Temperature

Upper Jurassic coral diversity appears closely correlated to ambient seawater temperatures and displays significant variations according to climatic changes and latitudinal positions [8]. The relatively large latitudinal window of Upper Jurassic reefs is generally used to support an equable global greenhouse climate [34,35]. Thus, it is unlikely that temperature was a predominant control-

ling factor at the scale of ‘medium- and high-frequency reef-growth phases’ of coral- or sponge-microbialite bioconstructions.

6. Conclusions

This study documents similar architectures in Jurassic coral- and sponge-microbialite bioconstructions on the northwestern Tethys margin. Independently of the palaeogeographical position (shallow lagoon to deep-shelf settings), the reef development corresponds to the stacking pattern of elementary units made of a primary skeletal framework and a multilayered microbialite encrusting. Contemporaneously with the edification of a coral or sponge framework, only a first and thin microbialite layer is locally observed. Then, a second and pluricentimetric-thick microbialite layer developed at the reef surface, playing the main building role. Finally, a third stromatolite layer, only observed in bioconstructions of constrictal growth fabric, covered the previous reef structures.

Reef composition and development were controlled by the proximity of siliciclastic sources. According to the amount of terrigenous material in the sedimentary environment, studied bioconstructions occurred in pure carbonate contexts, and in clay- or carbonate-rich mixed carbonate-siliciclastic contexts. Nutrients associated with terrigenous influx seem to have mainly controlled reef development and composition. Within an elementary unit, development of the second microbial layer, which entirely covered the reef surface, emphasizes an ecological disruption of coral or sponge assemblages. Whatever the trophic conditions (oligo- to mesotrophic) that occurred during coral or sponge growth, the microbialite development is related to a rapid increase in the amount of nutrients present in the water column. Mixed, carbonate-rich contexts are the more favourable environments to a rapid and important microbialite development. More clay-rich is the environment, more the microbialite development is marked by surfaces of growth interruption that are heavily bored and encrusted. A light limitation probably due to too turbid waters can be responsible for microbialite growth interruptions.

Growth mode of elementary units that composed sponge- and coral-microbialite bioherms provides precious information on the competition between reef growth and sedimentation rate. The presence of a large amount of microbialites, notably with different growth directions, suggests reduced-to-null sediment accumulation rates during the primary framework edification. The third stromatolite layer in bioconstructions of constrictal growth fabric is assumed to have recorded an increase

of the accumulation rate. Increase of the accumulation rate is assumed to be the main controlling factor in microbialite and elementary unit turn off. Main periods of sediment accumulation occurred during reef growth interruptions.

Along Jurassic shelves, ecological shifts from skeletal reef metazoans to microbialite crusts highlight high-frequency (millennial time-scale) palaeoenvironmental fluctuations. Architectures of the studied sponge- and coral-microbialite reefs emphasize three main orders of climatic oscillations that could have directly regulated the amount of terrigenous material and associated nutrients in the water column.

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