

## Paleoecology, Growth Parameters and Dynamics of Coral, Sponge and Microbolite Reefs from the Late Jurassic

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**Area of Study:** Portugal, Spain, Southern Germany, France, Poland

**Environment:** Shallow to deep carbonate platforms

**Stratigraphy:** Late Jurassic

**Organisms:** Corals, siliceous sponges, microbes, microencrusters

**Depositional Setting:** Brackish-lagoonal to deep ramp settings

**Constructive Processes:** Frame-building, baffling and binding (depending on reef type and type of reef-building organisms)

**Destructive Processes:** Borings by bivalves and sponges; wave action

**Preservation:** Mostly well preserved

**Research Topic:** Comparative facies analysis and paleoecology of Upper Jurassic reefs, reef organisms and communities

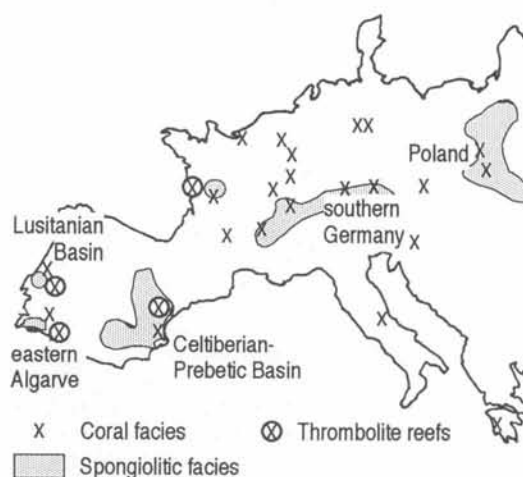


Fig. 1: Distribution of Upper Jurassic reefs studied in detail.

### Abstract

Reefs from the Late Jurassic comprise various types of coral reefs, siliceous sponge reefs and microbolite reefs. Upper Jurassic corals had a higher ratio of heterotrophic versus autotrophic energy uptake than modern ones, which explains their frequent occurrence in terrigenous settings. Coral communities changed along a bathymetric gradient but sedimentation exerted a stronger control on diversities than bathymetry. One coral community was adapted to brackish waters.

Reefal siliceous sponge biostromes and sponge microbolite mud mounds generally occur below the coral facies, and hexactinellid-dominated sponge communities generally occur below a zone of mixed "lithistid"-hexactinellid growth. This distribution mirrors differences in nutrient conditions, with coral facies related to stable, moderately oligotrophic to mesotrophic conditions whereas moderately oligotrophic could tolerate fluctuating levels and hence may range from extremely oligotrophic to strongly mesotrophic settings. This is due to the fact that hexactinellid sponges can largely live on osmotrophy and "lithistid" sponges develop deposits of living organic matter by hosting a huge mass of bacteria.

Microbolite crusts demand strongly reduced sedimentation and are important framework contributors in many coral and sponge reefs. Eutrophication or oxygen depletion may exclude reef fauna, giving rise to pure microbolite reefs.

Most Upper Jurassic reefs developed in ramp settings. High-energy reefs contain little preserved framework, whereas low-energy reefs may have excellently preserved

framework and pronounced relief whenever microbolite crusts provided stabilization. Reefs in steepened slope settings are generally rich in microbolites because of bypass possibilities for allochthonous sediment. Reef rimmed shallow-water platforms did occur but only developed on pre-existing uplifts. Upper Jurassic sponge-microbolite mud mounds grew in subhorizontal mid to outer ramp settings and reflect a delicate equilibrium of massive and peloidal microbolite precipitation and accumulation of allochthonous mud and fine allochems, determined by the distance to shallow-water carbonate factories. Disturbances in this equilibrium lead to the development of sponge biostromes or the disappearance of sponge facies.

The growth of Upper Jurassic reefs was largely restricted to, or strongly facilitated by, rising global or regional sealevel, reducing sediment influx occurring during 4<sup>th</sup> or 5<sup>th</sup> order transgressive pulses within the window of 3<sup>rd</sup> order sealevel rise. Consequently, transgressive/early highstand shallow-water reefs are rich in microbolite crusts and highly diverse, whereas the rare late highstand/lowstand coral reefs are of low diversity and have little framework preserved. In deeper waters, the frequency of sponge-microbolite mounds is correlated with the sealevel development. Together with basin configuration climatic and oceanographic response to sealevel rise account for a predisposition for eutrophication and oxygen depletion particularly around the Iberian Peninsula, giving rise to the occasional occurrence of pure microbolite reefs or repetitive successions of coral-microbolite to pure microbolite reefs at fairly shallow water depths.

The origin of Upper Jurassic reefs can only be unraveled by taking the paleogeographical, structural and sequence stratigraphic framework into account. On the other hand, the lateral and bathymetric distribution patterns of reef types from the Late Jurassic provide valuable tools for the better

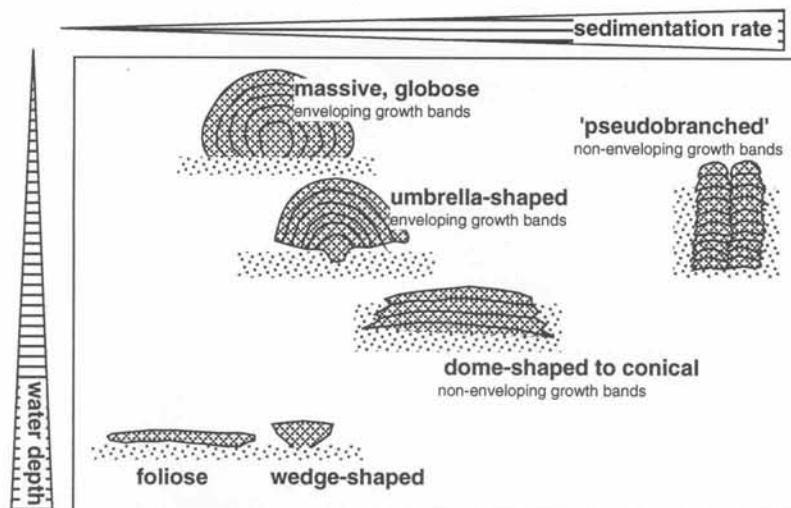


Fig. 2: The influence of sedimentation rate and water depth on the morphology of *Microsolena agariciformis* (after NOSE 1995).

understanding of shelf dynamics and climate of this epoch at a regional and even global scale.

more thorough discussion of selected aspects. Additional papers and monographs are in preparation.

## 1 Introduction

Reefs grew widespread during the Late Jurassic. Most were situated along the margins of the Tethys and its shelf seas but also developed in some parts of the North Atlantic rift systems and its adjacent epicontinental seas (central Portugal, northern Germany, southern England) as well as in the Pacific realm (e.g. southern Argentina, Japan). Along the Tethys they were particularly frequent at its northern marginal seas. We analyzed, in a comparative approach, the belt-like reef region at the tectonically stable northern margin of the Tethys (focusing on S-Germany, N-Switzerland, NE-France, NE-Spain and S-Portugal) as well as the reefs from the strongly differentiated and tectonically active Atlantic rift (Lusitanian Basin, west-central Portugal) and adjacent marginal seas (SW-France). Despite all differences in the settings, a common feature of most regions is the development of an Upper Jurassic, large-scale shallowing-upward succession, into which reefs are more or less frequently intercalated at different positions.

Reefs comprise very variable types and faunal communities of coral reefs, siliceous sponge reefs and microbolite reefs. These reefs were most widespread during the Oxfordian and, in some basins, during the Kimmeridgian, whereas they grew only locally during the Tithonian. Our main scope was to identify the factors responsible for the occurrence and differences of Late Jurassic reefs, and to discuss their mutual interdependence and interaction in a geological and paleogeographical framework. Our interpretation is based on qualitative and semi-quantitative paleoecological faunal analysis of reefal and non-reefal communities (constructional morphology, taxonomy and population dynamics of reef organisms), on the sedimentology of reefs (microfacies, petrography, geochemistry), as well as on their regional geological framework (biostratigraphy, sequence stratigraphy, field mapping, incorporation of pre-existing data on paleogeography and basin tectonics).

This paper summarizes results of a six-year research project on reefs from the Late Jurassic which was performed by the Stuttgart reef group in the course of the Priority Program "Global and Regional Controls on Biogenic Sedimentation – Reef-Evolution" of the "Deutsche Forschungsgemeinschaft". We present an overview of our research results at the current state of evaluation. We also give pointers to other papers already published by us for a

## 2 Paleobiology of Upper Jurassic Reef Organisms

Paleobiology of organisms in general can be deduced from the fossilized remains, which are the product of genetically fixed constructional characteristics specific for a certain organism (intrinsic factors, such as given microstructure and other general bauplan elements) and a flexible reaction or adaptation to environmental conditions or their change (extrinsic factors). The latter might be unraveled by well fixed or flexible morphology and growth rates, or isotopic signatures.

### 2.1 Corals from the Late Jurassic

The ecological demands of hermatypic scleractinian corals from the Late Jurassic are similar to those of modern zooxanthellate scleractinians, although some significant differences exist. In the Upper Jurassic, the associated facies and fauna (e.g. oolites, green algae) as well as the paleogeographical occurrence point to shallow, warm-water environments in which hermatypic scleractinians grew and formed reefs. Nevertheless, the low latitude reef belt was probably wider than today, since remarkable shallow-water coral reefs were also described from the Neuquén Basin in Argentina (50° paleolatitude) (LEGARRETA 1991), Northern Germany (39° paleolatitude) (BERTLING 1993a) and the Oxfordian of England (40° paleolatitude) (ALI 1984). This indicates a more equilibrated greenhouse-type climate during the Upper Jurassic (LEINFELDER 1993a, 1994a, LEINFELDER et al. 1993a).

In contrast to modern corals Upper Jurassic scleractinians frequently occur in siliciclastic environments. Beside forms adapted to elevated sedimentation already by their phaceloid growth (e.g. *Calamophylloipsis*) highly morpho-variable taxa (*Thamnasteria*, *Microsolena*) are able to cope with elevated sedimentation rates (Fig. 2). The latter exhibit a change to "pseudobranching" morphotypes with non-enveloping growth bands indicative of elevated sediment input (cf. JAMES & BOURQUE 1992, NOSE 1995) and a strong increase in growth rate (up to 10 mm/yr). The growth rates of Upper Jurassic scleractinians from the investigated European localities (see above) range between 1 mm/yr and a maximum of 10 mm/yr.

The abilities and ecological demands of Upper Jurassic scleractinian corals are strongly related to the question

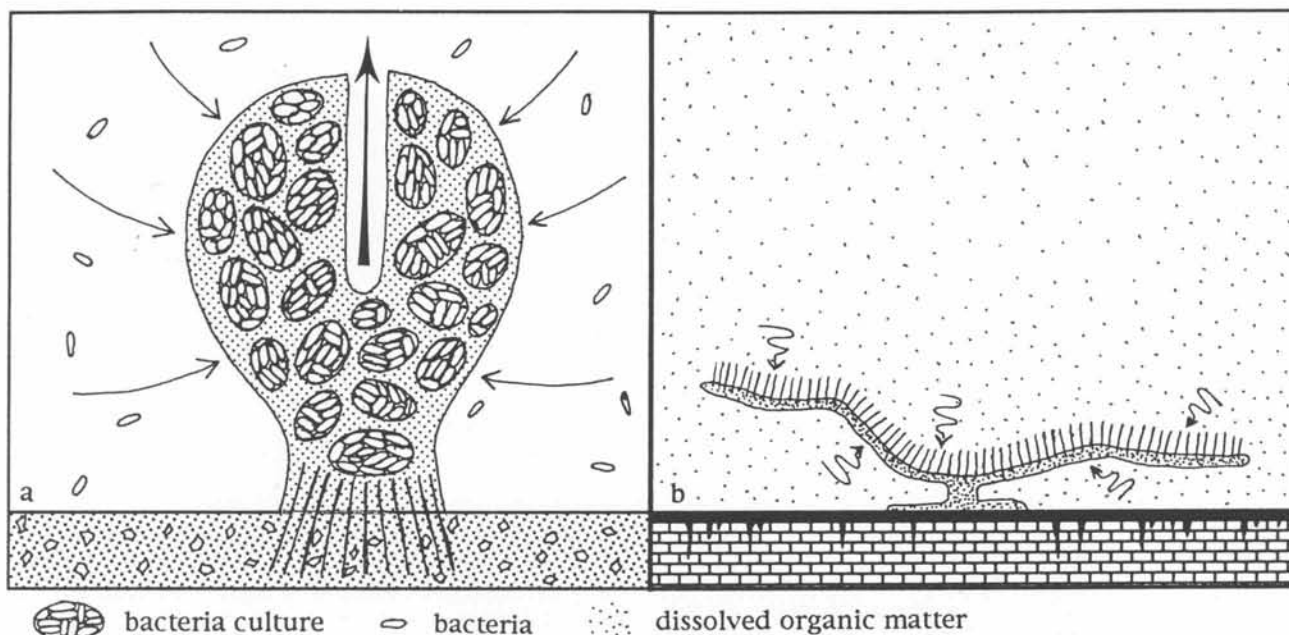


Fig. 3: a) Active filter feeding demosponge harboring bacteria cultures. b) Osmotrophic hexactinosean sponge. Dish shape favors collecting organic particles which may be harvested on the surface of the sponge.

whether they possessed phototrophic symbionts or not. It seems likely that this symbiotic relationship was initially developed in late Upper Triassic time, where the first large reef framework complexes, built by scleractinian corals, occurred (STANLEY 1981, 1988). Some Upper Jurassic shallow-water scleractinian species may be azooxanthellate (e.g. *Thamnasteria concinna*, STANLEY & SWART 1995). However, the symbiosis with zooxanthellae seems likely in many other highly integrated Upper Jurassic species, judged by the dominance of flattened and foliose morphotypes in deeper water (cf. BERTLING 1993a, b, LEINFELDER 1993a, NOSE 1995) or turbid settings. Additionally, flattening might be an adaptation to impoverished availability of particulate organic matter. In this case, a flattened morphology facilitates to effectively collect the available organic particles (SCHLICHTER, pers. comm.).

The relatively low growth rates, compared with modern scleractinians (with average growth rates of 10-15 mm/yr, up to 250 mm/yr) probably point to a lower efficiency of the symbiotic relationship in Upper Jurassic scleractinians. Further evidence for this hypothesis derives from the frequent occurrence of corals in shallow siliciclastic settings. Probably, scleractinians from the Late Jurassic were more dependent on particulate organic matter, for influx of fine siliciclastics is generally coupled with an increase in nutrients. Shallow siliciclastic settings were frequently colonized by genera of the family Microsolenidae (*Comoseris*, *Microsolenia*), corals exhibiting pennulae which probably supported a highly specialized gastro-vascular system like in the modern deeper water agariciid *Leptoseris fragilis*. This led to the improvement of suspension feeding and hence heterotrophic energy supply in settings where the high photosymbiotic activity of shallow-water corals was reduced due to great water depth (SCHLICHTER 1992, GILL & SANTANTONIO 1995). The existence of such features in Upper Jurassic shallow-water corals indicates that the efficiency of photosymbiosis was still lower than in modern shallow-water representatives, and that a considerable proportion of energy had to be gained by heterotrophic nutrition.

Additionally, in Upper Jurassic reef building scleractinians the ratio of low to high density growth bands is much lower than in modern zooxanthellate scleractinians under compa-

rable environmental parameters (e.g. low turbidity, warm and shallow water). Low density bands are considered to represent higher linear growth rates forming during episodes of high light availability (cf. WELLINGTON & GLYNN 1983, ALLISON et al. 1996). Hence, scleractinians from the Upper Jurassic apparently could not use light as efficiently as modern scleractinians for supporting skeletal growth.

## 2.2 Sponges from the Late Jurassic

Sponges are widespread in many Upper Jurassic reefs but are difficult to use for paleoenvironmental reconstructions because little is known about the biology of modern representatives, let alone their Jurassic counterparts. Siliceous sponges belong to various taxonomic groups within the demosponges (polyphyletic "lithistids") or to the hexactinellids. As the two major groups differ remarkably in their physiology, their biological organization and their ecological demands, they must be carefully distinguished for paleoenvironmental interpretation. "Calcareous" and "coralline" sponges belong to either demosponges or the Calcarea. Stromatoporoidea and chaetetids are now also considered to belong to the demosponges.

The "lithistid" demosponges are active filter feeding organisms. They feed on nutrition dominated by nanoplankton, mainly bacteria. Their retention rate is very high, normally attaining 90-100% (REISWIG 1990). Demosponges have a well developed mesohyl in which they can store large quantities of bacteria. These sponges can also consume the metabolic products of bacterial activity, gaining a certain independence of external supply by storing the microbes within their body (Fig. 3a). The bathymetric distribution of demosponges corresponds to a great extent with the bathymetric distribution of bacteria. The reason why demosponges mostly occur from the very shallow to moderately shallow water is that bacteria in the water column diminish towards greater depth (RHEINHEIMER 1980). The fairly high preservation potential of rigid demosponges is readily explained by a high amount of mesohyl-dwelling bacteria, causing rapid calcification after death.

Demosponges are able to close their inhalant pores (ostia) under episodes of slightly increased sedimentation, preventing clogging of the filter pathways. Some of them



can even reverse the water flow by sudden contraction and eject material which is already drawn into the inhalant pores (STORR 1976). This enables the animal to tolerate a certain amount of sedimentation, particularly if tube-like growth shapes are realized.

Retention rates of only 20-30 % show that most hexactinellid sponges are ineffective filter feeders. However, the tissue organization of hexactinellids allows them to absorb dissolved organic matter, making osmotrophy their predominant feeding strategy (REISWIG 1990) (Fig. 3b). Whereas this kind of food is depleted in the shallow water due to the consumption by living unicellular organisms in the photic zone (LEVINTON 1982), it is enriched in deeper-water low-energy settings, causing the majority of the hexactinellids to dwell in such habitats. As the mesohyl of hexactinellids is very thin, there is hardly any room to harbor bacteria (MACKIE & SINGLA 1983). This easily explains why microbially induced post-mortem calcification of the sponge animal by microbial automicrites occurs at a much lower rate so that fossilization potential is much lower in comparison with rigid demosponges.

Strongly reduced to absent sedimentation is a prerequisite for the settlement of hexactinellid sponges. Unlike demosponges, they are not able to close their ostia and sediment particles would easily clog the circulation pathways of the sponge. This sensitivity towards sedimentation makes fossil hexactinellids good bioindicators for sediment starvation: dish- and bowl-shaped hexactinellids demand close-to-zero sedimentation whereas narrow cup and tube morphologies intensify the exhalant water stream, which, to some degree, can shelter the animal from slow sedimentation (KRAUTTER 1995). Extremely low influx of sediment may cause severe nutrition problems for most other benthic organisms but the osmotic feeding strategy of hexactinellids together with the development of dish morphologies allowed the occupation of such hostile environments in the Late Jurassic by hexactinellid biostromes. Dish morphologies enabled the collection of available organic particles, which then were broken down by microbial activity into a form appropriate for the animal's nutrition (see 3.2.2).

Environments characterized by low water energy, dissolved organic matter and very reduced sedimentation are found mostly on the deeper shelf and in bathyal, abyssal and even hadal depth. These are the regions where modern hexactinellids are most frequent (TABACHNICK 1991, 1994). Independent bathymetric calibration by other methods shows that reefal communities of Upper Jurassic hexactinellids occur in lower mid-ramp to outer ramp settings. Depth distribution is additionally dependent on the amount of available nutrients at a given depth. The apparent restriction of extant hexactinellids to water temperatures colder than 15°C (LEYS, Victoria, pers. comm.) might be a result of evolutionary adaptation. However, isotope measurements show that during the Late Jurassic deeper shelf waters were noticeably cooler than the shallow water.

Most Upper Jurassic species of "coralline" demosponges and *Calcarea* are closely associated with coral reefs and therefore many might have had more or less effective cyanobacterial symbionts as have many modern counterparts. However, some species did occur in deeper settings (LEINFELDER et al. 1993a, b, WERNER et al. 1994). Bandings, if annual, show that growth rates of coralline demosponges were slower than those of corals. Like corals, they occur in both, purely carbonate and terrigenously influenced settings. They might also have demanded stable oligotrophic to mesotrophic conditions. Branching species as *Cladocoropsis mirabilis* might form entire bafflestone biostromes but only a few encrusting species are true contributors to reef frameworks, which appears to be related to their slow growth rate.

Concluding, the observed bathymetric zonation of a shallow coral-coralline sponge zone, followed towards deeper water by a mixed coral-"lithistid", "lithistid"-hexactinellid and hexactinellid-dominated zone in Upper Jurassic reef settings is largely a reflection of different nutrition strategies. Unlike modern coral reefs, Upper Jurassic coral and coral-coralline sponge communities were not restricted to oligotrophic settings but were in demand of stable nutrient conditions. Siliceous sponges, on the other hand, could better handle unstable and more fluctuating nutrient conditions reaching from predominantly oligotrophic to intermittently eutrophic situations. Both eutrophic and oligotrophic pulses could episodically cause predominance of siliceous sponges in areas otherwise occupied by reef corals.

## 2.3 Selected other Reef Organisms from the Late Jurassic

### Micro-Encrusters

In nearly every Upper Jurassic reef micro-encrusting, often problematic, organisms are present in great abundance. Many of these micro-encrusters have proven to represent very valuable paleoecological marker fossils (LEINFELDER et al. 1993b, SCHMID 1996). These include cyanobacteria (*Girvanella*, *Cayeuxia*), polychaetes (serpulids and the agglutinating *Terebella*), foraminifera (e.g. *Vinelloidea*), bryozoans, thecideid brachiopods as well as the problematica *Bacinella*, *Koskinobullina*, *Lithocodium*, and "*Tubiphytes*" *morroneis*. The last two organisms were studied in detail.

*Lithocodium aggregatum*, which has been regarded as an alga so far, could be shown by SCHMID & LEINFELDER (1995, 1996) to represent a Loftusiid foraminifera, most probably possessing endosymbiotic algae. Diagnostic features are the typical alveolar, micritic wall structure, the ability to agglutinate particles, and planispirally arranged chambers. Frequently occurring within the chambers of *Lithocodium* is another foraminifera, *Troglotella incrustans*. Most probably, this foraminiferal consortium represented a commensal relationship (op. cit.). It is clearly restricted to shallow-water settings with moderate water-energy.

"*Tubiphytes*" *morroneis*, having been very abundant in Late Jurassic times, has been regarded as a community consisting of a foraminifera and an overgrowth of some kind of algae or cyanobacteria (FLÜGEL 1981). It is interpreted by SCHMID (1995, 1996) as a miliolid foraminifera with a twofold test, the more or less thick outer test wall being formed with the help of endosymbiotic algae. Although occurring in a wide variety of different facies, "*Tubiphytes*" *morroneis* represents a valuable marker fossil for environmental conditions. This is due to the ability of this foraminifera to adapt to different conditions by developing different growth forms. For example, branching colonies are an adaptation to soft substrates (op. cit.). A specialty are trochospiral colonies, growing around the pores of different sponges (SCHMID 1996), clearly indicating syn-vivo encrustation (Fig. 4). Another important feature is the thickness of the outer test, apparently depending on the amount of light available for the algal symbionts. Shallow-water tests may show diameters of more than 1 mm, whereas the diameters of the outer test of deeper water forms strongly tends towards zero. Thus, bathymetric trends may be measured indirectly, provided that cryptic habitats such as reef caves, where test thickness is also strongly reduced, are not considered (Fig. 5).

By comparing communities from shallowing-upward successions of Portugal with those from Spain and southern Germany, the following standard micro-encruster communities were obtained:

*Girvanella*-community, indicating very shallow settings with fluctuating salinity; *Bacinella*-*Lithocodium* community

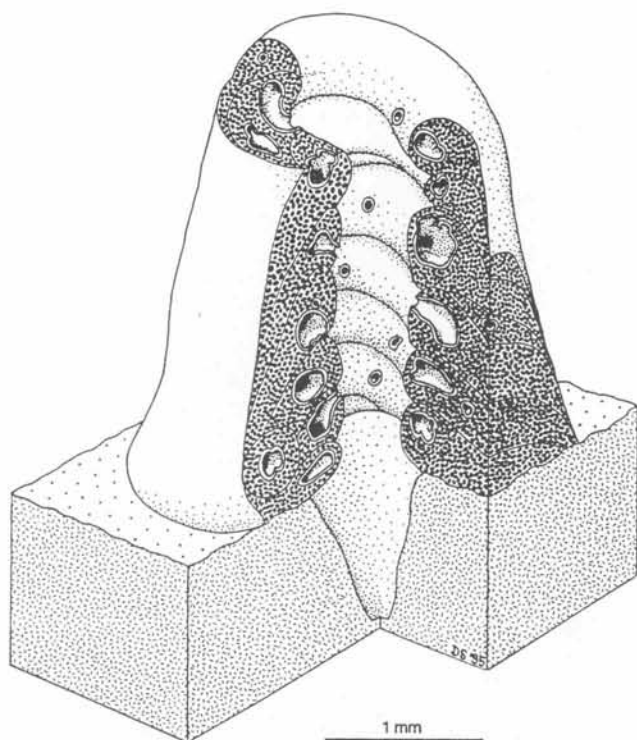


Fig. 4: Reconstruction of a "Tubiphytes" morronensis colony exhibiting a chimney-like growth form, encircling a sponge ostium and thus indicating syn-vivo-encrustation.

(slightly restricted, lagoonal to back-reef settings); high-diversity micro-encruster community (shallow water, "optimum" conditions); "Tubiphytes"-Koskinobullina community (occurring in middle ramp and moderately cryptic environments); and the Terebella-"Tubiphytes" community in deeper water and/or dysaerobic environments.

#### Bivalves

Many of the bivalves frequent in Upper Jurassic reef settings also occur in non-reefal settings (cf. FÜRSICH & WERNER 1986) and allow additional calibration of reef environments independent of the reef building organisms. Burrowing bivalves occur occasionally in sponge-microbolite mounds and, together with other burrowings, give evidence for the partial existence of soft mud within these structures. At least some of the boring bivalves, attacking microbolite reefs from the underside, show a mushroom-like shape freely above the sea-floor (LEINFELDER et al. 1993b). Encrusting bivalves show a substitution of several taxa along a bathymetric gradient (WERNER et al. 1994). The dysaerobic, flat clam *Aulacomya abadiensis*, a common element of Upper Jurassic bituminous deposits, may also occur in microbolite reefs, indicating pulses of oxygen depletion (see 4.2.4). A strong dominance of the oysters *Praeexogyra pustulosa*, *Nanogyra nana* and the bivalve *Isognomon lusitanicum* in *Amphiastrea* coral reefs gives further clues for the brackish character of these reefs (see below). The latter bivalves may also form oyster reefs and *Isognomon* clusters without the participation of corals (FÜRSICH 1981, LEINFELDER 1986, WERNER 1986).

#### Echinoderms

Crinoids are a frequent element of most Upper Jurassic reefs and occasionally even form crinoidal-microbolite reef patches (WERNER et al. 1994). In Lorraine, sand bars solely composed of crinoid ossicles separate episodes of reef growth which might be related to drowning events. Regular echinoids are frequent reef dwellers. Morphological analysis

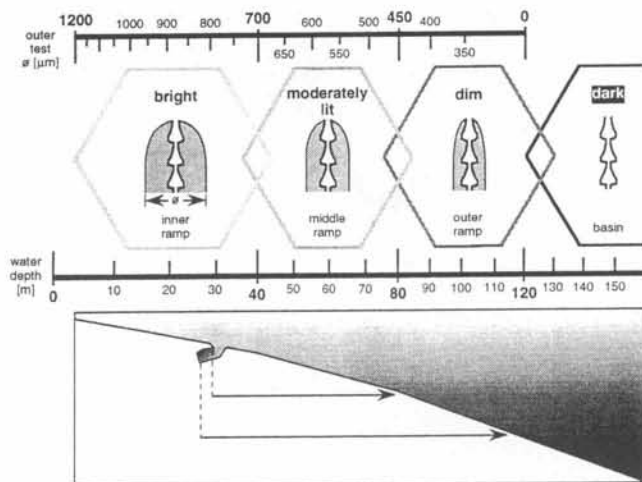


Fig. 5: The diameter of the outer test of "Tubiphytes" morronensis depends mainly on the light.

based on general shape and thickness of tests and characteristics of mamillae and ambulacral pores shows that several species show perfect adaptations to high water energy, soft bottoms, cavity dwelling or impoverished oxygenation (LEINFELDER 1986, BAUMEISTER & LEINFELDER in press).

#### 2.4 Origin, Types and Role of Reefal Microbolites from the Late Jurassic

Microbolites are organosedimentary deposits which have formed due to the activity of microbes. The term "microbolite", which is used here, has been introduced by RIDING (1991) as a substitute for the incorrect term "microbialite" (BURNE & MOORE 1987).

Microbolites are produced by a microbial community situated within a biofilm, generated by the activity of the microbes. In general, the microbes are mainly cyanobacteria and other bacteria (including heterotrophic bacteria), but other organisms such as algae or fungi may also contribute to the biofilm. Under certain conditions, the microbes may induce carbonate precipitation (CHAFETZ & BUCZYNSKI 1992). Apparently, these conditions were frequently realized in the Late Jurassic, resulting in widespread microbolite depositions, which possibly hints to a slightly elevated seawater alkalinity, supporting carbonate precipitation (cf. KEMPE & KAZMIERCZAK 1994). As the occurrence of Jurassic microbolite reefs far below the photic zone shows (DROMART et al. 1994), microbolite formation is not necessarily light dependent and can apparently take place without cyanobacteria. Considering the only partial organic character of this microbially induced carbonate precipitation, it is not surprising that stable isotopes yield carbon and oxygen isotope values close to seawater equilibrium (LEINFELDER et al. 1993b, SCHMID 1996).

SCHMID (1996) proposed a refined classification and nomenclature of microbolites, based on a combination of both microstructure (e.g. peloidal crusts) and macrostructure (e.g. thrombolites) (Fig. 6). In macroscopical scale, three types of microbolites can be distinguished: Thrombolites, stromatolites and leiolites (BRAGA et al. 1995), the latter being characterized by a dense structure. In earlier literature, some confusion was produced by mixing up structures of different dimensions and using them both for classification, often also involving growth forms such as oncoids (e.g. BURNE & MOORE 1987).

In mesoscopic scale, various growth forms do occur, ranging from massive, columnar microbolites to dendroid or reticulate forms as well as spheroidal forms (=oncoids). The

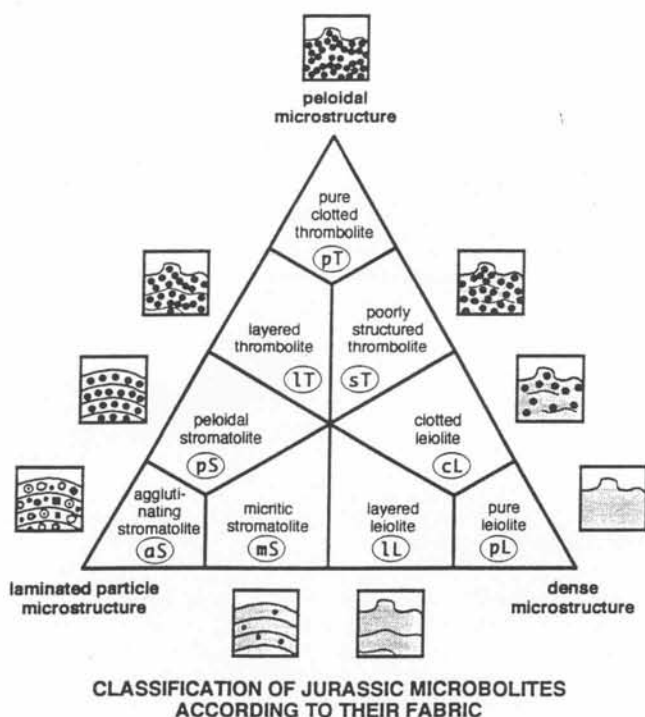


Fig. 6: Classification of Jurassic microbolites according to their fabric (see text for details).

growth forms depend mainly on sedimentation rate and water energy; for example, microbolites developed dendroid forms as a reaction to slightly elevated sedimentation at low-energy conditions (SCHMID 1996).

Thus, characterizing a microbolite-rich reef by considering microstructure, macrostructure, morphology and growth form(s), some conclusions concerning the environmental conditions can be drawn, whereas the occurrence of microbolites alone is not very helpful in reconstructing environments.

As discussed in Chapter 3.3, microbolites play a paramount role in reef building. Whereas in the past microbolites were mostly considered as secondary, merely binding organisms within the reef guild (FAGERSTROM 1987), they are acknowledged by now also as genuine constructors which, especially in Late Jurassic reefs, frequently are responsible for large parts if not the entire primary reef framework.

### 3 Reef Types, Reef Communities, and their Controlling Factors

#### 3.1 Coral Reefs from the Late Jurassic

Iberian reefal coral facies can be subdivided into 16 reef types which are grouped within 4 categories according to similarities in faunal composition, structure, participation of microbolite crusts and the content of carbonates and siliciclastics. The reef types are characterized by at least 15 coral communities (NOSE 1995). Some of these and additional coral communities are recognized on the Oxfordian Lorraine carbonate platform and in SW-Germany (e.g. Istein, Arnegg). The faunal composition and structure of the communities, the morphotypes of the principal faunal elements, and the preservation of the reef fabric reflect the physical parameters of the former reef environments. Medium to high-diversities are not restricted to a theoretical standard optimum but occur in several coral reef communities from different environments. This shows that coral faunas from the Late Jurassic could perfectly adapt to fairly

variable conditions in a wide environmental window (Figs. 7, 8).

#### High-Diversity Coral Reefs

The fundamental pre-requisites for high-diversity coral reefs from the Late Jurassic are low sedimentation rate, normal salinity, warm waters and illumination. However, within this frame high diversity coral reefs may occur in different environments according to the individual preferences and abilities of the reef organisms.

One of the most important Iberian reef types are debris-rich reefs dominated by corals, stromatoporoids and chaetetids. Medium to high diversity communities formed low relief biostromes or elevated reef bodies with cumulative thicknesses up to 150 m mostly in moderate to high-energy shallow-water environments. The high diversity fauna is dominated by corals (*Thamnasteria*, *Fungiastrea*, *Microsolena*, *Actinastrea*, *Amphiastrea*) but stromatoporoids and chaetetids occur as well (stromatoporoids: *Burgundia*, *Dehomella*, *Actinostromaria*; chaetetids: *Chaetetes*, *Ptychochaetetes*) (Algarve Basin, central Lusitanian Basin; NOSE 1995). Similar reefs grew also in the Oxfordian Swiss Jura chains on a huge carbonate platform system (St. Ursanne formation).

Similar to modern high-energy coral reefs, massive to hemisphaeroidal growth forms prevail. This widespread Upper Jurassic reef type is characterized by an imbalanced sediment budget (i.e. skeletal debris production exceeds biogenic growth plus export of skeletal debris). The lack of effectively binding organisms such as algae or microbes prevented the formation or preservation of stable frameworks. These reefs mostly exhibit an indistinct morphology having the aspect of debris piles. They are mostly situated on ramps, but may also occur at the margins of intrabasinal structural uplifts, contributing to the formation of rimmed isolated platforms. In the latter case, physical debris is effectively exported via the steep fore reef slope. Hence, such reefs exhibit a equilibrated sediment balance which gives way to an intense development of binding microbolite crusts, resulting in platform-rimming coral-microbolite-debris reefs (Ota reef, LEINFELDER 1992, 1994b).

Other reef types characterized by high-diversity communities are reefs with sporadic short-term input of fine siliciclastics (marly coral-microbolite-reefs, NOSE 1994, 1995). High diversity in this case is in accordance with the assumption that Upper Jurassic scleractinian reef corals favor higher nutrient levels than their modern counterparts since the ratio of heterotrophic versus autotrophic nutrition is still higher than in modern reef corals (see 2.1).

Provided illumination is available, differences in water depth did not have a strong impact on the diversity of coral reefs in the Late Jurassic. This is probably due to the higher ratio of heterotrophic vs. autotrophic energy uptake of Jurassic scleractinians. On the other hand, the composition does change along a bathymetric gradient and different coral communities substitute each other. This can be deduced from shallowing upward profiles in the Lusitanian Basin where high diversity coral communities (*Microsolena-Trocharea*-community) occur even in deeper water settings (transition from mid to outer ramp, possibly about 40 m of water depth, Figs. 8, 9). These reefs represent coral microbolites containing occasional siliceous sponges, developed as low relief biostromes or small patch reefs. In shallow mid-ramp settings, coral microbolites are characterized by a high-diversity coral-coraline sponge community developed as larger patch reefs with a pronounced relief (Pl. 1/1).

#### Stressed Coral Reefs

Upper Jurassic coral reefs also occurred in environments with, at first glance, rather unfavorable conditions for coral growth. These coral communities and reefs are generally



characterized by their reduced diversity and by the occurrence of especially adapted corals which is partly reflected by specialized coral morphologies.

#### Salinity

Corals of the Upper Jurassic, just as those of the modern world, only rarely lived in environments with reduced or fluctuating salinities. However, the distribution of the *Amphistrea piriformis* patch reefs in Upper Oxfordian to Lower Tithonian brackish lagoons and bays of the Lusitanian Basin shows that this community was adapted to generally lowered salinity. The formation of small flat to knobby patches up to 1 m in height by this eurytopic ceroid coral was probably due to its ability to cope to some degree also with fluctuations of other occasionally occurring adverse factors in these environments such as sediment influx, water turbidity and higher energy. Apart from the bivalve dominated fauna (oysters, *Isognomon* shell banks) the low diversity and sedimentologic as well as isotopic data of bivalve shells suggest fluctuations within the brachyhaline to mesohaline range (YIN et al. 1995).

#### Sedimentation

Sedimentation was the paramount factor on determining faunal composition and structure of Iberian coral communities. It obviously had a stronger impact on diversity than bathymetry and related factors. This is clearly demonstrated by the fact that sediment-stressed coral communities in shallow water show stronger reduction in diversity than many coral communities from slightly deeper ramp envi-

ronments, provided the latter are not smothered by sediment influx (Fig. 8). The pronounced vertical growth of the phaceloid coral *Calamophylloids* represented a good adaptation towards elevated sedimentation rates. Hence, the coral frequently dominated communities in lagoons, prodelta and mid-ramp positions (LEINFELDER 1986, WERNER 1986, NOSE 1995). Similar growth strategies were developed in some dendroid and ramose genera (e.g. *Ovalastrea*, *Convexastrea*, *Enallhelia*) which dominate low to moderate diversity communities of protected mid and distal ramp environments (NOSE 1995). Another adaptational trend is realized by some highly morphovaryable taxa (*Microsolena agariciformis*, *Thamnasteria lobata*) which developed "pseudoramose" colonies with non-enveloping growth bands and elevated growth rates (see also 2.1). Episodic sedimentation stress could be tolerated even by platy to leaf-shaped corals provided the undulous "leaves" were oriented oblique to the substrate, so that sediment could be easier removed by gravitational support (Liesberg beds, Swiss Jura chains; TAKACS in prep.)

Sediment-stressed reefs always grew as low relief meadows due to the almost lack of binding microbolites. The latter only occurred under low sedimentation but then were capable of forming rigid reefal frameworks considerably elevated above sea floor (cf. LEINFELDER et al. 1993b).

Beside stress by fine siliciclastics, strong input of carbonate mud may also have a negative impact on diversity and may also shape coral morphology. Consequently, low diversity coral-coraline sponge-mud reefs occur in the central

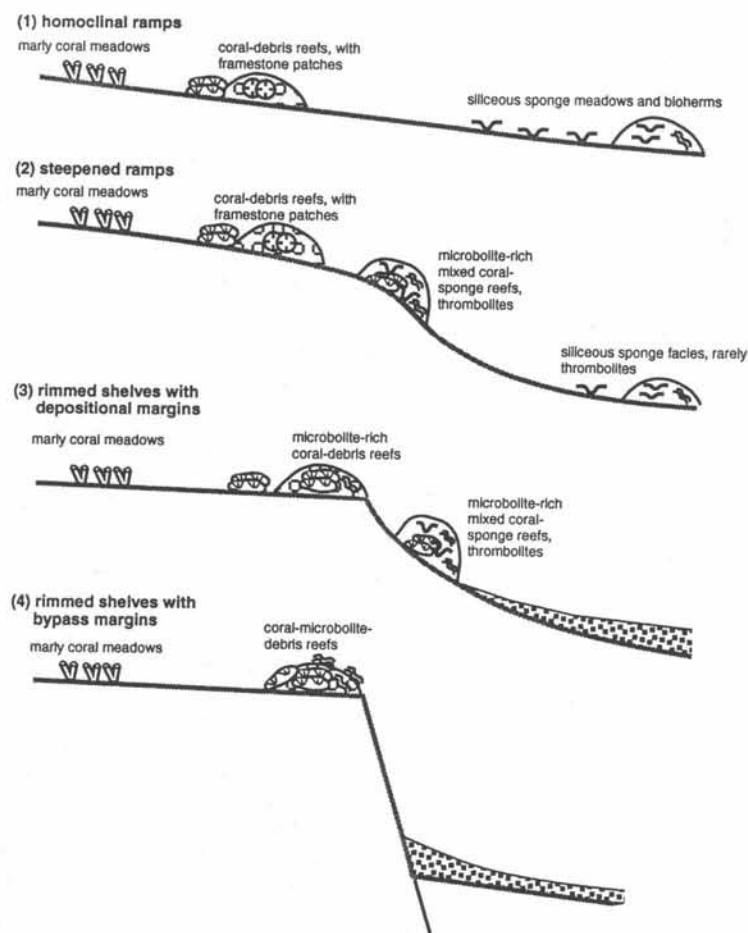


Fig. 7: Upper Jurassic reef types related to different shelf configurations. Pure siliceous sponge facies is restricted to subhorizontal mid to outer ramps (1). Mixed coral-siliceous sponge reefs may be diagnostic for the existence of steepened slopes (2, 3). Coral-debris sand piles, representing remains of high-energy reefs, are indicative of shallow ramp and shelf depositional margin situations (1-3), whereas microbolite-rich coral-debris reefs grew atop bypass margin situations (4). Rimmed shelves with steepened slopes were particularly characteristic of the southern Tethys and North Atlantic realm, whereas ramp configurations prevailed on the northern Tethys margin (from LEINFELDER 1994b).

Lusitanian Basin within protected inner ramp settings (*Microsolena-Convexastrea*-community). Branching growth forms predominate the reef building fauna (LEINFELDER et al. 1994, 1995).

#### Water Depth

Coral communities changed along a bathymetric gradient, giving evidence of differentiated light demands of many Upper Jurassic corals just as in modern ones. However, for most part of the photic zone, this had no major influence on diversities which can be explained by their higher uptake of heterotrophic energy relative to modern reef corals (see 2.1). Only towards the lower boundary of the euphotic zone, many coral taxa disappear, and plates of microsolenid coral colonies up to 1 m in diameter may dominate the community, being accompanied by "lithistid" demosponges (LEINFELDER et al. 1993a). Similar to modern *Leptoseris fragilis*, horizontal platy shape not only helped catching the available light but also digestible particles in order to support nutrition. Due to the supposed higher demand of heterotrophic food of Jurassic microsolenids, this community lived shallower than modern *Leptoseris* communities.

Depth-related stress was enhanced when waters were turbid. Microsolenid-rich communities in terrigenous settings include bioindicators of fairly shallow water such as *Lithocodium* and adaptations of regular sea-urchins to a moderately, or occasionally elevated water energy (BAUMEISTER & LEINFELDER in press). However, stress due to diminishing illumination was accompanied by sedimentation stress. This was solved by the development of flattened, but inclined and undulous "leaf" morphology as a compromise solution between enlarging and flattening surfaces in order to increase light uptake, and inclining them in order to facilitate sediment removal, making these communities real sediment bafflers quite similar to some modern *Agaricia agaricites* communities with strikingly similar growth

shapes. The Upper Jurassic counterparts are medium-diversity biostromal reefs dominated by microsolenids, *Thamnasteria* and *Isastrea*. (e.g. Thamnastreen-marls and Liesberg-beds, French and Swiss Jura) (Pl. 1/2).

#### Water Energy

Although high-energy debris reefs often consist of moderate to high diversity communities, reefs exposed to extreme wave action in inner ramp settings may also show low-diversity communities. The fauna in such wave-stressed environments is mainly composed of massive cerioid and meandroid corals like *Actinastrea*, *Amphiastrea* and *Psammogyra* (e.g. *Actinastrea*-*Lithophaga*-community, NOSE 1994, 1995). Boring bivalves occur abundantly, which further increased an already high rate of debris production. In sheltered gaps between the massive coral heads, delicate branching forms like *Goniocora* and *Enallhelia* could grow. Apart from their limited faunal composition, these wave-stressed reefs largely resemble the coral-coraline sponge-debris-reefs (see 3.1.1).

### 3.2 Siliceous Sponge Reef Facies from the Late Jurassic

#### Siliceous Sponge Microbolite Mud Mounds

Siliceous sponge microbolite mud mound facies developed extensively on the northern shelf seas of the Tethys, particularly in Romania, Poland, Southern Germany and the French Jura Range (LEINFELDER & KEUPP 1995).

The mud mounds range from a few decimeters to more than 70 m in size. Their shape varies from flat lenticular to upward extended to very irregular buildups (Pl. 1/3). Large sponge mounds are sometimes formed by clustering of much smaller buildups (LEINFELDER 1993a).

In general, the siliceous sponge mud mounds consist of frequent to rare calcified siliceous sponges, a light gray,

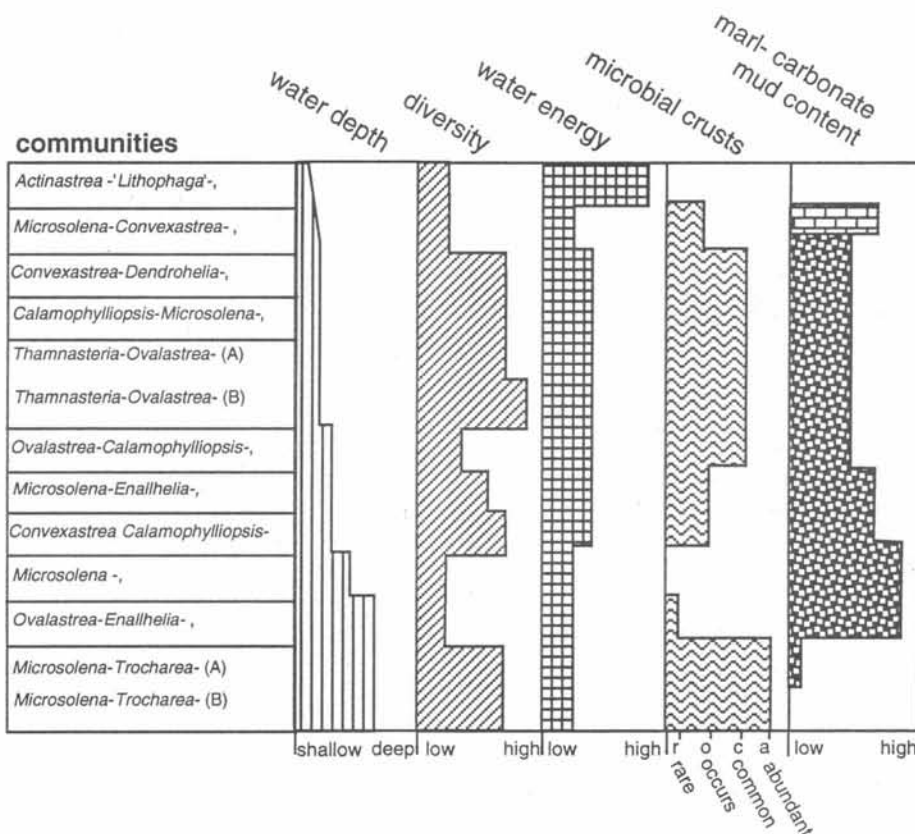


Fig. 8: Coral communities of the central Lusitanian Basin with some significant sedimentary features and their relation to bathymetry and water energy. Note that diversity shows no correlation with bathymetry but is apparently dependent on sedimentation rate. Sediment input can be deduced from the marl or carbonate mud content in combination with the intensity of encrustation (modified after NOSE 1995).



often peloidal micritic matrix and variable proportions of darker, thrombolitic to leiolitic to rarely stromatolitic microbolites. Major areas are dominated by microbolite boundstones which are characterized by a dominance of crustose and non-crustose microbolites with irregular patches, lenses or even layers of lighter, partly mottled mud interpreted as allomicrites (Fig. 10e). Both pure microbolite boundstone buildups containing siliceous sponges (Fig. 10a) and mounds consisting of a rhythmical alternation of peloidal packstones, sponge-microbolite boundstones and peloidal wackestones (Fig. 10b) exist. Very frequently, mud mounds exhibit an indistinct spatial zonation of different micrite-dominated microfacies types (Fig. 10c). Siliceous sponge-bearing microbolite boundstone is the most dominant facies. Allomicritic siliceous sponge floatstones can interdigitate with microbolite boundstones but more frequently overlie the latter and form the top of mounds (Fig. 10d). Peloids and minute coated grains are particularly frequent in the microbolites but also occur in the light micrite areas. They are partially cemented by sparites, resulting in a packstone to grainstone fabric, often occurring as patches. In-place relics of sponge skeletons within such patches, the dominance of peloidal fabric in microbolitic sponge mummies,

the occasional occurrence of sponge spicules serving as nucleus for ooid-type coated grains, and the minute size and frequent irregular shape of these particles evidences that they represent the products of microbial activity. However, some of the younger sponge-dominated buildups of southwestern Germany may contain abundant particles, including true ooids, oncoids, cortoids and rounded peloids, occurring as layers within predominantly micritic mounds or even dominating parts of some buildups (cf. SCHALLER & KOCH 1996). Occasionally, these mounds grade upwards into coral and particle-rich buildups which in southern Germany developed in selected localities at the end of the Kimmeridgian, whenever the underlying sponge mounds have developed a pronounced relief and a probable, short-term sealevel drop accounted for further shallowing.

Frequencies of siliceous sponges within a sponge microbolite mud mound range from very rare to abundant. Sponges comprise both Hexactinellida (Hexactinosa, Lychniscosa and Lyssakinosa) and the polyphyletic "lithistid" demosponges. The accompanying fauna is of fairly high diversity, consisting of different taxa of echinoderms, gastropods, bivalves, brachiopods, ammonites and belemnites. Encrusting organisms include polychaetes

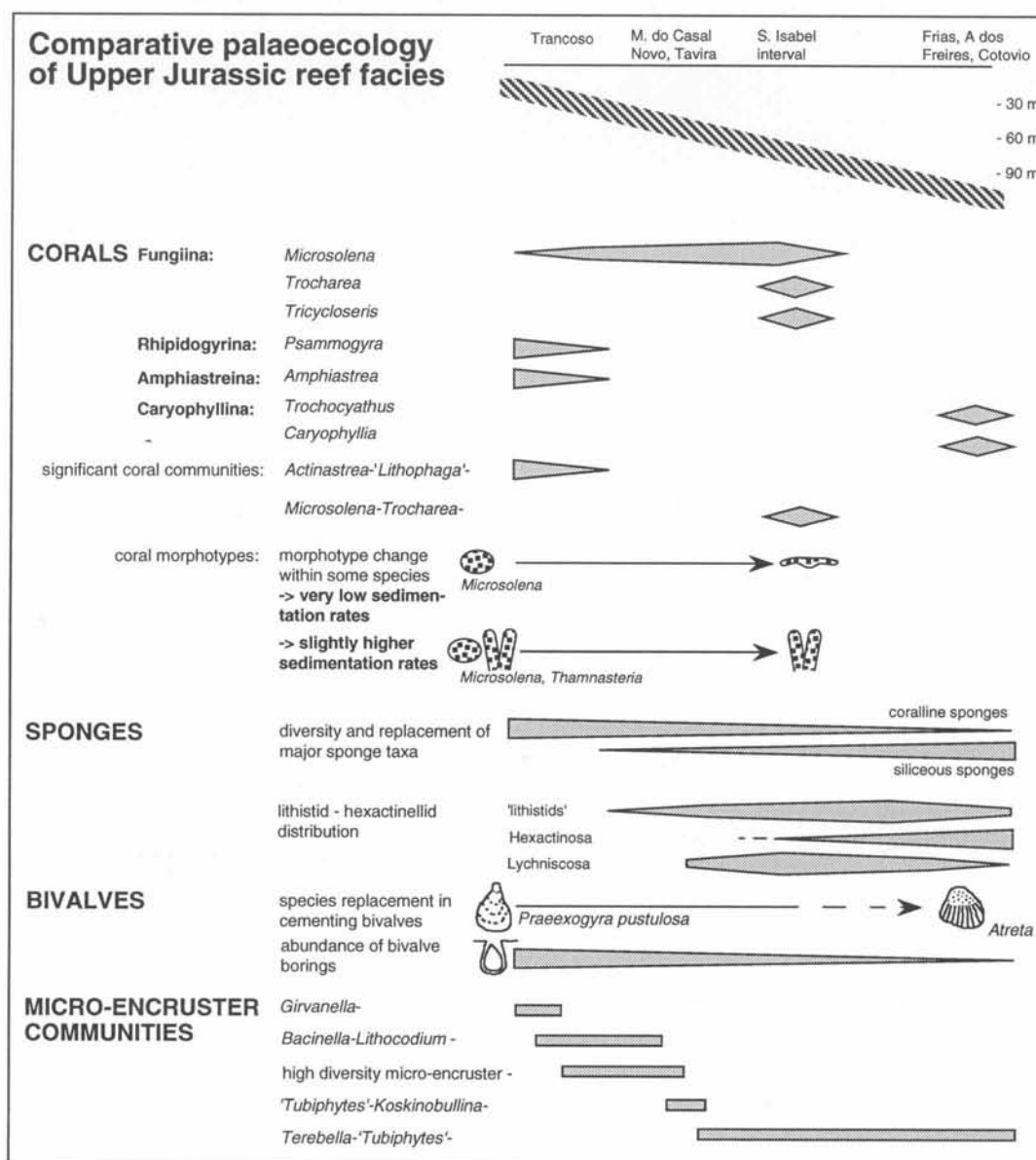


Fig. 9: Bathymetric distribution and comparative paleoecology of Upper Jurassic reef organisms from Iberia; modified and expanded from LEINFELDER et al. (1993a, 1993b) and WERNER et al. (1994).

(serpulids and *Terebella*), bryozoans and foraminifera including "*Tubiphytes*". Among the encrusting fauna, bryozoans are entirely restricted to the surfaces of siliceous sponges whereas polychaetes (serpulids and *Terebella*) and particularly the encrusting foraminifera "*Tubiphytes*" are

also frequent on surfaces of microbolites evidencing the primary hard consistence of the latter. On the other hand, bivalves found in the dense, lighter micrites include some burrowing species, which together with the ichnofossil *Chondrites* and other indistinct burrowing traces is evidence

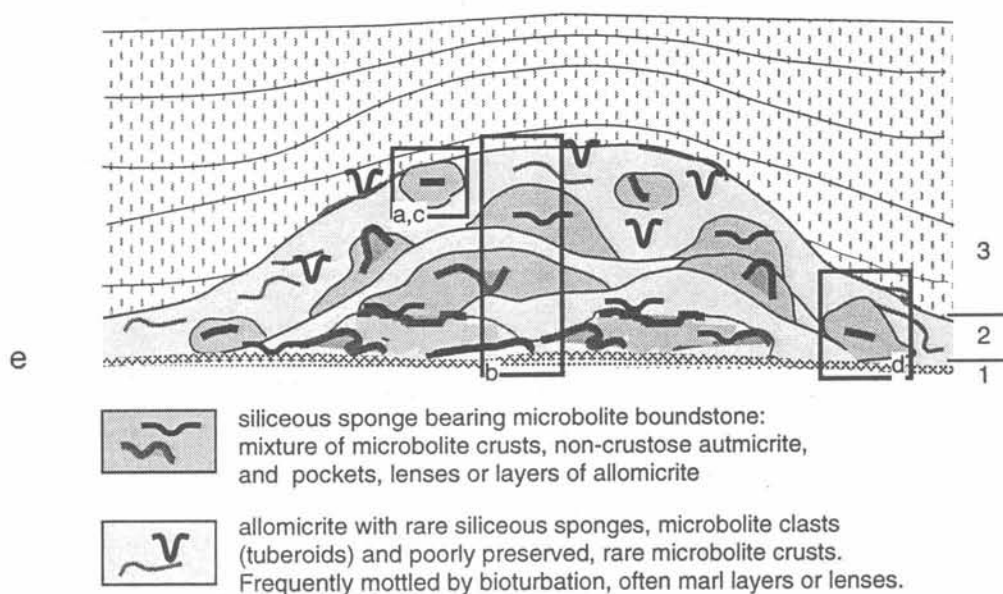
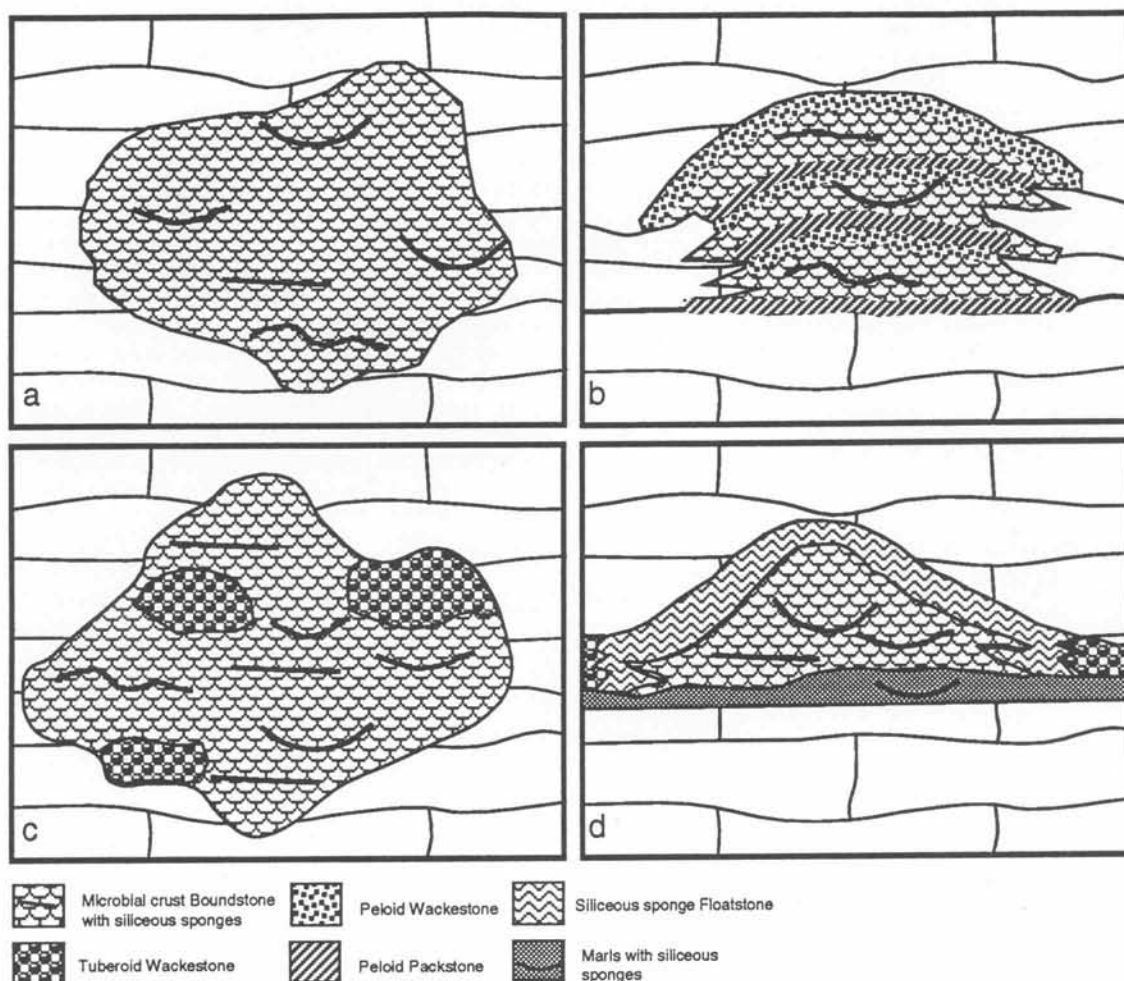


Fig. 10: Sponge microbolite mud mound types, based on examples from Southwestern Germany. a-d) Small, microbolite-dominated mound structures. e) Growth history of a composite larger mound (compiled from various examples): 1) Mound initiation on a flooding surface. 2) Formation of mound by various episodes of dominance of automicritic microbolite precipitation and dominance of allomicrite accumulation. 3) Cessation of reef growth due to an increase in sedimentation of allomicrites. Further explanation see text.

of the soft original consistency of parts of the mounds. Most of the fauna of the mounds (hexactinosean sponges, encrusters, epibenthic macroorganisms) indicates that sedimentation rates often must have been very low, but arborescent growth forms of some microbolites and the partial lack of siliceous sponge fauna and distinct microbolites shows that they were variable, though never high. The combination of these features demands a combined model for mud mound growth where episodes of microbolitic automicrite precipitation alternated with episodes of trapping allochthonous carbonate mud probably being exported from shallow, more productive coral-dominated carbonate platforms (LEINFELDER & KEUPP 1995, see 4.1).

In southern Germany, "lithistid" sponges outnumbered the hexactinellids towards the end of Kimmeridgian reflecting the general shallowing-upwards trend which, due to the strong submarine relief developed by the sponge mounds by this time (cf. GWINNER 1976), shows a very differentiated spatial pattern: Coral facies developing on top of former mound apices was coeval with siliceous sponge facies continuing on earlier mounds with a less pronounced relief.

### Siliceous Sponge Biostromes

In most regions, siliceous sponge biostromes occur subordinate to sponge microbolite mud mounds with the exception of northern Switzerland and particularly eastern Spain.

In the Oxfordian of the Iberian and Prebetic Basins (eastern Spain), sponge biostromes prevail and exhibit an enormous lateral continuity (KRAUTTER 1995). The siliceous sponges settled on a flat unstructured deeper shelf environment below storm wave base. The Oxfordian sponge facies reaches a maximum thickness of 40-45 m with an average of 10-15 m which might be reduced to less than two meters in many regions. Leiolitic, rarely thrombolitic microbolites occur throughout the sponge biostromes but do not dominate. The matrix is micritic and *Chondrites* which occurs abundantly in some horizons is evidence of the originally soft character of at least parts of this matrix. Iron-hydroxide-stained, partly bored hardgrounds developed very frequently and may be stacked, suggesting extremely low sedimentation rates. This is in accordance with the great abundance of epibenthic and nektonic fauna, the first of which is strongly dominated by the sponge fauna. Sponges are almost exclusively representatives of hexactinosean siliceous sponges. *Lychniscosa* and "lithistid" demosponges are extremely rare. Calcareous and coralline sponges are absent. 80 % of all sponges regardless of their taxonomic position are developed in thin dish shape. Hexactinosa are always developed in dish morphologies. The sponge fauna is of low diversity with only 25 species being classified to date. The density of the sponge population was nevertheless high evidencing stable environmental conditions for the represented taxa (Pl. 1/4).

There are some puzzling features of these biostromes: Despite very low sedimentation rates hardly any epizoa such as serpulids or bryozoans occurred, and microbolite mounds did, apart from a very few exceptions, not develop. Other accompanying benthic fauna is scarce, of low diversity and dominated by brachiopods.

The setting was a moderately deep, uniform low-energy ramp with extremely reduced carbonate and terrigenous background sedimentation. This is due to the lack of marginal shallow-water platforms and a rising sealevel, leading to the stacked, hardground terminated condensed successions. Obviously, the very reduced terrigenous influx resulted in an extremely low nutrient level, which is reflected by a strong reduction in filter-feeding organisms and the almost exclusive occurrence of the osmotrophic hexactinellids (see 2.2). Probably, oligotrophy was too pronounced to

even allow enhanced growth of microbolites despite the favorable cessation of allochthonous sedimentation. Mud mounds could not develop because together with the lack of pervasive microbolite growth the complete lack of allochthonous mud did not allow building up such structures.

The regular echinoid *Rhabdocidaris* aff. *rhodani*, occurring rarely, shows adaptations towards impoverished oxygenation (BAUMEISTER & LEINFELDER in press). Perfectly developed *Chondrites* horizons are evidence of episodic depletion of oxygen in the bottom sediment due to the lack of water exchange and microbial activity.

The Birmenstorf sponge biostromes from northern Switzerland are similar in their richness of dish-shaped siliceous sponges but differ completely by their diversity and the more equal distribution of sponge taxa (*Hexactinosa*, *Lychniscosa* and "Lithistida") and other accompanying fauna. Rich epizoa fauna and the dominance of filter feeding organisms show that nutrition was improved relative to the above example. Position in the aphotic zone would not necessarily exclude microbolites, for they also occur in Jurassic deep water facies (DROMART et al. 1994) and are thus facultatively aphotic. The scarcity of microbolites might be due to a, though very low but noticeable, influx of terrigenous and carbonate mud apparently inhibiting growth of microbial mats and hence the development of mud mounds.

Additional increase in terrigenous sedimentation might result in sponge biostromes dominated by tube-shaped siliceous sponges. Such a situation was realized in southern Portugal: a set of very thin (0.1 m) mainly siliceous sponge biostromes is intercalated within a 30 m thick pure microbolite mud mound. The biostromes could only develop over a very limited period of time because return to dysoxic conditions (see below) terminated the growth of the sponge population at a very early stage, leaving small juvenile sponge individuals (LEINFELDER et al. 1993a). Tube shapes in this case might also have had the advantage to elevate the animal rapidly above the sea floor which might still have been subject to oxygen depletion.

In general, both siliceous sponge biostromes and siliceous sponge microbolite mud mounds developed in the same depth range. However, an unfavorable sedimentation rate (too low or too high for mud mound growth) and factors suppressing pervasive growth of microbolites (oligotrophy or continuous background sedimentation) favor biostrome over mound development. The development of mounds reflects a balanced equilibrium of intermittent allochthonous carbonate sedimentation providing material for accumulation and episodes of zero sedimentation allowing the growth of stabilizing microbolites and automicrite formation (LEINFELDER & KEUPP 1995). The given water depth (below the upper euphotic zone) and the given nutrient concentration determine the composition of the sponge taxa and other organisms.

### 3.3 Microbolite Reefs from the Late Jurassic

Microbolites play a key role for the majority of Late Jurassic reefs, either building reefs together with metazoans or building reefs on their own (LEINFELDER et al. 1993b, SCHMID 1996). This is due to the fact that microbolites account for the genuine reef framework, and reef metazoans are often merely accompanying organisms, contributing comparatively little to the reef framework. Mud mounds, a mud-rich reef type in which microbolites often play a major role, are discussed in Chapter 3.2.1.

#### Pure Microbolite Reefs

More or less pure microbolite reefs, with reef metazoans never accounting for more than 10 %, occur in different growth forms. They include large bioherms up to 30 m thick as well as cup-shaped, conical patch-reefs (see Pl. 1/5 and



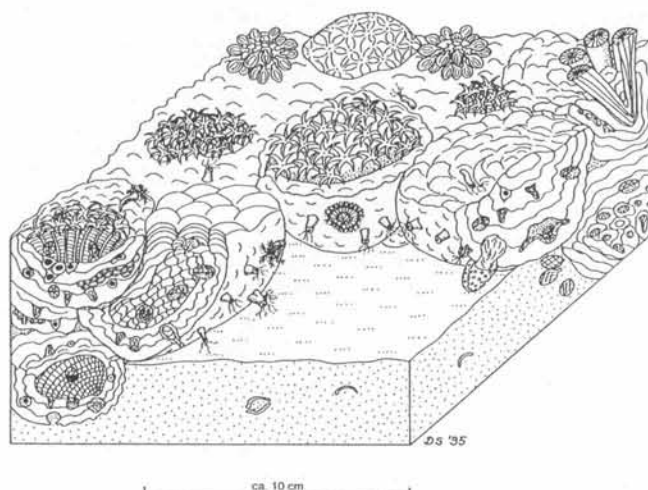


Fig. 11: Reconstruction of a coral-microbolite reef occurring in mid-ramp settings. Several corals and stromatopores are being encrusted by downward facing hemispheroid microbolites as well as some micro-encrusters ("Tubiphytes"-Koskinobullina community). Abundant reef-dwellers are echinoids; reef-destroyers are lithophagid bivalves and excavating sponges (from SCHMID 1996).

LEINFELDER et al. 1993b: Pl. 38, Figs. 6-7). This special growth form developed due to the settling of microbes on isolated hard substrates and subsequent upward and sideways growth. Microbolite reefs consist mainly of layered thrombolites, whose growth forms in mesoscopic scale largely depend on sedimentation rate and water energy (see 2.4).

Pure microbolite reefs must have grown under conditions that were unfavorable for reef metazoans, at least for most of the time. For quite some of these reefs, there are several hints for dysoxic conditions during reef growth (LEINFELDER et al. 1993b, 1994; see below), whereas others might have been subject of extended periods of eutrophication. Both processes inhibited settling of metazoans except for the episodes of better oxygenation, which resulted in sparsely distributed, mostly small-sized metazoans or, in other cases, intercalations of metazoan biostromes.

Pure microbolites are characterized by a very low-diversity micro-encruster community, dominated by *Terebella* and "Tubiphytes" morronensis. This community also appears in well oxygenated and oligotrophic deeper water settings, but dysoxic conditions are at least quite probable whenever the community is shifted towards a strong dominance of *Terebella*, and accessory encrusters such as bryozoans are lacking.

#### Microbolite Dominated Metazoan Reefs

In the Upper Jurassic, microbolites often built up reefs together with corals or, in middle to outer ramp settings, with siliceous sponges. Only with the help of microbolites

these reefs were able to rise distinctly above the sea-floor and thus to build bioherms. In coral-microbolite reefs, thrombolites are clearly prevailing; in siliceous sponge reefs, thrombolites are also abundant (Pl. 1/6), but leiolites (= dense, poorly structured microbolites; see above) are a common feature as well.

A special growth form, widespread in coral-microbolite reefs, is downward-facing hemispheroids (see LEINFELDER et al. 1993b, SCHMID 1996), being particularly abundant in some Spanish reefs and in the reefs of La Rochelle (Aquitainian Basin). At the reef base, microbolites seem to be the prevailing reef-builders, but closer examination shows that the hemispheroidal microbolites are mostly concealing large phaceloid corals inside the reef body. Between some of these microbolite-rich reefs, reef caves could develop. Inside the caves, a special type of microbolites, so-called "pseudostalactites" (TAYLOR & PALMER 1994), can be found. These reef-cave microbolites are associated with a cryptic micro-encruster fauna where thecideid brachiopods, bryozoans and serpulids are clearly dominating (unpublished results, see also op. cit.).

The dominating downward growth direction of the microbolites is due to the fact that the surface of the corals can only be encrusted after their death. Another limiting factor for microbolite growth is the grazing activity of cidarid echinoids and rasping gastropods. By growing downwards and sideways, thus building balcony-like structures, the microbolites enable the reefs to extend laterally and vertically, rising above the sea-floor (Fig. 11).

In the mound-shaped and mostly mud-rich siliceous sponge reefs, downward facing hemispheroids never occur. Instead, massive to columnar or dendroid growth forms prevail, depending on the rate of sediment input.

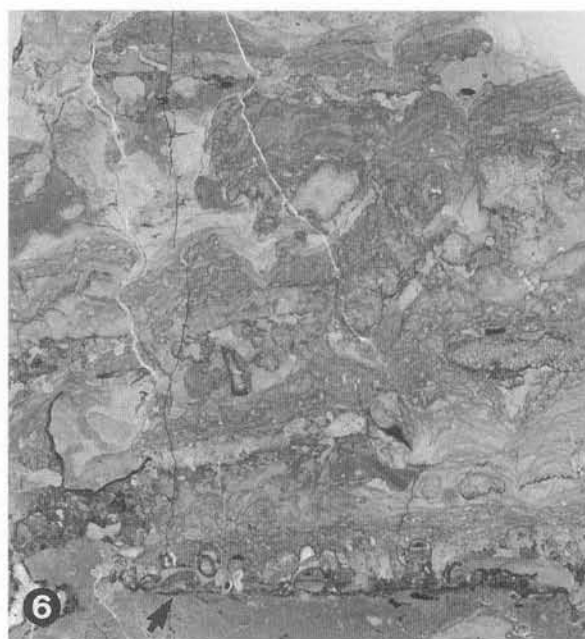
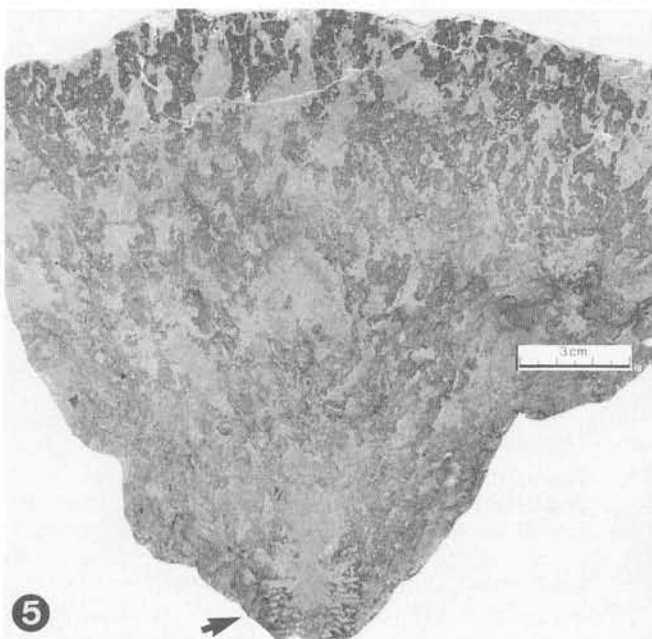
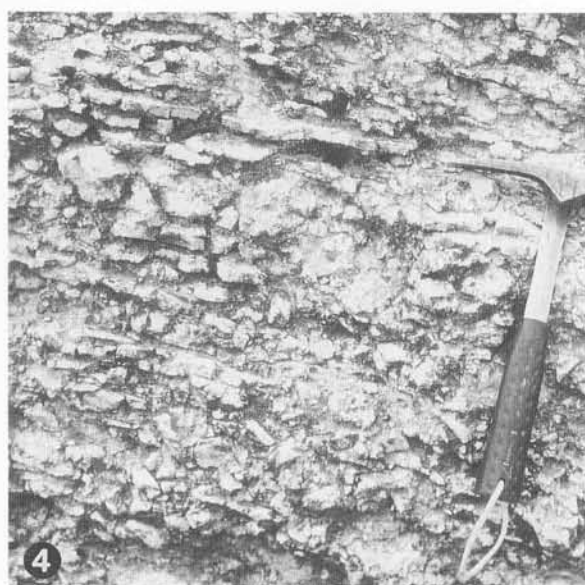
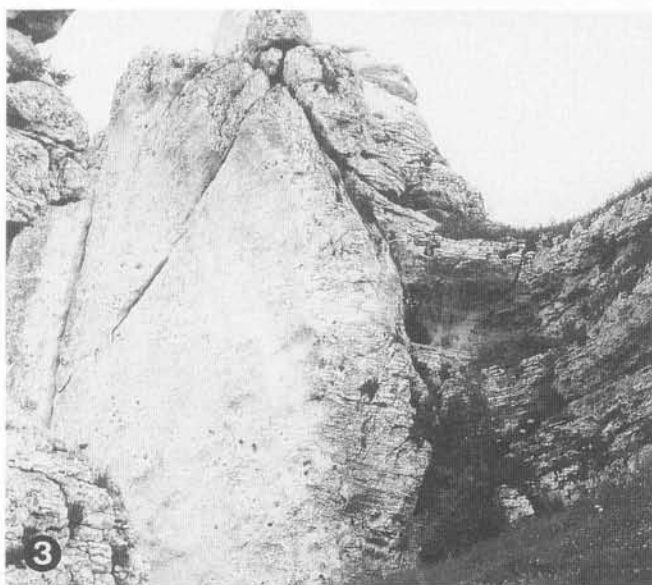
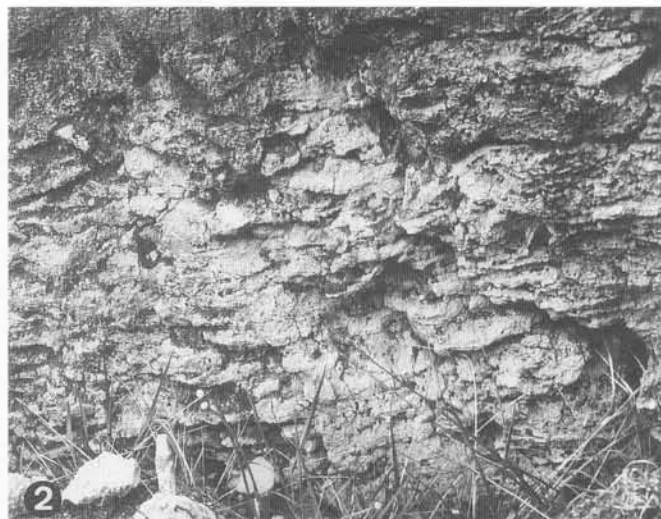
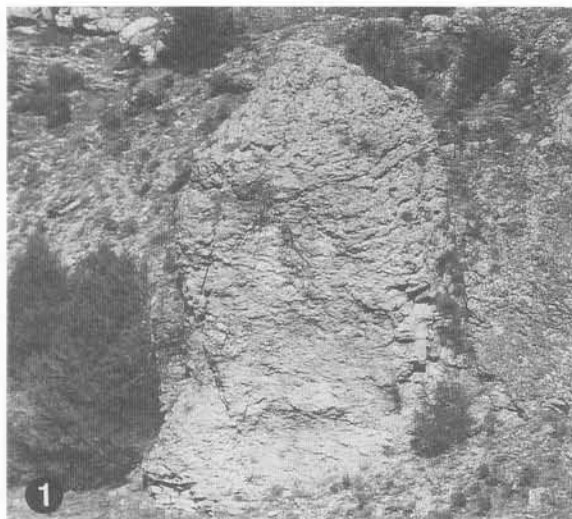
Metazoan reefs with a high amount of microbolites were probably growing under conditions where a certain but not too high amount of nutrients was favoring microbolite growth (LEINFELDER 1992). In metazoan reefs where levels of nearly pure microbolites are intercalated, these levels very probably grew during phases of oxygen depletion, which becomes quite evident if supported by other diagnostic features such as enrichment of pyrite, glauconite and clusters of the "flat clam" *Aulacomyella* (see 4.2.4).

#### 4 Reefs of the Late Jurassic within their Regional and Global Geological Framework

The importance of allochthonous sedimentation, substrate characteristics (consistency, inclination), bathymetry (and related factors such as illumination, temperature and water energy), nutrients and oxygen was highlighted in the previous chapters (Fig. 12). Such strong dependence of reef occurrence and composition on abiogenic factors demands an additional analysis of the geological framework which was responsible for the setting and switching of these control parameters. This also emphasizes the importance of

#### Plate 1

- Fig. 1: Coral-microbolite reef, approximately 10 m in height. Kimmeridgian; Jabaloyas (Celtiberian Basin, Spain).
- Fig. 2: Coral biostrome, predominantly consisting of platy microsolenid corals (*Microsolena Isastrea* and *Fungiastrea*). Height of figured section is 1 m. Middle Oxfordian; Euville (Paris Basin, France).
- Fig. 3: Siliceous sponge-microbolite mud mound, approximately 10 m in height. Oxfordian (Bimammatum zone); Podzamcze (Poland).
- Fig. 4: Siliceous sponge biostrome. The plate-shaped hexactinoid sponges are very densely spaced. Yçtova Formation, Oxfordian; Pozo Cañada (Prebetic Basin, Spain).
- Fig. 5: Conical, cup-shaped microbolite in longitudinal section, exhibiting dendroid growth form. The base of the thrombolitic microbolite body is formed by a hexactinellid sponge (arrow). Lower Peral beds, Oxfordian; Cotovio (Algarve, Portugal). Polished slab.
- Fig. 6: Layered thrombolite exhibiting a columnar to flat growth form; densely structured leiolites are also appearing. The arrow points to the base of a dish-shaped siliceous sponge which has been attacked by numerous lithophagid bivalves. Yçtova Formation, Oxfordian; Calatorao (Celtiberian Basin, Spain). Polished slab; natural size.



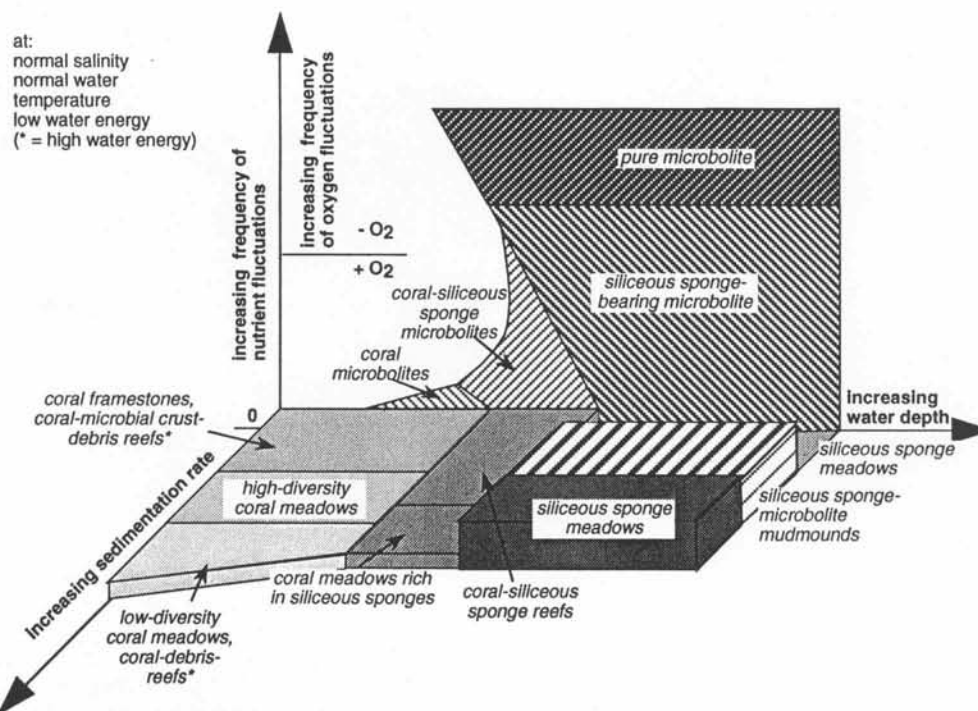


Fig. 12: The triple factor model of Upper Jurassic reefs. Differences in background sedimentation rate, bathymetry, nutrients and oxygen levels are the dominant factors determining the occurrence and character of Upper Jurassic reefs. Microbolite crusts only occur when sedimentation is very low or ceases. The higher ratio of heterotrophic versus autotrophic energy uptake in Upper Jurassic corals indicates upper oligotrophic to mesotrophic settings. Siliceous sponge reefs might span lower oligotrophic to upper mesotrophic settings and are more tolerant towards nutrient fluctuations. Pulses of eutrophication and/or oxygen depletion may exclude calcifying reefal metazoans to give rise to pure microbolite facies (modified after LEINFELDER 1993a).

reefs as an excellent paleoindicator of regional and global, ecological and structural parameters and changes for the Late Jurassic world.

#### 4.1 Control by Basin Configuration

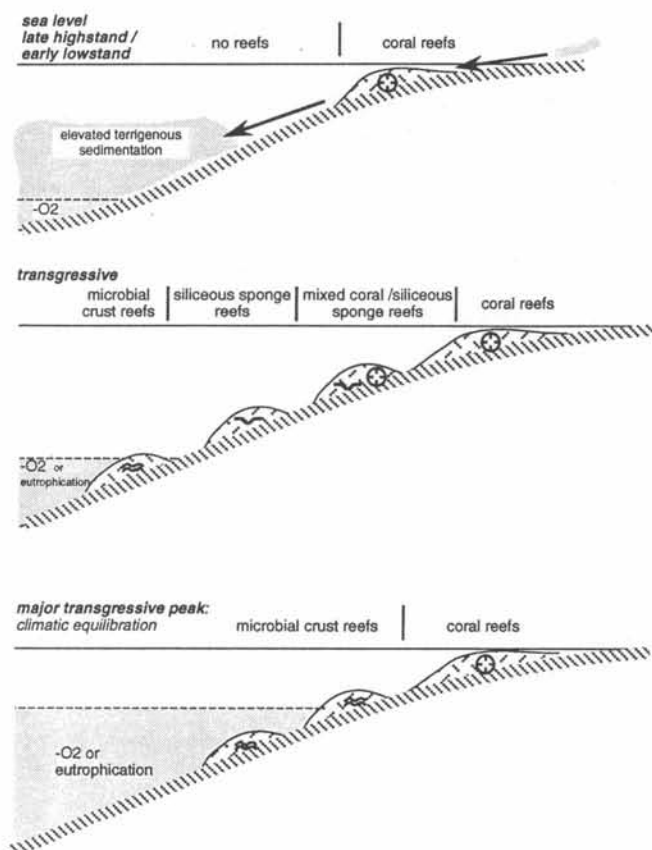
The strongest influence of basin configuration (cf. Fig. 7) and related parameters on reef growth was detected in the Lusitanian Basin of West-Central Portugal. Syn-rift sedimentation during the Oxfordian and Kimmeridgian created many steep slopes, basement uplifts, rise of salt pillows, strongly prograding siliciclastic slope settings, siliciclastic estuarine and fan deltas as well as marginal embayments all of which showed occasional reef and even platform growth at various depths, slope angles and sedimentation rates (ELLIS et al. 1990, LEINFELDER 1986, 1992, 1994a, LEINFELDER & WILSON 1989, LEINFELDER et al. 1993a, b, NOSE 1995, SCHMID 1996, WERNER 1986, WERNER et al. 1994). General morphology, fabric and particularly faunal composition reflects the various abiogenic factors associated with these settings, and their changes in a very dynamic way. As to coral reefs, allochthonous sedimentation and episodes of oxygen depletion are the most important modifiers of faunal diversities, whereas different bathymetries are reflected by different faunal communities rather than drastic changes in diversity. Particularly in areas undergoing a strong terrigenous influx reef growth was restricted to optimum episodes characterized by a cessation of tectonic activity together with a regional or global sealevel rise (see below). A well developed type hardly realized in other regions are high-energy coral-debris-microbolite crust reefs which are restricted to shallow-water steep slope breaks enabling export of the majority of reef debris (LEINFELDER 1992, 1994a, b). A similar tectonic control on slope accentuation occurs at the margin of the Aquitaine Basin towards the North Atlantic rifts and at the shallower deeper water break in the eastern Algarve where the Tethys

seaway narrowed considerably. Steep slopes may be occupied by coral-microbolite or pure microbolite reefs enabling allochthonous sediment or reef debris being bypassed around these structures. Very reduced water convection in these narrow seaways created a predisposition for eutrophication and shallow-water oxygen depletion which was established in the course of sealevel rise (see below).

Subhorizontal ramps existed in the Oxfordian of eastern Spain and southwestern Germany, with little signs of syn-sedimentary tectonic activity. These were the preferred sites of sponge biostrome and mud mound formation provided sufficient distance to sediment-exporting shallow-water platforms was given. Pervasive growth of mud mounds could, in the course of time, change such a flat-bottom topography to a rugged submarine relief, providing habitats for shallow-water reefs similar to tectonic uplifts in active rift basins. In the vicinity of large shallow-water platforms, as in the Swiss-French Jura Range reef growth was suppressed on the slopes to be reestablished only in distal areas in the form of sponge biostromes or sponge microbolite mud mounds. Cumulative sediment thicknesses show that increased accommodation on the slope due to half-graben subsidence might have trapped major parts of shallow-water derived sediments there.

The vast, originally nearly horizontal shallow-water Oxfordian carbonate platform of eastern France developed in the course of reduction of terrigenous influx by the ability of nutrient-dependent and sediment tolerant microsolenid corals which created laterally extensive coral biostromes. Once the carbonate platform was established, these biostromes disappeared and other coral reefs occurred scattered across the platform. However, many of these reefs are of moderate diversities with only minor percentage of microbolites and a considerable amount of carbonate mud or bioclastic particles. Many suffered from the incapacity of exporting mud and particles and apparently frequently suffocated by sediment accumulation. Some communities were





**Fig. 13:** Simplified sequence stratigraphic model for reef occurrences in terrigenously influenced settings. During high and falling sealevel reefs could only grow in the constantly wave-washed zone. Sealevel rises allowed reefs to develop over a wide bathymetric range due to a general reduction in background sedimentation. Some rises caused an additional climatic equilibration, which may have resulted in a slowdown of water circulation. This gave way to eutrophic or even oxygen-depleted settings in fairly shallow water, conditions to which only pure microbolites were adapted.

adapted to fairly high sedimentation rates, resulting in the development of several meters high bafflestones composed of only one or a few species of thin branching corals. An additional factor to explain the reduced occurrence of coral reefs might be the assumption that the lack of terrigenous influx caused very oligotrophic waters on this vast carbonate platform, a situation which the majority of Upper Jurassic corals, and possibly also the microbial mats, were not adapted to. Later differentiation of topography was probably due to a certain tectonic control as well as due to autocyclic platform dynamics. For instance, the development of submarine, encrinite sand dunes provided topography more suitable for coral growth, and reefs developing on the crests or flanks of these dunes show slightly higher diversities, a higher percentage of microbolite and better preservation than many other ones (LATERNSE in prep.).

In vast level-bottom ramp-type platforms unpredictable minute differences in current and hence sediment accumulation patterns determined the points of reef initiation, which may either have rapidly ceased or developed further by positive feedback mechanisms. Moreover, the distance to the hinterland, climate and tectonic activity determines the rate of terrigenous influx and hence strongly controls nutrient levels. These controls both, were working on shallow ramp-type platforms and determined the frequency, type and composition of coral and sponge reefs. Control of reef growth by basin configuration and dynamics is naturally more pronounced and direct in rift basins and tectonically

steepened ramps, and distribution and composition of reefs is an important tool in basin analysis.

#### 4.2 The Paramount Role of Sealevel Dynamics on Reef Growth in the Late Jurassic

Regional or global sealevel fluctuations may change environmental parameters for reef growth considerably (Fig. 13). Our examples show that effects of actual changes in water depth are only important in very shallow reefs, whereas the effects of reduction of terrigenous material and the overall reduction of sedimentation rate during times of sealevel rise are the most important conditions for enabling reef growth. Climatic changes related to sealevel change as well as low-stand condensation in deeper settings may considerably complicate the picture. Geometries of carbonate platforms from the Late Jurassic are more dependent on syndimentary tectonics than on sealevel development but analysis of keep-up vs. catch-up vs. give-up trends of aggrading reefs can provide valuable clues as to the interplay of both (LEINFELDER 1994b). Frequencies of sealevel change are very variable. The first to second-order, nearly continuous Jurassic sealevel rise gradually improved the overall conditions for reef growth particularly on the northern margin of the Tethys, but only third order floodings provided a direct predisposition for reef growth. In some cases reef growth continued during major parts or even stacks of third order rises, whereas in other examples it was fourth and higher order floodings within the third-order rise which then actually opened the reef window to allow widespread growth of reefs along a broad bathymetric gradient. Cyclicity of faunal communities show that nutrient and oxygen fluctuations were frequent during certain transgressive time intervals and probably were also associated with low-amplitude sealevel oscillations. Occasionally, there are even hints for annual cyclicities of reef growth.

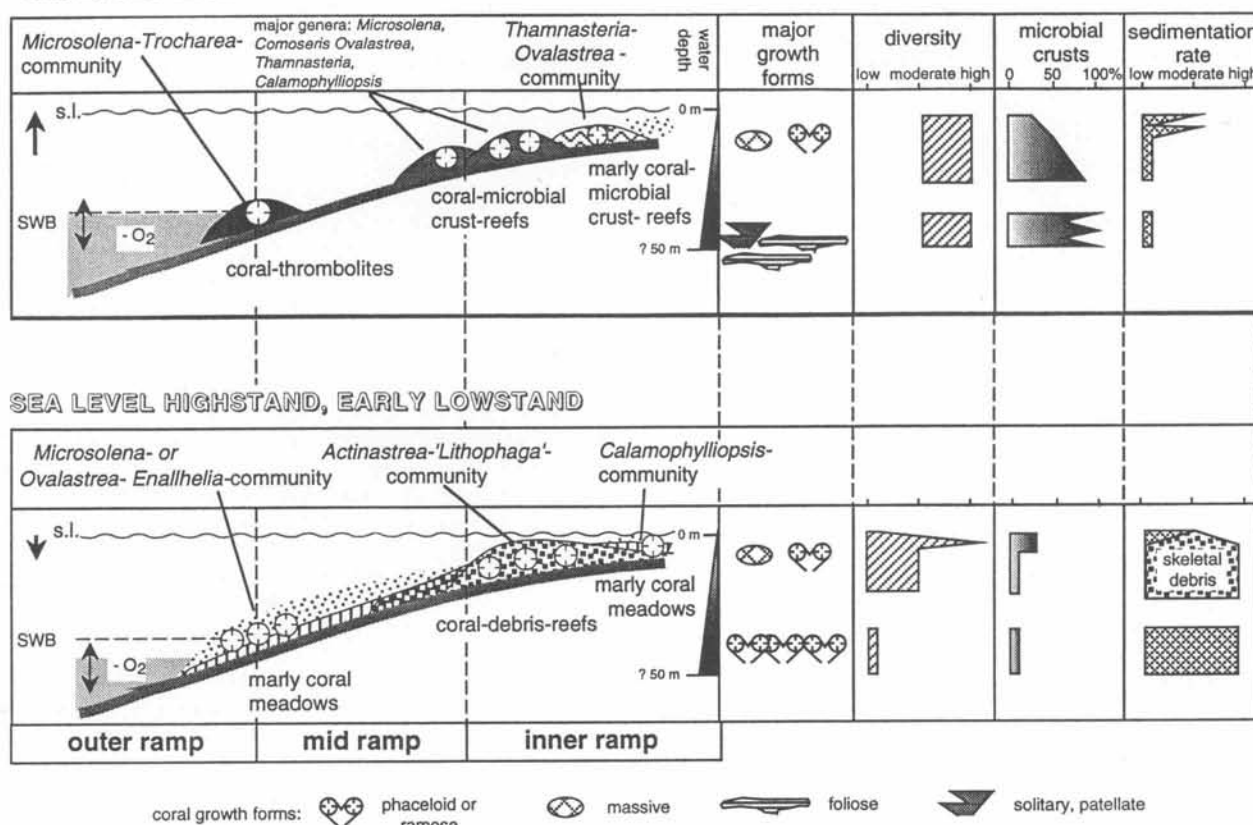
#### Sealevel Related Patterns of Reef Occurrence and Composition in Siliciclastically Influenced Settings

The major effect of sealevel rise on reef growth, particularly in settings strongly influenced or dominated by siliciclastic sedimentation, such as during the Kimmeridgian of the Iberian Peninsula, was sediment trapping in landward stepping coastal swamps or estuaries, resulting in the necessary reduction of allochthonous sedimentation in shallow-water and deep-water settings.

In terrigenous settings of the Late Jurassic, there are many criteria other than the sudden occurrence of reefs, allowing for the interpretation of time-dependent, regional sediment reduction. Such levels are frequently characterized by a short-term return to carbonate sedimentation, by higher concentrations of both benthic and nektonic fauna, by telescoped transitions from soft bottom to firm-bottom faunal communities (sedimentary condensation), including the occasional development of bored and iron-stained hardgrounds which may be encrusted by microbolite crusts, as well as by the enrichment of glauconite (LEINFELDER 1993a, b, WERNER et al. 1994).

Transgressive and early highstand reefs: Most reefs consequently formed during sealevel rise. A special feature of "transgressive" reefs is their richness in microbolite crusts. Although microbial films and mats might possibly be tolerant to sedimentation, extensive development of the typical thrombolitic to, rarely, stromatolitic crust fabric only occurred when no allochthonous sediment was trapped, making these crusts perfect indicators of zero or very low sedimentation (LEINFELDER et al. 1993b; see 2.4). The growth form of these crusts allows to decide whether sedimentation was generally very low or was interrupted by sedimentation events, the latter case leading to digitate

## SEA LEVEL RISE



**Fig. 14:** Distribution of Upper Jurassic coral communities from Iberia in relation to sealevel, water energy and sedimentation rate. Sealevel rise: Sealevel rise creates widespread shallow water shelf areas, which give way to an intensive reef development with various reef types. Rising sealevel holds back siliciclastic sedimentation in coastal regions, a major prerequisite for the vigorous development of microbial crusts and the settlement of hermatypic scleractinian corals. This sealevel state is characterized by moderate- to high-diversity coral communities both in shallow (*Thamnasteria-Ovalastrea*-community) and deeper (*Microsolena-Trocharea*-community) water. Sealevel highstand, early lowstand: In the highstand and early lowstand siliciclastics are deposited across the entire ramp and bioclastic debris may be exported from inner ramp settings to more distal areas. Reef development is hampered by elevated sedimentation rates and strong skeletal debris accumulation in areas exposed to strong wave action. Marly coral-meadows may grow both in sheltered inner ramp settings and deeper mid ramp environments, whereas coral-debris-reefs develop in strongly wave exposed areas. The fauna mostly represents moderate to low diversity coral communities. The elevated influx of siliciclastics is responsible for both low diversity and the meadow/biostrome geometry of coral communities.

branching crust growth (SCHMID 1996). Other good measuring sticks of the actual rate of reduced to zero sedimentation are morphological features of corals and diversity characteristics of coral communities (see 3.1.1) (Fig. 14). Consequently transgressive reefs in the shallow water are frequently high-diversity coral reefs rich in microbialite crusts. Their framework is often perfectly preserved which is due both to the enormous participation of microbialite crusts as well as to a very low fragmentation rate pointing to mostly low-energy environments, which were maintained due to the ongoing sealevel rise. High-energy reefs also occurred but these are mostly preserved as piles of bioclastic debris with variable, mostly low proportion of original framework. Microbolite crusts occur subordinately, probably due to their suffocation within bioclastic debris. In very marginal settings, coral meadows even occur within fine siliciclastics, pointing out to the fact that sedimentation rate was sufficiently reduced to allow growth of low-diversity communities adapted to such settings.

Towards the deeper water (several tens of meters), mixed coral-siliceous sponge reefs, then pure siliceous sponge reefs occurred. Most of them were also thrombolitic, showing a high amount of microbialite crusts. Towards still deeper waters, pure microbialite reefs could develop which show signs of adaptations towards elevated nutrient values or even oxygen depletion (Fig. 13). During the transgressive *hypselocyclus/divisum* time episode such reefs may ap-

pear already below or even within the coral zone, suppressing and substituting the sponge reef bathymetric zone. Repetitive changes of such conditions resulted in the development of successions of pure microbialite reefs to coral reefs to pure microbialite reefs, and so on (see below).

Late highstand and lowstand reefs: Favorable conditions in terms of reduced sedimentation prevailed until early highstand. The return of siliciclastic sedimentation killed most of these reefs during later highstand; consequently late highstand and lowstand situations are mostly devoid of reefs in such siliciclastically influenced basins. Only in the very shallow, high-energy zone, where constant wave agitation prevented settlement of terrigenous mud and silt, reefs may have survived into the late highstand or even early lowstand. Such reefs are frequently not recognized as such because they are mostly composed of bioclastic debris without major areas of framework preservation and a very low proportion or complete lack of microbialite crusts (see 3.1.1) (Fig. 14). These features are due to the high-energy character of these reefs and the lack of accommodation space caused by the falling sealevel. Termination of growth of such reefs was mostly caused by subaerial exposure and karstification (LEINFELDER 1993a, LEINFELDER et al. 1993a, b, NOSE 1995).

In areas where sedimentation rate was generally low, and terrigenous influence was more reduced than above, such as the Swabian Alb, reef development (in this case mostly

sponge-microbolite mud mounds) could, at favorable places, persist during all phases of sealevel fluctuations (LEINFELDER 1993a). However, reefs expanded laterally during sealevel rise, enabling time-limited reef growth in areas which were subject of non-tolerable allochthonous sedimentation during times of falling sealevel. During the Early Kimmeridgian reef growth was widely suppressed even in southern Germany due to the strong influx of terrigenous material across entire Europe. Only during the transgressive episode of the *hypselocyclus/divisum* zone specialized reefs (*Lacunosa* reefs) developed (see 4.2.4).

#### Reef Occurrence and Sealevel Change in Carbonate Dominated Settings – Differences to the Classical Sequence Stratigraphic Interpretation

Whereas during the Kimmeridgian and Tithonian most areas of Europe were subject to mixed carbonate-terrigenous sedimentation, the Oxfordian was largely dominated by carbonates. Among the differences to siliciclastically dominated or mixed successions are:

**1) Lowered nutrient values of carbonate systems:** Since it must be assumed that Jurassic corals not only tolerated but rather demanded higher nutrient values than modern reef corals due to their still imperfect photosymbiotic relation with algae (see 2.1), minimum nutrition becomes another critical value for the establishment of Jurassic reefs. Whereas in siliciclastic or mixed settings, sealevel rise may lead to an overnutrition of reefs (causing reefs other than microbolite reefs to vanish), the same sealevel rise may be of paramount importance in carbonate settings to create a minimum concentration of nutrients necessary for the growth of Jurassic reefs. This may be an additional reason why we noted the expansion of south German sponge-microbolite mud mound growth during sealevel rise (LEINFELDER 1993a) as well as the restriction of sponge meadow development to transgressive episodes in eastern Spain (see 3.2.2, cf. KRAUTTER 1995).

**2) The various control of mud mound genesis** was already discussed in Chapter 3.2.1. In basins with elevated influx of micritic mud from proximal platforms, mud mounds may occur only during sealevel rise, whereas in wider ramps with a more moderate influx from distant shallow-water carbonate factories mound development may be more persistent but frequently expands during sealevel rises (LEINFELDER 1993a).

**3) Lowstand condensation:** If slope and basinal carbonate settings are accompanied by a very shallow, level-bottom carbonate shelf, sealevel fall might expose the entire shelf and shut off export of carbonate mud. This may lead to lowstand condensation in deeper settings which can complicate dynamic analysis of reef growth. It may be difficult to distinguish this from transgressive condensation but deeper water hardgrounds with incorporated proximal allochthonous particles such as ooids, dasyclad algae and lignite litter are good indicators for lowstand condensation. Signs of bottom water oxygen depletion appear to not be compatible with lowstand condensation. An example for lowstand condensation in association with sponge meadows stems from the Oxfordian of Southern Portugal (LEINFELDER et al. 1993a, NOSE 1995). Due to the rarity of reef or shoal-rimmed level-bottom carbonate shelves and due to the availability of calcareous nannoplankton it is predicted that lowstand condensation was rare during the Late Jurassic.

**4) Climatic changes related to sealevel change:** Regional or global lowstand of sealevel might result in regional or global aridization so that terrigenous material, even if available in the hinterland, will not, or only at a low rate, be transported towards the seas, maintaining the purity of carbonate systems. This might change when as a response to

sealevel rise the climate grades towards higher humidity. In such a scenario, terrigenous material is preferably introduced into the marine realm and deposited during late rise and early highstand, rather than during lowstands (LEINFELDER 1993a), contrasting the classical theory of sequence stratigraphy. The Zementmergel of the South German Upper Jurassic seems to represent such an inverse situation. New biostratigraphic results show that the Zementmergel of the Swabian Alb are topmost Kimmeridgian in age (SCHWEIGERT 1996). This was a time of rapid sealevel rise as detectable in other parts of Europe (cf. LEINFELDER 1993a, PONSOT & VAIL 1991). Tongues of allochthonous sediments (Hattingen-Trümmerkalk, Brenztal-Trümmeroolith) were shed from nearby shallow-water, probably steeply confined isolated platforms developing on top of earlier, major sponge-microbolite mounds, into the Zementmergel basins and may be interpreted as highstand shedding. Whether deposition of the terrigenous clays of the Zementmergel was merely caused by stronger humidity associated with rising and high sealevel or was additionally caused by a certain tectonic hinterland activity, is not yet fully solved, but the change from a kaolinite dominance to a illite/smectite dominance of the insoluble fraction in the upper part of the middle Kimmeridgian (CHRISTMANN et al. 1994) might be indicative of a continuously more humid climate.

#### Geometries and Successional Trends of Carbonate Platforms and Reefs: Expressions of Sealevel Change?

As outlined above, most Upper Jurassic platforms owe their geometries to pre- and syndimentary tectonic activity rather than sealevel change. On the other hand, the differentiation, within aggradational geometries, of catch-up, keep-up or give-up trends is a tool for deciphering the various importance of tectonics and sealevel change. Particularly give-up trends of shallow-water platforms and coral reefs point to tectonic disturbances accompanied by sealevel rise. Examples for this are the Barreiro-coral buildup from the eastern margin of the Lusitanian Basin, which shows a pronounced deepening trend to be finally buried by fine sediments with a high proportion of siliciclastics (cf. ELLIS et al. 1990, LEINFELDER 1994b) or the Montegordo reef which exhibits a deepening-shallowing trend indicative of very rapid subsidence along the strike-slip eastern margin of the Lusitanian Basin (LEINFELDER 1994b). On the other hand, very rapid shallowing-up from siliceous sponge facies to coral facies on isolated platforms is often facilitated by falling sealevel, although changes in nutrient situation must not be neglected (see 2.2). For the Arnegg reef of southwestern Germany this is evident by the following observations: Preserved geometries show that autochthonous coral communities grew on debris shed by the main coral reef. These coral meadows developed in the same horizontal level than did the mixed coral-siliceous sponge reef earlier. Sealevel must consequently have dropped.

Purely aggradational platforms can be due to tectonic control (Ota Platform) or represent transgressive platform stacks developing on a prograding siliciclastic slope system (Amaral Platform, NOSE 1995). Final blanketing of such platforms by oolites during sealevel rise might have resulted even in retrogradational architecture.

#### Special Sealevel Related Reef Development During the Jurassic

The generally rising and, during its late epoch, high sealevel of the Jurassic, together with the frequent sealevel fluctuations of various order caused some unique characteristics of Jurassic reef development.



### Jurassic Reefs Through Time

Jurassic reefs became increasingly frequent in the course of the Jurassic period. The rarity of Early Jurassic coral reefs is still explainable by the rarity of scleractinian taxa. However, the latest by the Mid-Jurassic, available coral taxa were sufficient to allow coral reef growth in various settings. Siliceous sponges appear to have been available with many different taxa during the entire Jurassic. LEINFELDER (1994a) gave arguments that the general increase of reef occupation through time was largely controlled by tectonics and sealevel rise, with the first being the dominant factor for reef development on the southern margin of the Tethys and the latter playing the key role along the northern margin of the Tethys. The continuing sealevel rise caused a nearly constant retreat of the coastline, accompanied by the development of transgressive sedimentary traps such as swamps and estuaries. On the ramp-configured shelf of the northern Tethys and its adjacent shelf seas, this led to the nearly continuous decrease of terrigenous influx (at places earlier than at others) and hence to the continuous improvement of conditions for reef growth.

### Effects of Sealevel on Global Distribution of Upper Jurassic Coral Reefs

All evaluated Upper Jurassic coral reefs include many taxa which obviously possessed photosymbionts (see 2.1) and are associated with dasyclad algae and oolites, making them good indicators of warm surface waters. A look at the global distribution of Upper Jurassic coral reefs shows, however, that they also appeared in fairly high paleolatitudes (cf. compilation in LEINFELDER 1994a). Whereas reefs mentioned by BEAUVAIS (1984) from Sakhalin or Greenland are poorly known and moreover might partly be situated on exotic terranes (Sakhalin) of unknown position for the late Jurassic, reefs from southern Argentina and Chile are somewhat better studied. These represent coral reefs accompanied by dasyclad algae and oolites. Diversities are low but in the light of the other features this is interpreted as stress caused by sedimentation (LEGARRETA 1991, see LEINFELDER 1994a for additional references). Consequently, these reefs should be indicative of fairly warm surface waters (at least 20°C?). This is contradictory to global circulation models provided by MOORE et al. (1992) or ROSS et al. (1992) (for discussion see LEINFELDER 1994a). It appears that the high global sealevel of the Late Jurassic equilibrated the climate much more than previously thought, highlighting the strong and to date insufficiently understood interaction of surface waters and global climate.

### Eutrophication and Oxygen Depletion of Reef Settings Accompanying Sealevel Rise

In an equilibrated climate (as highlighted above), cold, oxygen-rich surface waters are not available and accumulation of organic matter possibly coupled with oxygen depletion will easily occur in the deeper waters which is not only shown by widespread development of black shales and bituminous deposits of Late Jurassic age but also by our reef examples (deeper water microbolites). Our examples also show that in narrow seaways, such as the Tethys off the Iberian Peninsula and the narrow Atlantic rift, pulses of strong nutrient accumulation which occasionally even caused strong bottom water oxygen depletion occurred during episodes of additional climate leveling provided by intra-Late Jurassic sealevel rises. Such events happened particularly in a third-order transgressive episode at the end of the Early Kimmeridgian (hypselocyclum-divisum chrons) where shallow-water, oxygen-depleted or eutrophic reefs

developed in the Celtiberian Basin, southern Portugal, central Portugal and southwestern France (cf. LEINFELDER 1993a, 1994c, WERNER et al. 1994). Deeper water reefs in southern Germany also show signs of increase of nutrients (the brachiopod-dominated *Lacunosa* reefs) and are associated with poorly oxygenated sediments (*Pseudomonotis*-Bank). It is noteworthy that these peculiar reefs grew in a time-episode of siliciclastic dominance (caused by widespread tectonic movements across Europe). The lack of carbonate platforms might have deprived the shallow ocean waters of an important carbon sink so that the shallow seas became supersaturated by carbon which was expelled to the atmosphere where it helped heating up the globe and further diminished thermic convection of ocean waters (LEINFELDER 1993a, 1994a, LEINFELDER & SEYFRIED 1993).

### Short-Term Sealevel Oscillations

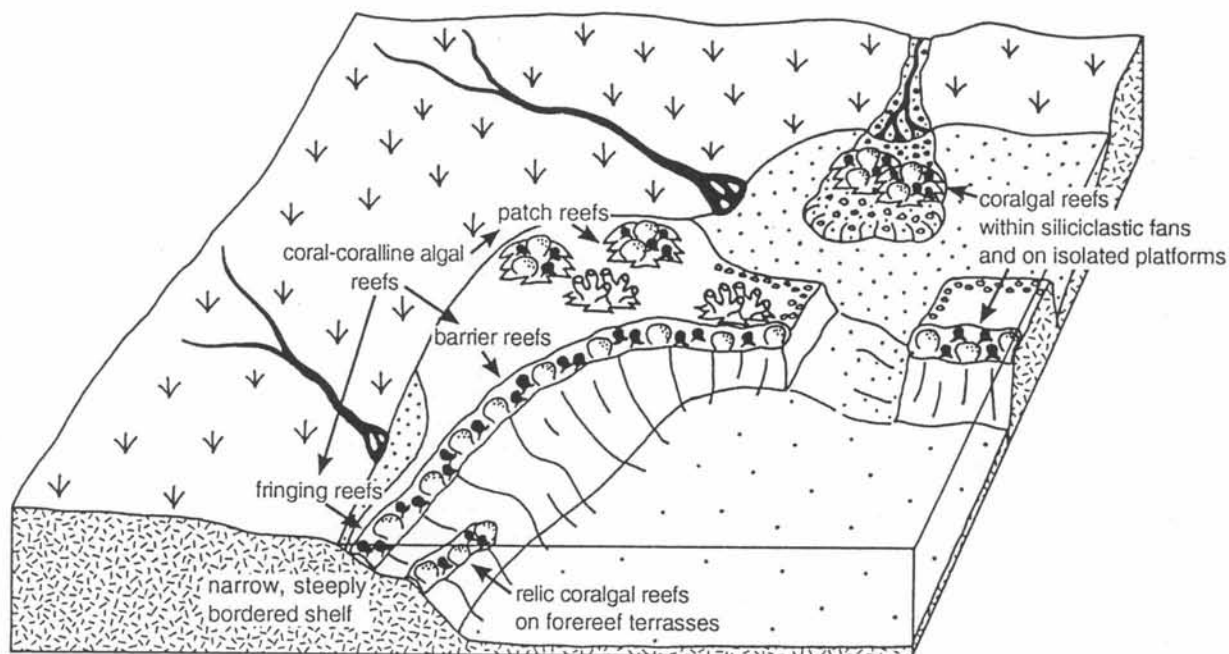
Orbital forcing of shallow-water peritidal cycles is well documented for Purbeckian sediments, that is for the latest part of the Jurassic (STRASSER 1988, JOACHIMSKI 1991). However, the lack of polar icecaps in the Late Jurassic world suggests that amplitudes were narrow, thus separation from short-term autocyclicality is very difficult. The coral-reef rimmed peritidal cycles of the Ota Platform (central Portugal) are not laterally correlatable despite perfect outcrop conditions even across short distances, and consequently were interpreted by LEINFELDER (1994b) as being dominantly of autocyclic origin. Within shallow-water reefs subaerial exposure horizons may frequently be developed and restriction of dissolution to aragonitic particles shows that this occurred syndesimetrically (LEINFELDER 1994b). Internal correlation of sediments of the coraliferous Amaral formation (central Portugal) as well as the nearly coeval Kimmeridgian shallow-water carbonate platform of eastern Spain shows that fourth and even fifth order cycles may be represented, but to date there are no means for an accurate time resolution of this complex pattern (NOSE 1995).

Sequence stratigraphic interpretation shows that reef growth is often associated with environmental ameliorations (particularly with the push-back of siliciclastic influence) accompanying third order sealevel rise (see above). On the other hand, measurements and evaluations of growth capacities of Upper Jurassic corals and microbolites show that the growth of individual Upper Jurassic reefs must have been actually much more rapid, being in the range of thousands to ten thousands, rarely hundred thousands of years (SCHMID 1996). This shows that reef growth events occurred within the window of third-order sealevel rise but are actually often associated with other events, i.e. probably sealevel rises of higher frequency. Short-term, partly repetitive stacked successions of eutrophic/dysaerobic pure microbolite reefs to mesotrophic sponge or coral reefs (LEINFELDER et al. 1993a, b, LEINFELDER 1994a) show that environmental conditions can have changed rapidly, possibly in a fifth or higher order frequency.

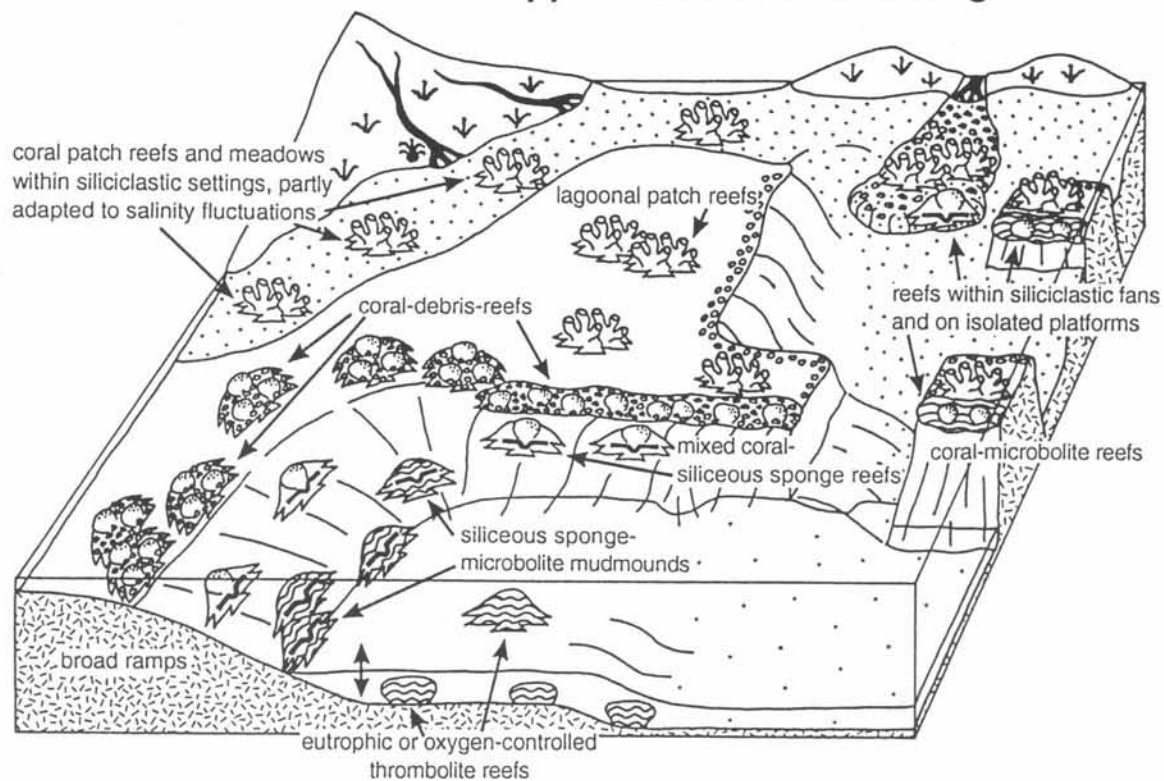
Nearly pure microbolite reefs, even those interpreted as dysoxic due to their association with glauconite, pyrite framboids, *Chondrites* levels and the dysaerobic bivalve *Aulacomyella*, often contain scattered, small-sized, oxygen dependent fauna such as siliceous sponges or, if shallower, reef corals. This shows that dysaerobic conditions were not stable across the entire time of development of the reef, e.g. during a fourth or fifth order sealevel rise but must have oscillated at a higher frequency. Whether or not these oscillations were again correlated to sealevel fluctuations of high frequency or represent random oscillations of environmental factors is debatable.

Fig. 15: Comparison of general reef settings in the Late Jurassic and the modern world. For explanation see text (redrawn after LEINFELDER 1993a).

## Modern reef settings



## Upper Jurassic reef settings



Even if no macrofauna is present in the above pure microbolite reefs, an intimate association of the microbolite crusts with "*Tubiphytes*" is obvious. Occasionally, minute layers dominated by "*Tubiphytes*" alternate with layers without these although in most cases intergrowth is very intimate probably due to the ragged and irregularly domed outer surfaces of the respective reefs. The Upper Jurassic "*Tubiphytes*" is interpreted by SCHMID (1995, 1996) as an encrusting foraminifera associated with endosymbiotic algae and also occurs in very shallow, obviously oxygenated coral reef environments (LEINFELDER 1992, LEINFELDER et al. 1993b). It therefore must have been either a very euryoxic or at least eurytrophic organism, or is indicative of high-frequency oxygen or nutrient fluctuations within the dysaerobic or eutrophic microbolite reefs. Judging from its photosymbiotic relation, the latter interpretation is more likely. Since foraminifera grow at the rate of days and weeks, shifts from "*Tubiphytes*" to non-"*Tubiphytes*" dominance might even represent annual cycles.

## 5 Conclusions

Upper Jurassic reefs are non-actualistic reefs although coral reefs share quite some features with their modern representatives (Fig. 15). Both modern and Upper Jurassic coral reefs grew on preexisting shelf and intra-platform margins but also might occur within siliciclastic fan deltas and turbid waters. However, the Upper Jurassic coral reefs occurred more frequently in terrigenously influenced turbid waters of coastal settings, even entering brackish environments. This is interpreted as a reflection of a higher proportion of heterotrophic metabolism in Jurassic reef corals although distinct bathymetric zonation, morphological adaptations to decrease of illumination and distinct annual growth banding shows that photosymbiosis has already been developed in many taxa albeit of a lower efficiency. Another difference is the frequent position of Jurassic coral reefs in ramp settings, mostly forming low-relief structures in both low- and high-energy settings. Framework was only preservable in settings of low to moderate energy where microbolites reflecting microbial activity largely accounted for reef stabilization. They anticipated the tasks of the modern reefs coralline red algae which only existed as precursor forms (LEINFELDER & WERNER 1993). Though being able to tolerate elevated water energy, microbial mats were not efficient enough to bind the high amount of debris produced in most of these settings, so that Upper Jurassic high-energy coral reefs are largely preserved as originally unstabilized debris deposits with only a minor fraction of framework preservation (LEINFELDER 1992, 1994b, NOSE 1995). Besides microbial mats many other encrusting microorganisms, such as photoautotrophic foraminifera (SCHMID & LEINFELDER 1996, SCHMID 1996) contributed to sediment fixation of Upper Jurassic coral reefs.

Although modern communities dominated by siliceous sponges do exist (e.g. DAYTON 1978, VAN WAGONER et al. 1989, CONWAY et al. 1991, HENRICH et al. 1992) they differ greatly from their Jurassic counterparts in frequency of occurrence, lack of mound formation and environmental demands. Judging from independent sedimentological, sequential and paleoecological evidence, siliceous sponge biostromes and mounds occurred on near-level bottom ramps, in shallow to moderately deep, carbonate dominated shelf waters but below the zone of reef coral growth. The exact bathymetric position was strongly dependent on nutrient characteristics and a fairly broad overlap zone with coral growth existed. Upper Jurassic reef corals needed stable upper oligotrophic to mesotrophic levels whereas siliceous sponges were adapted to fluctuating nutrient levels,

and hexactinosan biostromes could handle even extremely oligotrophic settings (KRAUTTER 1995). Upbuilding of microbolite sponge mounds was due to a mutual, and often alternating, accumulation of dense to peloidal carbonate by trapping of allochthonous sediment and by microbially induced precipitation, both processes of which were related to microbial activity. Sponges were no framebuilders but rather sought such settings for the following reasons:

- 1) Filter feeding is optimized by a higher position,
- 2) "lithistids" let themselves get intensely "infected" by bacteria which appears to help them through times of insufficient food supply and
- 3) hexactinellids need an environment where indigestible organic matter is broken to a useful form by microbial activity.

Microbolites were an important constituent of both coral and sponge microbolite reefs from the Late Jurassic. Without their participation, no positive structures could have been produced. The dependence of microbolite formation on low sedimentation rates makes microbolite-rich reefs good indicators for generally reduced sedimentation and explains why such reefs are largely restricted to episodes of rising sealevel. Given low sedimentation microbolites can occur at any water depth, defining them as facultatively aphotic. They also can cope with deteriorated environmental factors which exclude other organisms. Consequently, pure microbolite reefs developed during episodes of strong eutrophication or oxygen depletion. In hypersaline, hyposaline, intertidal or freshwater settings, microbolites were also frequent during the Late Jurassic.

In general, reef communities from the Late Jurassic occurred within a much wider range of environmental conditions than their modern counterparts, but distinctly changed their composition and structure relating to environmental variations. Provided detailed paleoecological analysis is performed, this variability allows to use them as perfect indicators for paleoenvironmental parameters, structural situations, as well as for general paleogeographic, -oceanographic and -climatic reconstructions. Analysis of Upper Jurassic reefs suggests that the Late Jurassic was an epoch of equilibrated, warm climate, with a stable body of warm surface waters enabling coral reef growth up to high paleolatitudes. These waters were superimposed to slightly cooler waters occupied by siliceous sponge communities, provided flat ramp-configured shelves existed. Lack of strong oceanic circulation resulted in occasional eutrophication or oxygen depletion even in shallow waters. This happened particularly in the narrow seaways surrounding Iberia, giving rise to extensive development of pure microbolites at certain time-intervals.

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