Digital informal reprint of

Leinfelder, R.R. (2001): Jurassic Reef Ecosystems.- In: Stanley, G.D.Jr. (ed.), The History and Sedimentology of Ancient Reef Systems, pp. 251-309, Kluwer Academic/Plenum Publishers, New York.

please see remarks for use and other comments on last page.

Chapter 8

Jurassic Reef Ecosystems

REINHOLD R. LEINFELDER

1. Introduction 251
2. Jurassic Reefs 252
2.1. Distribution of Jurassic Reefs 252
2.2. General Types of Jurassic Reefs 253
2.3. Abilities and Demands of Jurassic Reef Organisms: The Key to Paleoenvironmental Reconstruction 259
2.4. Controlling Factors of Jurassic Reef Ecosystems: The Comparative Approach 279
3. Intrajurassic Reef Development: Faunistic Evolution or Environmental Change? 293
3.1. Evolutionary Aspects of Reef Organisms 293
3.2. Sea-Level Development 297
3.3. Tectonic Control 297
4. Conclusions 299
References 302

1. Introduction

Corals and sponges from Jurassic reefs have attracted both amateur and professional paleontologists for a long time. In particular, the often beautifully preserved corals, which may look just like a coral skeleton from an extant coral, nourished the idea that Jurassic reefs were quite similar to modern representatives. Also, Jurassic reefs often are considered to have been very prolific, having outcompeted even the modern Great Barrier Reef by forming a reef belt at least 7000-km long.

This view persisted not only among amateur paleontologists but also among many geoscientists. Many Jurassic reefs contain a wealth of sponges and therefore were labeled in major revisions of Phanerozoic reef systems as ,,coral—sponge“ reefs, at least until the last decade (e.g., James, 1983; Fager-

REINHOLD R. LEINFELDER • Institute for Palaeontology and Historical Geology, University of München, D-80333 München, Germany.

The History and Sedimentology of Ancient Reef Systems, edited by George D. Stanley Jr., Kluwer Academic/Plenum Publishers, New York, 2001.

strom, 1987; Scott, 1988). However, this was not generally considered a major difference from modern reef ecosystems, because sponges also may play prominent roles in reefs today, such as Caribbean reefs. The common implication was that Jurassic reef ecosystems were fairly similar to modern reef systems in terms of composition, structures, and ecological requirements.

Some earlier studies (e.g., Crevello and Harris, 1984) and particularly recent comparative analysis of Jurassic, chiefly Upper Jurassic reef systems (e.g., Geister and Lathuilière, 1991; Leinfelder, 1993a, 1994b; Nose, 1995; Schmid, 1996; Leinfelder *et al.,* 1996; Insalaco *et al.,* 1997; Matyszkiewicz, 1997) have shown that the reefs comprise a wide variety of different types and that companison with modern reefs must occur with great caution.

2. Jurassic Reefs

This chapter illustrates Jurassic reef ecosystems by focusing on similarities and differences of reef fauna, reef structure, and ecological demands between modern reefs and Jurassic reefs. This contribution is based on analyses of reefs from the late epoch of the Jurassic period, because it was at that time that reefs developed most vigorously, and comparative studies can be performed best using this time interval. However, the temporal development of reef growth in the course of the Jurassic period also will be briefly discussed.

2.1. Distribution of Jurassic Reefs

In terms of the general tectonic setting, Upper Jurassic coral reefs occurred predominantly in variable positions on pure carbonate to mixed carbonate— siliciclastic, flat, or steepened ramps. Quite a few of them grew very close to the shoreline, whereas others were situated in fairly deep settings, possibly down to several hundreds of meters.

Examples of coral reefs on flat, partly near level-bottom ramps are widespread in Europe (e.g., Germany, France, Spain, Portugal, England: e.g., Ah, 1983; Aurell and Badenas, 1997; Bertling, 1993; Errenst, 1990a,b; Fezer, 1988; Flügel *et al.,* 1993; Geister and Lathuilière, 1991; Insalaco *et al.,* 1997; Leinfelder, 1993a; Leinfelder *et al.,* 1996; Nose, 1995). Coral reefs at the margins of and behind steepened ramps occur, for example, in Switzenland (Gygi and Persoz, 1986; Pümpin, 1965; Pittet *et al.,* 1995; Takacs, in pnep.) and in central and southern Portugal (Ellis *et al.,* 1990; Leinfelder, 1994b, Nose, 1995; Schmid and Jonischkeit, 1995). Coral reefs also may rim platforms with depositional or bypass margins, with examples coming from central Portugal (Leinfelder, 1992, 1994b), Austria (Steiger, 1981; Steiger and Wurm, 1980), Italy (Sartonio, 1989), the Caucasus (Scott, 1988), Monocco (Steigen and Jansa, 1984), and the US Gulf Coast (Baria *et al.,* 1982; Montgomery, 1993, 1996), among many other localities.

Sponge reefs also were widespread, with prominent occurrences in Romania (Draganescu, 1976; Herrmann, 1996), Poland (Trammer, 1988; Matys-

zkiewicz, 1996),southern Germany (Gwinner, 1976; Wagenplast, 1972; Meyer and Schmidt-Kaler, 1989; Brachert, 1992; Leinfelder *et al.,* 1994, 1996; Matyszkiewicz, 1997; Werner *et al.,* 1994; Keupp *et al.,* 1996; Pisera, 1997), Switzerland (Takacs, in prep.), France (Gaillard, 1983; Palmer and Fürsich, 1981), Spain (Deusch *et al.,* 1991; Krautter, 1995, 1996), but also developed in Portugal (Ramalho, 1988; Leinfelder *et al.,* 1993a), Italy (Krautter, 1996), and Morocco (Wiedenmayer, 1980; Warme *et aL,* 1988), among many other places. Microbolite reefs are particularly common in Iberia, Portugal (Leinfelder *et al.,* 1993b; Schmid, 1995), and offshore Nova Scotia (Jansa *et al.,* 1989). For a more complete list of references on occurrences of Jurassic coral, sponge, and microbolite reefs, see Leinfelder (1994a). Important occurrences are also indicated in Fig. 1.

Focusing on the plate tectonic setting of the Jurassic most reefs grew on the stable and wide shelf of the northern Tethys margin. Particularly during the Late Jurassic, sea level was about 100 to 150 m higlier than today (Haq *et al.,* 1988), which in Europe resulted in many pericontinental and epicontinental shallow to moderately deep shelf seas connecting the Tethys. In a belt extending from Russia to Rumania through Poland, Germany, Switzerland, Eastern France, eastern Spain, Southern Portugal to Texas and New Mexico, reefs developed extensively, especially during the Oxfordian. However, no continuous barrier reef developed; instead, reefs occurred as isolated bodies of variable extent in a beltlike yet broad shelf area. Another seaway with reef development was the North Atlantic rift systems and adjacent epicontinental seas, which during the Late Jurassic connected the Texas realm with the Portuguese Lusitanian rift basin, western France, England, and Northern Germany. Many seaways connected the epicontinental seas adjacent to the northern Tethys with those adjacent to the North Atlantic rift system. Reefs were less widespread, yet existing on the southern Tethys shelf (see Section 3). During the Late Jurassic, warm-water coral reefs and coral associations also grew in fairly ~~low~~ *(correction: high)* latitudes, such as in northern England (Ali, 1983; Insalaco *et al.,* 1997) and southern Argentina (Leggareta, 1991). This is evidence of very equilibrated seawater temperatures (Leinfelder, 1994a).

2.2. General Types of Jurassic Reefs

Jurassic reefs contain various proportions of ,,parazoans“ (sponges) and/or ,,true“ metazoan reef building organisms (corals and others), microbial crusts, mud, and peloidal to calciclastic particles, as well as highly variable proportions of framework development or preservation. The basic types of Jurassic reefs can be grouped into the following categories, although a great variety of transitional and successional types exist (Fig. 2):

- Coral reef types
- Siliceous sponge reef types
- Pure microbolite reef types

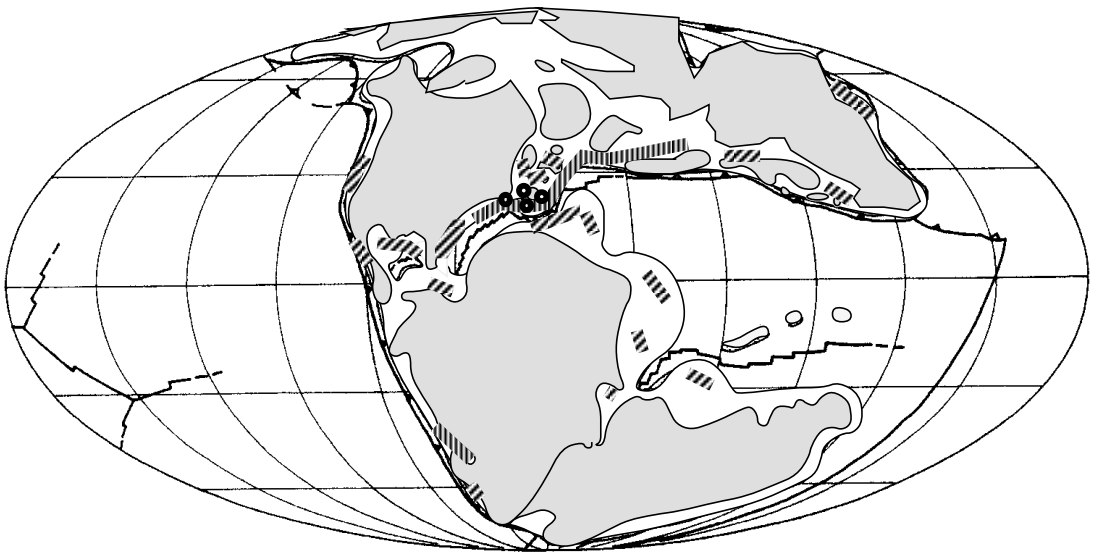


FIGURE 1. The global distribution of coral, siliceous sponge and pure microbolite reefs during die Late Jurassic. (Modified after Leinfelder, 1994a.)
Pangea paleogeography after Scotese *et al.* (1993). Reefs are more frequent along the northern Tethys shelf. Note occurrence of warm-water coral reefs in high paleolatitudes, indicating equilibrated water temperatures. Reefs were less frequent during die Early and Mid-Jurassic (see sketch maps in Leinfelder, 1994a).

(Note Figure is originally in landscape format, it was turned here 90° for better readability of this online-copy)

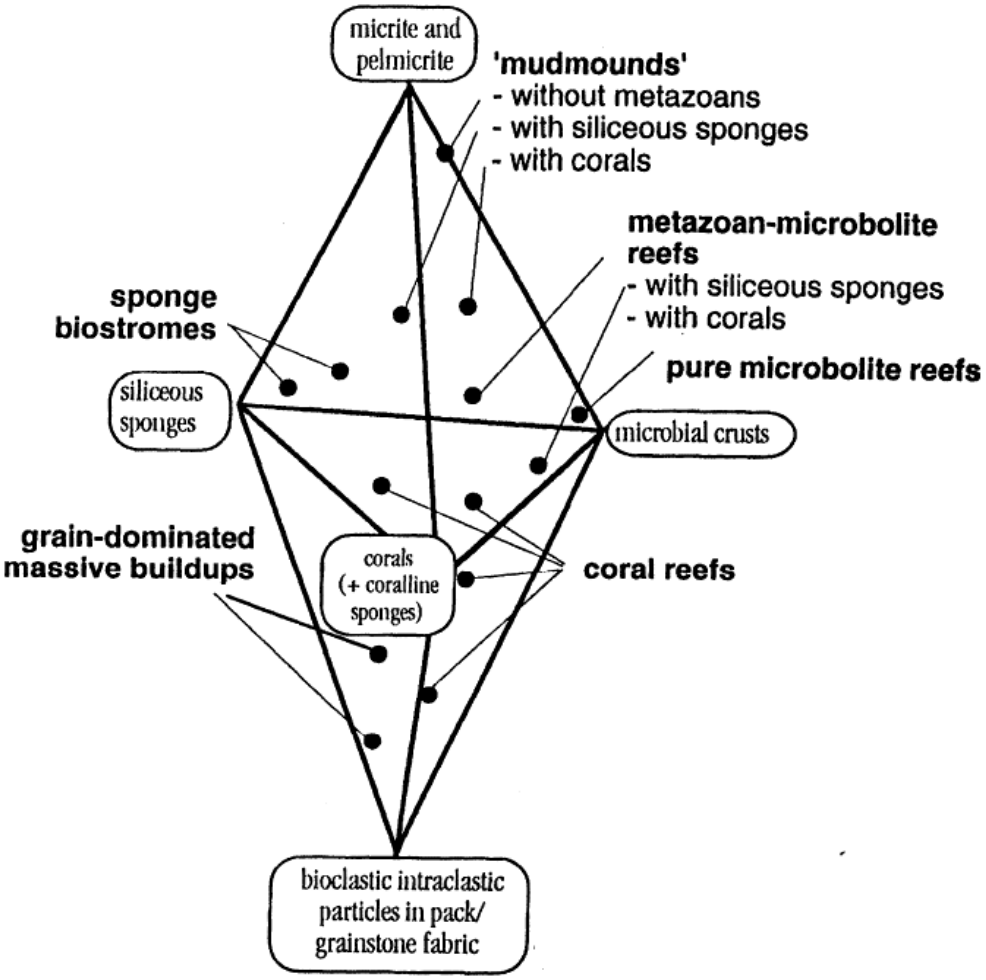
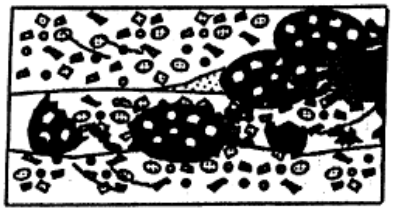


FIGURE 2. Compositional types of Jurassic reefs. The end-members coral reefs, siliceous sponge reefs, microbolite reefs, mudmounds, and bioclastic sand shoals form .many transitional types. Most common types are indicated by dots. (After Leinfelder, 1993a, and Leinfelder and Keupp, 1995, modified.)

2.2.1. Coral Reefs

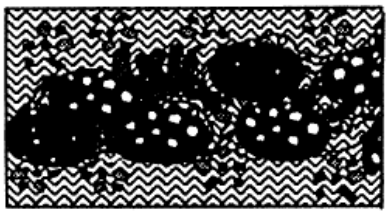
Recent literature on Upper Jurassic coral reef types exists (e.g., Leinfelder, 1993a, 1994a,b; Leinfelder *et al.,* 1996; Nose, 1995; Insalaco 1996a,b; Insalaco *et al.,* 1997), therefore only a short review of coral reef types is given here in tabular form (Fig.3). The dominant fauna of these reefs are scleractinian corals that may or may not be preserved in life position. If preserved *in situ,* in rare cases they may build true framestones with massive corals growing on top of each other. Coral bushes forming baffiestones, however, are more frequent and in rare examples may grow up to 4 m. In general, dimensions are from a few

CORAL-DEBRIS REEFS



Small patches of massive corals with indistinct, irregular outline, embedded within coarse bioclastic debris. Bioeroders frequent, binding organisms rare to lacking. Massive, nodular coral colonies prevailing. Low to medium diversity coral fauna. important genera are *Actlnastrea, Psammogyra, Amphiastrea, Convexastrea* and *Pseudocoenia.* Low-diversity types dominated by *Actlnastrea.*
Framestone patches metre-sized and smaller, coral debris. facies may however amount to thickness of tens of metres

CORAL - MICROBOLITE - DEBRIS REEFS

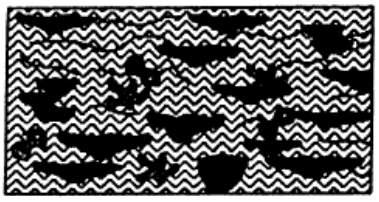


Similar to above, but microbolite crusts and other microencrusters frequent. High-diversity coral fauna. Stacked reeefs up to150 metres thick.

CORAL - MICROBOLITE BIOHERMS

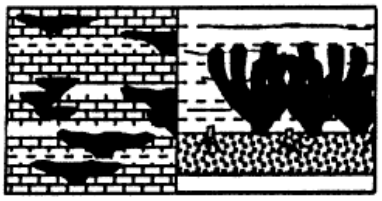
Steepiy bordered, distinct biohems ot several metres height. Medium to high-diversity coral fauna. Phaceloid corals *(Calamophylliopsis)* and ramose corals are very important, particularly during initial stages of growth. May contain clayey matrix. Microbial crusts abundant, offen forming framework. Reef caves frequent, partly occupied by downwards facing microboilte hemispheroids and cave fauna.
Reefs may be stacked, partially interbedded with pure microboilte reefs.

CORAL - MICROBOLITE BIOSTROMES



Medium to high-diversity coral fauna, composed largely of foliose and patellate corais. *Microsolena, Thamnasterla, Fungiastrea* and *Trocharea* particulary
frequent. Diametres of platy corals up to 1 metre. May contain abundant dish-shaped lithistid sponges, occasionally grading into mixed coral-siliceous sponge biostromes. Individual biostromes are metre-thick but may be amalgamated.

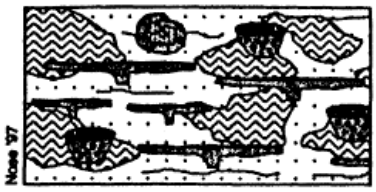
CLAYEY CORAL MEADOWS



Low-diversity coral fauna, either with broad, dish- to tunnel like, irregular coral morphologies, or with a dominance ot phaceloid *(Calamophylliopsis),* ramose *(Ovalastrea)* corals as well as sediment-sticking variabilities of morphovariable corals *(Microsolena, Thamnasteria, Convexastrea).* No microbial crusts. Individual biostromes may attain heights of several metres.

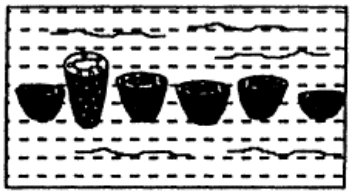
FIGURE 3. The most prominent reef types of the Late Jurassic (Simplified after Nose and Leinfelder, submitted for publication).

SILICEOUS SPONGE - MICROBOLITE MUDMOUNDS



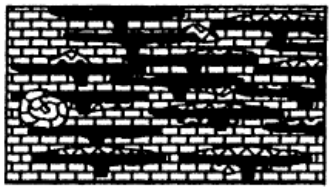
Mounds wlth dlstinct, partly steep outlines, metre to tens of metres high; often composite structures. Composed of highdlversity liithistid and/or hexactinellid sponge fauna, microbolite crusts and calcareous mud, partly peloidal or intraclastic. Additional organisms. such as encrusters , bivalves, brachiopods, belemnites and ammonites frequent.

CLAYEY SILICEOUS SPONGE MEADOWS



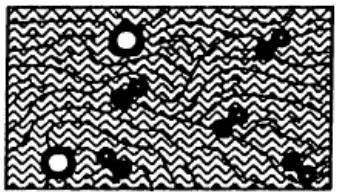
Mostly dominated by small, tube and vase shaped hexactinosan sponges, forming decimeter-thick levels. Occasionally also dominance of dish-shaped sponges. No microbial crusts.

CALCAREOUS SILICEOUS SPONGE MEADOWS



Typically of very low-diversity, dominated by dish-shaped hexactinosan sponges in rock-forming quantities. Microbial crusts regularly occurring but thin. Individual meadows cm-thick, stacked to several metre thick biostromes. Ammonites abundant. Additional fauna very impoverished.
Occasionally higher diversity biostromes, with more microbial crusts and a muddy, peloidal matrix. Additional fauna diversified.

PURE MICROBOLITE REEFS



Steep-walled structures, sometimes with overhangs, from decimetre size up to 30 metres thick. Microbial crusts in rockforming quantities. Microencrusters, such as Terebella and Tubiphytes may be frequent, arranged in distinct zones. Siliceous sponges may occur but generally are limited to distinct levels. Framboidal pyrite end authigenic giauconite frequent. Dysaerobic bivalves (Aulacomyella) and Chondrites may be abundant between reefs. Occasionally interbedded with metazoan-microbolite reefs.

FIGURE 3. *Continued.*

decimeters height up to stacked reefs attaining the cumulative thickness of 100 m and more. Most frequent are coral reefs with thickness ranging from several meters up to 15 m. Upper Jurassic coral reefs can be typified by their faunal composition, dominance, and frequency of coral species, their sedimentological characteristics, and their general shape and dimensions. In general, medium- to high-diversity coral reefs with 40 and more coral species in one coral association should be distinguished from low-diversity coral reefs. [Turnsek *et al.* (1981), recorded 109 species of corals, hydrozoans, and

chaetetids in a barrier-type reef complex of Slovenia, but this appears to be a bulk number from all reef bodies.] Medium- to high-diversity coral reefs comprise coral—debris pile reefs, coral—microbolite—debris pile reefs, marly coral—microbolite reefs, coral mudmounds, and coral—microbolite bioherms, and biostromes. Low-diversity coral reefs encompass low-diversity coral—debris pile reefs, *Amphiastrea* patch reefs, various types of marly coral meadows, and coral—stromatoporoid mudmounds (Fig. 3).

2.2.2. Siliceous Sponge Reefs

These reefs are either of biostrome type or exhibit a mudmound character due to the large contribution of fine-grained carbonate, part of which corresponds to microbial crusts. Siliceous sponges are composed of various proportions of hexactinellid sponges and ,,lithistid“ demosponges. Siliceous sponges are the most characteristic element of these reefs, but often do not dominate volumetrically over microbial crusts and calcareous mud. Mudmounds may be from a few decimeters up to several tens of meters high. The larger mounds are often composed of stacked, smaller mounds (see Section 2.4.4). Siliceous sponge—microbolite mudmounds are normally of medium to high diversity in terms of sponge taxa, although a great deal of work is still to be done to determine sponge associations in a quantitative way at the species level. Besides the various types of sponge mudmounds, there are a lot of sponge biostromes, which in the case of the Oxfordian sponge beds from eastern Spain stretch across more than 70,000 km^2, with their original extension certainly having been much broader (Krautter, 1995). Sponge biostromes or sponge meadows are variable and mostly of low faunal diversity. Marly meadows dominated by vase- and tube-shaped sponges are distinguished from calcareous biostromes dominated by dish-shaped sponges. Abundance of sponges may be very high, with sponges being almost the only rock element, such as in the case of the Spanish sponge biostromes (see Section 2.4.4). Somewhat muddier, thick-bedded biostromes have less frequent sponges but contain a lot of microbial crusts (Fig. 3)

2.2.3. Pure Microbolite Reefs

An interesting reef type is the one that is almost completely composed of microbolite. Such reefs were widespread in some areas during the Late Jurassic and are also known from the Early Jurassic. Microbolite crusts, dominated by clotted, thrombolitic fabric, form a dense framework, building up bioherms from a few decimeters up to 30 m in height (Leinfelder *et al.*,1993a,b). Macrofauna is either virtually absent, confined to narrow levels, or in rare cases scarcely scattered irregularly throughout the reefs in miniature forms. Whenever fauna appears, it is mostly siliceous sponges, chiefly of the hexactinellid type. Serpulids, terebellid worms, and enigmatic encrusting microorganisms may be occasionally very frequent. An interesting feature is that such pure microbolite reefs also may occur in a repetitive, stacked manner within some coral reefs (see Section 2.4.4).

2.3. Abilities and Demands of Jurassic Reef Organisms: The Key to Paleoenvironmental Reconstruction

Reef organisms are strongly dependent on each other, and thus play many different roles in reef systems, which are often referred to as ,,cities under water“ due to the formation of preservable structures and the intense interdependence of the reef biota. In such comparisons, the reef organisms are described as belonging to different guilds, thus having different ,,jobs,“ such as chief constructors, cementers, recyclers of building material, gardeners, shopkeepers, water filterers, waste recyclers, and much more (e.g., Fagerstrom, 1987, Ginsburg, 1997; Leinfelder and Ginsburg, 1998). All jobs are necessary to keep the reef city system running and no single chain or web link can be missing. In order to accomplish their tasks, reef organisms have very special demands and abilities. In the fossil example, it is absolutely necessary to uncover those abilities and demands of extinct reef organisms in order to evaluate their role and efficiency in the fossil reef system. Only by doing so is it possible to reconstruct the factors controlling the growth of fossil reefs. This is the ultimate goal in analysis of fossil reefs and allows using fossil reefs as paleoenvironmental and paleostructural monitors (Leinfelder, 1994a; see also Section 2.4).

2.3.1. The Master Builders: Reef Corals

The major constructors of modern reefs are the scleractinian corals, which depending on taxa have variable growth rates, shapes, and fragility. The paramount feature of the great majority of modern reef corals is their perfect symbiotic relationship with zooxanthellate. corals, making them largely independent of the heterotrophic feeding mode. Besides the tropical reef corals, there are nonzooxanthellate species, some of which form reeflike (though normally not preservable) meadows in deep and cold waters (Henrich *et al.*, 1996).

Jurassic scleractinians had a high and across the epochs of the Jurassic generally increasing taxonomic diversity (see Section 3). During the Late Jurassic, coral associations generally appeared in large-scale, shallowing upward successions in a broad variety of environments whose general environmental parameters in many cases can be determined by criteria independent of corals. This enables paleontologists to evaluate the abilities and demands of Jurassic corals. Once calibrated, coral associations then can be used as environmental monitors for settings that cannot be reconstructed by other criteria. In this chapter 1 want to particularly emphasize similarities and differences of Jurassic corals from modern corals.

2.3.la. Bathymetry and the Photosymbiosis Question. One of the key questions is whether Jurassic reef corals already possessed a photosymbiotic relationship with algae, which in modern reef corals is paramount in determining the environmental necessities and physiological abilities of corals and

in particular allows them to grow fast. Despite diagenetic alteration Jurassic corals do often show a distinct macroscopic banding of their skeletons. Microstructures of the individual bands are astonishingly similar to modern zooxanthellate corals, showing low- and high-density bands, which in modern corals are attributed to seasonal differences in illumination. Higher illumination allows for a more rapid linear growth, as it is reflected as a band of lower structural density (Allison *et al.,* 1996). The distinct development of high and low-density banding in many Upper Jurassic corals supports a good argument over whether many of them already possessed zooxanthellae or other algal symbionts.

The following additional arguments support such interpretation: (1) Many Jurassic taxa are highly integrated forms, which means that they developed complex calical features, such as thamnasterioid and meandroid types with perforate septae, dissepiments, and pennulae (Nose, 1995). Such forms are exclusively zooxanthellate today (Coates and Jackson, 1987), whereas simpler forms may be both zooxanthellate and nonzooxanthellate. (2) Within shallowing-upward successions, Jurassic coral associations are restricted to the upper part. (3) Jurassic coral associations are commonly associated with high-energy sediments such as oolites or shallow lagoonal sediments, like dasycladacean limestones and intertidal loferite sequences. (4) Jurassic coral associations may span a larger bathymetric framework than modern reefal coral associations and even show a partial overlap with siliceous sponge associations of deeper waters. Nevertheless, distinct associations change characteristically along the bathymetric gradient, with deeper water or turbid settings characterized by a dominance of plate-shaped corals. Plate shape is a widespread adaptation toward lower illumination. There are some Jurassic morphovariable coral taxa that show nodular growth in shallow water, flattened, irregular to plate-shaped growth in low-light settings, and branching growth form under elevated sediment influx (Nose, 1995; Nose and Leinfelder, 1997). Deeper-water associations might be completely composed of plate-shaped taxa, such as the many microsolenid associations from Iberia or France (Errenst, 1990a,b; Leinfelder *et al.,* 1996; Insalaco, 1996a). In the transitional zone with lithistid demosponges, some Jurassic microsolenid corals may develop thin plate shapes measuring more than 1 m across (Leinfelder *et al.,* 1993a). However, platy shapes might also be an adaptation toward poor plankton availability or osmotic nutrition, and moreover a two-dimensional plate-shaped cross-section through a coral colony need not necessarily correspond to a similar three dimensional plate shape (Fig. 4).

Additionally, but not unequivocally, partial support for the occurrence of photosymbionts in Mesozoic reef corals comes from carbon and oxygen isotopes. Stanley and Swart (1995) have argued that a positive correlation of these isotope ratios as well as oxygen ratios above —6 ΔO^{18} are characteristic of nonzooxanthellate forms due to near-equilibrium conditions with the ambient seawater. Strong clustering of values around —3 to + 1 ΔC^{13} and —5 to —3 ΔO^{18} is interpreted as the reflection of the vital effect of zooxanthellae.

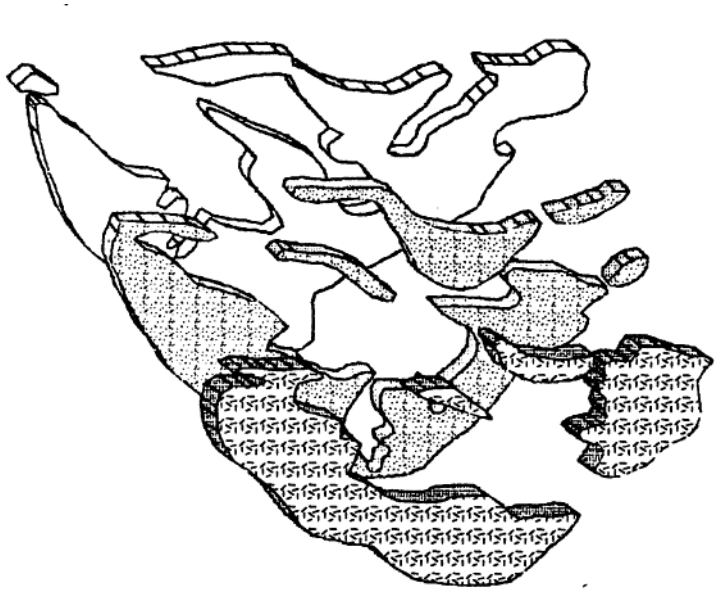


FIGURE 4. Three-dimensional reconstruction of microsolenid corals from the Swiss Liesberg Beds (Oxfordian). The irregular funnel to spiral shape may appear dish-shaped in a fragmental, two-dimensional cross-section. Growth form is interpreted as ‚best-fit' adaptation toward both reduced illumination and background sedimentation. (From Tacaks, unpublished data.)

The authors used Mesozoic corals that were still preserved as aragonite. However, not all these results are compatible with the above criteria. Using Polish material, the species *Thamnasteria concinna* should be a nonzooxanthellate form according to Stanley and Swart (1995), whereas this species and its close relative *Thamnasteria lobata* show clearly developed growth banding, highly integrated calices, and flattening interpreted to be from greater water depth. Isotopic values of Iberian (nonaragonitic) material show no isotope correlation and plot in the zooxanthellate field with their ΔC^{13} values but are depleted in oxygen, which might be a diagenetic effect (Nose and Schmid, unpublished results). This contradiction may be due to the fact that in both aragonitic and neomorphic material, diagenetic overprinting could be too intense to use this method or rather that the isotope signals of Jurassic corals were not as strong as in modern corals because the efficiency of the photosymbiotic relation was still much lower than in modern corals (Nose and Leinfelder, 1997).

There are a couple of important arguments that support the last statement. Despite showing the distinct bimodal growth bands of modern zooxanthellates, growth rates of Jurassic corals were considerably less than those of modern corals, being in the range of 3 to 5 mm/year in comparison with the modern zooxanthellate corals' average rates of 10 to 15 mm/year (Fig. 5).

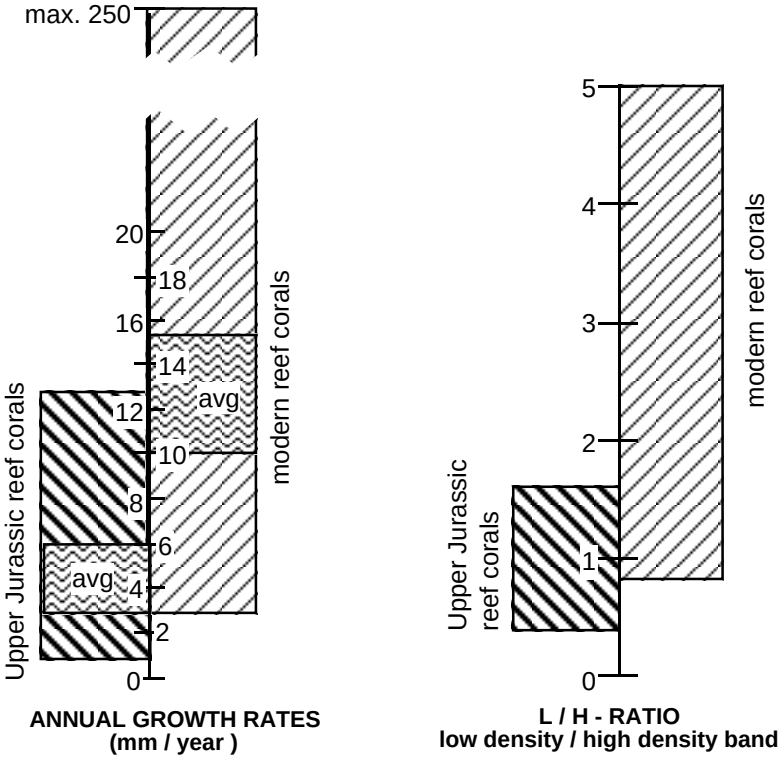


FIGURE **5.** (Left) Linear growth rates of Upper Jurassic and modern reef-building scleractinians; avg, average. (Recent data after Buddemeier and Kinzie, 1976; Schuhmacher, 1976.) (Right) Ratio of low to high density band thickness in Upper Jurassic and modern reef building scleractinians (recent data after Highsmith, 1979). (Modified after Nose and Leinfelder, 1997.)

Maximum values of modern corals are 280 mm/year and more, whereas the highest growth rates of Jurassic corals measurable to date are about 13 mm/year (Bertling, personal communication,1998). This lower growth rate is accompanied by a lower ratio of low- versus high-density band thickness, which in modern zooxanthellate reef corals ranges from 0.8 to 5, whereas in Upper Jurassic taxa the ratios average around 1 and never exceed 1.6. This shows that despite a different calcification pattern due to elevated light availability, there was no major push in growth rate, suggesting that the photosymbiotic relationship was not yet as effective as in modern forms. Corals also may have been apozooxanthellate, i.e.,switching from zooxanthellate to nonzooxanthellate state (Stanley, personal communication, 1998). Another important argument is that highest species diversity of Upper Jurassic coral associations appears in settings with a highly reduced yet clearly noticeable siliciclastic influx rather than in pure carbonate settings (Section 2.4.4). Again, this indicates that the photosymbiotic relation was not yet perfected so that these corals were not yet adapted to strongly oligotrophic

settings and moderately oligotrophic to mesotrophic sites were preferred for at least some Upper Jurassic coral associations.

2.3.1b. Sedimentation Rate. In contrast to the above-mentioned positive effect of a very low terrigeneous influx, raised sedimentation rates were as just a threat to Jurassic corals as they are to modern ones (Rogers, 1990; Riegl, 1995) and strongly elevated sedimentation rates could not be tolerated. Nevertheless, there was a considerable range of tolerable background sedimentation among Jurassic corals. In general, coral growth forms and calical types may be adapted to sedimentation to a variable degree. Growth form strategies are straightforward, with cylindrical solitary forms and bushy corals better adapted than massive colonies. Among massive colonies, domal forms are less vulnerable than flat, encrusting, or plate-shaped corals. Also, number of septae (as an expression of available tentacles that can be used for cleaning) and calical types of massive colonies may be good indicators of potential adaptation. Cerioid forms with deep calices and strong calical walls are poorly adapted, whereas thamnasteroid and meandroid shapes pose fewer problems in sorting out unwanted particles by tentacle activity (Hubbard and Pocock, 1972; Leinfelder, 1986, 1994b). However, there are many exceptions to such morphological concepts. Poorly adapted corals might have grown under the shelter of larger and better-adapted forms. Colonial skeletal morphologies must also express factors other than sedimentation, such as illumination. Corallum shapes are multifunctional and may represent a best-fit compromise toward different adaptations. An example are the dominantly platy shapes of many microsolenid associations interpreted as a low-light adaptation in deeper or turbid settings (Bertling, 1997b; Errenst, 1990a,b; Leinfelder et al., 1993a, 1996; Insalaco, 1996a). Microsolenids have been compared with the modern zooxanthellate tabular deep-water form Leptoseris fragilis (Leinfelder, 1992; Insalaco, 1996a). Leptoseris fragilis occurs down to 150 m in the clear waters of the Red Sea by combining both a very sophisticated indirect photosymbiotic relationship and enhanced suspension feeding morphologies (Schlichter, 1992). Insalaco (1996a) presented a key study on such associations based on comparative study of occurrences from eastern France, Switzerland, and England. He also interpreted pure carbonate, low-diversity microsolenid associations with plate shape dominance as deeper water settings, whereas the ,,microsolenid window“ was raised in areas with terrigeneous influence due to turbid waters. However, such interpretation might be biased due to two-dimensional interpretation of growth forms. Actually, detailed analysis of growth forms from the Swiss and French occurrences showed that microsolenids are not generally platy, but commonly exhibit intermittent pustular growth, enabling calical growth to keep up with episodes of sedimentation (Takacs and Stuttgart, unpublished results). Three-dimensional reconstruction based on parallel slabs shows that many platy growth forms measured from two-dimensional slabs actually refer to broad funnel-shaped to irregular colonies (Fig. 4), which represent the best adaptational fit toward (1) surface enlargement necessary because of turbidity, (2) removal possibilities of alloch-

thonous material settling down from the water column, and (3) rapid upward growth to cope with sedimentation.

Bertling (1997b), in an Oxfordian example from northern Germany, pointed out that biostromes composed of platy corals also may develop under strong sediment stress, when sedimentation is intermittent. Growth banding shows that coral growth is limited to about 20 years of nonsedimentation, whereas strong sediment pulses are reflected by the siliciclastic matrix. In many other cases, however, microsolenids underwent more frequent, probably seasonal terrigeneous influx, triggering the irregular, broad funnel shapes described above. Moreover, coral calices also may be oriented downward, rejecting the simplified low-light theory for broadened microsolenid corals. In Switzerland and France, clayey microsolenid associations are overlain by pure carbonate microsolenid associations, both dominated by broadened, two-dimensional platy growth forms. They occur within a generally shallowing upward succession and it appears that the lower, clayey association grew in deeper waters than the compositionally distinct, superimposed, calcareous association (Laternser, 2000), which is a contrasting view to the interpretation of Insalaco (1996a). This new interpretation is corroborated by the occurrence of diagnostic shallow-water organisms, such as *Lithocodium* and *Bacinella* (see Section 2.3.4), by a dominantly bioclastic ground mass and by echinoid types indicative of elevated water energy (see Section 2.3.3).

Besides general growth and calical forms of corals, additional criteria are necessary to identify the degree of sedimentation rate in a Jurassic coral association, particularly since many modern corals have a good capability of cleaning themselves through mucus secretion. This has no direct expression in the morphology of the corallite or the general growth form. Other useful criteria are:

- Corals may show steplike rugged undersides or nonenveloping growth bands that demonstrate that corals became partially buried while growing. Rugged margins are indicative of occasional sedimentary events, whereas smooth margins with nonenveloping growth band are characteristic of continuously elevated sedimentation (Nose and Leinfelder, 1997).
- Thick microbial crusts with frequent microencrusters on coral surfaces are good indicators of very reduced background sedimentation.
- Microencrusters alone or associated with thin microbial crusts might be indicative of strongly reduced but intermittent sedimentation.
- Very low diversities of coral associations point strongly to sedimentation stress, if other stress factors, such as great depth, strong abrasion, or abnormal salinities can be ruled out.

2.3.1c. Water Energy. There are some additional differences between Jurassic and modern corals and coral associations. The dominance of distinct morphology in comparable hydraulic settings is not compatible between

Jurassic and modern corals. Jurassic high-energy settings are dominated by massive hemispherical rather than branching forms as in modern coral reefs. In the Jurassic, branching forms were largely restricted to lower energy settings. However, some species of *Calamophylliopsis, Stylosmilia,* and *Dermosmilia* do occur in higher-energy reefs of Portugal and Lorraine (France), which could indicate strategies similar to modern acroporoids, such as rapid regeneration potential after storms. Flat encrusting forms, which may occur in modern, highly abrasive settings, are not similarly developed in Jurassic reefs owing to the fact that such environments were normally unsuitable for colonization (see Section 2.3.5). However, loaf-shaped, broad, nonencrusting morphologies are a typical element of unstable, sand-ground, high-energy reefs and probably represent stabilization strategies by a broad, lower resting surface.

2.3.1d. Salinity. A few Jurassic coral taxa were very euryhaline. *Amphiastrea piriformis,* for instance, formed small, monospecific reef bodies up to 1 m large in an oyster—*Isognomon* association within delta embayments in Kimmeridgian and Tithonian rocks of Portugal (Fürsich, 1981; Fürsich and Werner, 1986; Leinfelder, 1986).

2.3.1e. Temperature. No Jurassic cold-water corals are known. Astonishing coral productivity occurred in fairly high paleolatitudes (e.g., Germany: Bertling, 1993, 1997b; Southern England: Insalaco *et al.,* 1997). Low coral diversities of southern Argentinean Oxfordian coral associations are interpreted as the result of siltation stress (Morsch, 1989), rather than climatic stress, since coral colonies are large and co-occur with dasycladacean algae and calcareous oolites (Morsch, 1989; Matheos and Morsch, 1990; Leggareta, 1991).

2.3.2. **Multipurpose Workers: The Sponges**

Most of the sponges in modern reefs are soft sponges belonging to the demosponge group. Much rarer are coralline sponges that exhibit a basal coral skeleton, are normally small, and often are restricted to reef caves. The sponges are often described as the water filter system of the reef, by their abilities to filter huge amounts of water in order to feed on bacteria, a principal food source. They also serve partly to stabilize loose substrates that subsequently become cemented by other organisms, reducing abrasive influence of sand-sized particles within the reef (Greb *et al.,* 1996). Many modern sponges live outside modern coral reefs in nearly all water depths. The home of most modern siliceous sponges (lithistid demosponges and hexactinosan sponges) are deeper waters, down to bathyal depths (Reid, 1968; compilation of additional references in Krautter, 1997). Only rarely do they form siliceous sponge meadows (Henrich *et al.,* 1992), and only a few localities are known to date where rigid hexactinosan sponges occur in deep shelf mudmounds

(Conway *et al.*, 1991; Conway and Barrie, 1997). However, the latter locality is not a direct analogue to Jurassic siliceous sponge mudmounds because the modern example is composed of terrigeneous mud, whereas the mud in the Jurassic examples is largely carbonate. Recently, Pisera (1997) pointed to some possible modern analogues for siliceous sponge settings on deeper carbonate-dominated shelves, such as the bathyal lithistid associations on the slopes of New Caledonia (Lévi and Lévi, 1988; Roux *et al.*, 1991). Detailed analysis is still lacking and further studies will show whether these occurrences could serve as models for Jurassic sponge reefs. To date, it appears that none of the known modern sponge settings are directly comparable with those of the Jurassic, particularly the spectacular sponge mounds.

Whereas not much is known about Jurassic soft sponges, those with a rigid skeleton occur frequently in Jurassic reefs. In coral reefs, stromatoporoids (now generally assigned to the coralline sponges that have an identical basal calcareous skeleton) and other sponges with calcareous skeletons (Calcarea) are common elements and occasionally even dominate to form meadows (Fürsich and Werner, 1991; Werner *et al.*, 1994). Nearly all of them are restricted to shallow water. Siliceous sponges are rare in Jurassic coral reefs but are the dominant element in the sponge reefs. In general, there may be either a dominance of lithistids with additional hexactinosan elements or a dominance of hexactinosans without lithistids. Taxa diversity ranges from high to very reduced, with distinct growth forms clearly predominating in the low-diversity associations (dish shape dominance or tube-vase shape dominance; see Section 2.4.4).

The biology of modern siliceous sponges is not fully understood. Recently, Krautter (1997) compiled available data on modern sponges and, based on both modern and Jurassic examples, developed morphological criteria to highlight demands and abilities of Jurassic sponges. Of particular interest is that the two major groups of siliceous sponges differ considerably in their biology and physiology.

2.3.2a. Energy Uptake. The normal feeding strategy of sponges is active filtering of minute planktic organic matter. Since ostia are rarely larger than 200 μm, the usable particle size is below this limit, down to 1 μm; hence, sponges largely filter on the micro-, nanno-, and picoplankton, most of which arew free living bacteria. The amount of free bacteria rapidly diminishes in greater water depth (Hobbie *et al.*, 1972; Rheinheimer, 1980), a fact for which sponges compensate by enormous water pumping activity or by additional forms of energy uptake. Many sponges of the demosponge group (including the important Jurassic lithistid sponges) cultivate enormous amounts of bacteria or cyanobacteria, which can amount to more than 80% of the soft tissue of sponges. This appears a useful strategy to deal with major strong fluctuations in nutrient availability. Whereas the symbiotic relationship with cyanobacteria is evident (Wilkinson and Trott, 1985; Wilkinson and Evans, 1989), the same is also plausible for the settlement of pure bacteria. Bacteria probably benefit from the chemical microenvironment and the waste products of the host

sponge, whereas the sponge can feed on metabolic products of the bacteria or the bacteria themselves, especially in times of reduced availability of external food. This strategy enables them to inhabit environments that are depleted in external planktic food. In fossil examples, lithistid sponges with very large thick body walls appear to have used this strategy. This is particularly obvious if in morphovariable forms the same species appears thin in some environments but thickened and globoid in other settings. In lithistid-dominated associations, low nutrient availability may be indicated if:

- Thick-walled forms dominate, whereas thin-walled, morphoconstant forms are missing.
- Morphovariable forms are of the nodular to globoid, i.e., the highvolume-per-surface type.
- The diversity of the entire association is low.

Hexactinellid sponges have a completely different bauplan, and thus are considered an independent phylum by some authors (discussion in Reiswig and Mackie, 1983). The volume of their organic tissue is extremely thin, just coating the silica spicule skeleton. Their filter-feeding capacity is much poorer than in lithistid sponges, but their tissue characteristics enable them to feed largely on dissolved and colloidal organic matter by osmotrophy. Dissolved and colloidal organic matter become strongly enriched in deeper waters through the decay of sinking dead plankton and other organic particular material. Dissolved organic material in shallow water is recycled directly by the wealth of unicellular living plankton that is lacking largely in deeper water, making deeper settings the preferential site of hexactinellid growth. Even if dissolved organic material is rare due to general low productivity of the surface waters or from thermohaline stratification preventing dead material from sinking to the bottom, some hexactinellids can still adapt to such impoverished conditions by enlarging their surface-to-volume ratio. Superoligotrophic conditions are to be assumed by the following criteria:

- Strong dominance of thin-bodied, dish-shaped hexactinellid sponges.
- If nonmorphovariable, only such taxa with an original thin dish-shape are represented.
- If lithistid sponges are present, they are of the massive to nodular type (Fig. 6).
- Low- to very-low-diversity associations, with hardly any additional faunal elements.

Such a peculiar association is known from the Oxfordian of eastern Spain (see Section 2.4.4).

2.3.2.b. Sedimentation Rate. Sponges, like any other fixosessile organism, are vulnerable to elevated sedimentation rates but have a variety of adaptations that are also recognized in fossil examples and help define the ancient environment where sponge associations lived. Development of a tube shape is one of the primary adaptations toward sedimentation. Tube shape

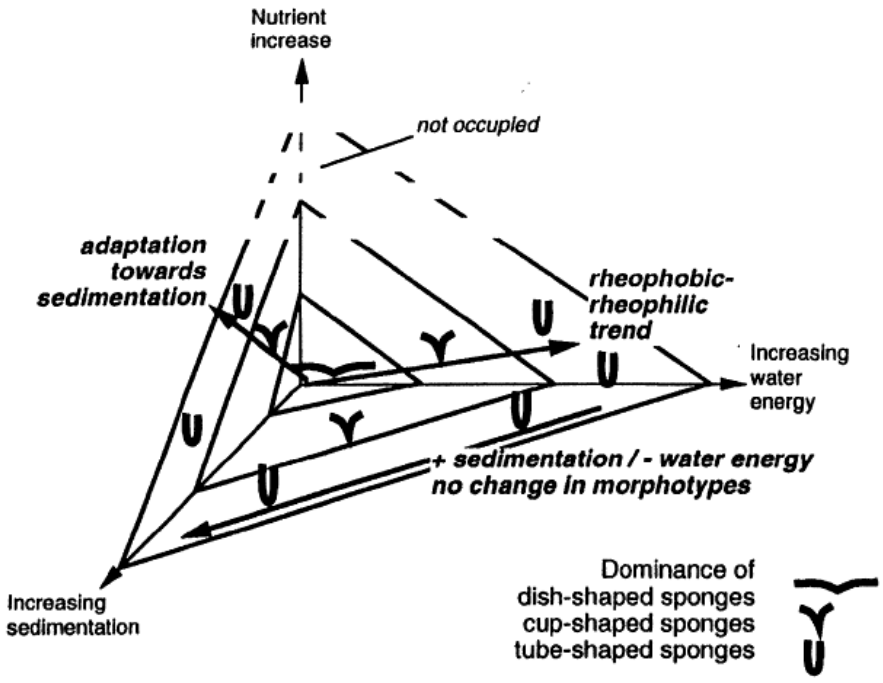


FIGURE 6. Selected environmental factors controlling morphologies of Jurassic siliceous sponges (strongly simplified). Dominance of morphologies varies from thin dishes to thick-walled knobs, to cup and tube shape along environmental gradients. Distinct trends may occur along increasing water energy and increasing sedimentation, which is normally coupled with increasing nutrient availability. Note that dominance of tube shapes may both be indicative of slightly elevated water energy and elevated sedimentation. See text for details.

helps in filtering through the ,,chimney“ (Bernoulli) effect, provided slow horizontal currents are available. In completely quiet settings, the exhalant current becomes bundled in tube-shaped sponges, and thus prevents fine material from settling down. Associations of small, tube- and narrow vase-shaped sponges occur frequently (Leinfelder *et al.*, 1993a; Fürsich and Werner, 1991; Werner *et ul.*, 1994). Dish-shaped sponges are completely unprotected. However, the sponges do have some abilities to cleanse themselves of material that actually penetrates the sponge. Demosponges have multipurpose cells, the so-called archaeocytes, which can capture unwanted particles, transport them to the outer surface of the sponge, and release them there, although this does not work well in lithistid demosponges because the denseness of their spicular skeleton strongly restricts motility of archaeocytes. Consequently, this group of demosponges is largely restricted to clear waters. Hexactinosan sponges have the ability to let particles migrate through their tissues, although the process and especially the limitations of it are not yet fully understood (Krautter, 1997). Yet, the fossil examples show that hexactinosans are often the only sponges appearing in clayey deposits that show other features of elevated

sedimentation rate, such as lack of microbolite crusts (see Section 2.4.4). A couple of calcareous sponges were able to cover their lower, older inhalant pores by a secondary skeleton, hence allowing them to cope with sediment accumulation. This was detected in the Jurassic sponge *Eudea clavata* by Krautter (1994).

2.3.2c. Temperature. Another important feature of paleoenvironmental implication is the restriction of modern hexactinosan sponges to water temperatures colder than 15° Celsius (Mackie *et al.,* 1983; Dayton *et al.,* 1994), although this might be an evolutionary adaptation and not necessarily transferable to the ancient examples.

2.3.2d. Growth Rate. The growth rates of sponges, though poorly known and apparently very variable, appear to range around the average of 2 cm/year for modern siliceous sponges (M. Krautter, personal communication, 1998). Upper Jurassic siliceous sponges occasionally may be more than 2 m in diameter. Such individuals thus should have attained an age of several hundred years, making growth rates and individual life spans comparable to scleractinian corals.

2.3.3. Bioeroders: The Recyclers of Building Material

In a modern reef a wealth of organisms are continuously eroding the coral skeletons by rasping, gnawing, and biting off pieces of the surface or even by drilling into them. Most bioeroders, such as herbivorous snails, parrot fish, or many sea urchins are doing so in search of food, which is often soft algae. Prokaryotic, microscopic cyanobacteria and fungi drill into coral skeletons for protection, as do the frequent lithophagid bivalves and boring sponges. Bioeroders are important and in a healthy reef, they are in perfect equilibrium with reef growth. They remove old, sick, and dead stone corals and other calcareous skeletons before the surfaces are lost by settlement of a soft algal cover. If bioeroders attack living corals, it is particularly the old ones that already suffer from partial necrolysis, hence giving the larvae of both nondominating and dominating taxa improved chances for settlement. By doing so, they maintain high coral diversity. Paleozoic reefs often show time-dependent, intrinsic change from a pioneer, through intermediate (high-diversity) to a dominance stage, without any apparent extrinsic environmental changes (e.g., Walker and Alberstadt, 1975). Aging of a reef, as expressed by the intrinsic change of reef associations, is largely unknown from Mesozoic and Cenozoic reefs and might be an expression of the much lower availability of bioeroders during the Paleozoic, and hence the lack of the „rejuvenescance“ mechanism provided by these organisms.

Bioeroders break the reef material into particles of variable size. Cobble- and sand-sized pieces, if cemented by other organisms, become recycled by forming a hard foundation for the new settlement of larvae. Most of the smaller generated material, including silt- and mud-sized bioeroded particles, also is

removed from open surfaces in the reef. Part of this material fills the open cavities of the underlying dead reef, and by doing so stabilizes the entire living reef. Another large fraction is winnowed into the open ocean or the lagoon by waves and storms, thus preventing the reef from getting choked by its own debris. This is particularly important for productive reefs growing in a nonsubsiding tectonic setting. The available ecospace can be used much longer by this strategy.

In Jurassic reefs, quite similar bioeroding organisms were active. Boring microbes were ubiquitous in coral reefs and back reef sands, as evidenced by typical microcrystalline rims with an irregular inner margin (coated grains *pro parte).* Even the oldest boring foraminifer, *Troglotella incrustans,* known from the Jurassic, developed a peculiar commensal lifestyle within the test of another foraminifer and did not contribute much to general bioerosion (Schmid and Leinfelder, 1996). Lithophagid bivalves often mined massive skeletons to their complete destruction. Bertling (1997a) demonstrated that taxonomic composition of the boring fauna also was related to the degree of sedimentation.

While clionid boring sponges were not yet as important in Mesozoic reefs as in Neogene reefs (Bertling, 1997a), the boring haplosklerid sponge *Aka* was widespread in deeper sponge reef settings (Reitner and Keupp, 1991). Sea urchins are a very frequent element in both Jurassic sponge and coral reefs. In rare cases, scratch marks from sea urchins on bivalve shells are known from the Upper Jurassic (Leinfelder, 1986), providing evidence for the existence of algal turfs or microbial coatings on these shells.

Regular echinoids are frequent in many Jurassic reefs containing microbial crusts. As in modern reefs, they appear to have had the task of keeping growth of microbial films under control. Interestingly, some coral reefs do show an upward and outward increase of microbial crusts, which is astonishingly paralleled by a relative decrease rather than an increase of regular sea urchins. Despite the potential higher food availability provided by prolific microbial growth, this fact indicates environmental deterioration at least for sea urchins, such as intervals of poor oxygenation, which many have speeded up the turnover from coral dominance to exclusive microbolite domination (see Section 2.4.1). Also, sea urchins are less frequent in monospecific coral reef meadows struggling with sedimentation. It seems that in the latter example there was too little food for the urchins because the strategy of the phaceloid to ramose corals was to have their branches partially buried by sediment (see Section 2.3.1).

To date, it is impossible to calculate mass balance budgets of reef construction versus reef destruction in Jurassic reefs, although bulk accretion rates can be determined in some cases. Nevertheless, the patterns show that bioerosion was an important factor in Jurassic reefs as well. However, some Jurassic bioeroders may be valuable indicators of specific environmental factors. For example, analysis of constructional morphology of regular Upper Jurassic echinoids particularly allows for the interpretation of water energy, oxygen availability, and water depth (Fig. 7) (Baumeister, 1997; Baumeister and Leinfelder, 1998).

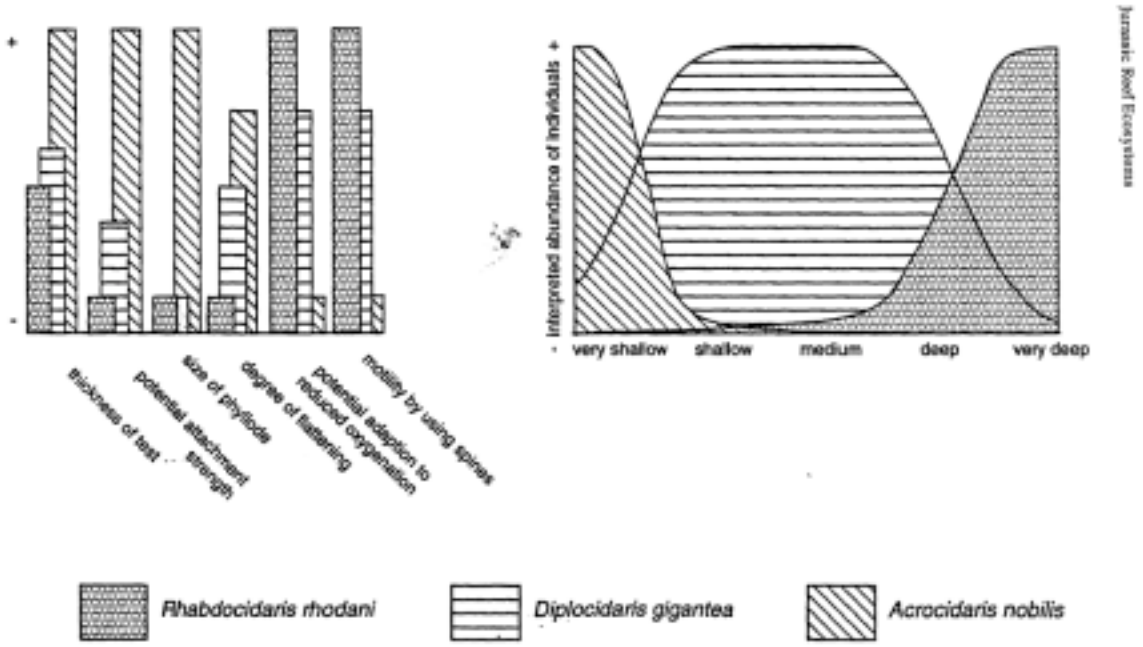


FIGURE 7. Analysis of constructional morphology of Jurassic regular echinoids for environmental interpretation. The three chosen examples represent a well-adapted and specialized deep-water form *(R. rhodani)*, a largely ubiquitous. poorly specialized form of moderate water depth *(D. gigantea)*, and a specialized shallow-water high-energy taxon *(A. nobilis)*. (Data from Baumeister, 1997, and Baumeister and Leinfelder, 1998.)

(Note Figure is originally in landscape format, it was turned here 90° for better readability of this online-copy)

Thickness of the test of a regular echinoid is a first indicator of water energy. Jurassic *Acropora nobilis,* for example, has a very thick test similar to modern *Colobocentrotus atratus.* Similarly, *A. nobilis* also exhibits saddle-type broadened short spines serving as a partial secondary test. Another good environmental indicator is the morphology of oral spine mammillae. Attachment surfaces allow interpretation of motility and strength of spines, and hence are indicative of substrate characteristics. Probably the best environmental criteria, however, are the ambulacral pore systems of Jurassic reef echinoids. An enormous number of oral P3/4-type pores, which relate to strong muscular ambulacral sucker feet, indicate the ability of the taxon to withstand high water energy, and hence are highly indicative of very shallow, high-energy reefs. Such forms may be accompanied by echinoids with a slightly lower resistivity toward water energy (P2/3 isopore sucker disk) that lived in more protected areas within the reefs and so forth. However, it is the form with the highest potential resistance that characterizes the energy setting.

Another interesting feature is regular echinoids which show an increase of ambulacral pore rows with P1 isopores related to nonsucking ambulacral feet or forms such as *Rhabdocidaris rhodani,* a taxon that exhibits slitlike C1 isopores across its entire test. C1 isopores correspond to flattened, bladelike respiratory ambulacral feet. Such foot modification is normally typical of the aboral surfaces of irregular echinoids, which by their burrowing life habit had to improve their respiratory system. The epibenthic regular *Rhabdocidaris rhodani* evolved this independently and the increase of nonmechanical ambulacral P1 feet in the other examples also is diagnostic of either increased activity or reduced oxygen availability of these forms. Actually, the latter type occur in siliceous sponge reefs, and independent evidence shows that these reefs were positioned in outer ramp settings. *Rhabdocidaris rhodani* actually lived in fairly restricted settings as reflected by the low-diversity host association (see Section 2.4.4).

2.3.4. Binding and Cementing Organisms: Keeping It All Together

Binding and cementing organisms are extremely important in the reef ecosystem, since they fix loose surplus material that could not be stored in lower reef cavities or exported from the reef. Much of the material is produced by bioerosion, but the more exposed the reef, the higher the portion of additional debris generated by waves and storms. As a consequence, high-energy reefs need very effective binding and cementing organisms, such as the modern encrusting coralline red algae. Many other organisms such as soft corals, encrusting sponges, bryozoans, and microbial films help stabilize the loose material, but it was only after the adaptation of coralline red algae to highly abrasive settings that reefs could inhabit the high-energy environment (see Section 4).

Calcareous red algae did exist in Jurassic reefs, but they did not play important roles in reef stabilization, save for very few exceptions where solenoporid bindstones cover coral reefs (Nose, 1995; Helm, 1997). A direct

ancestor to the coralline algae, *Marinella lugeoni,* arose during the Late Jurassic and also inhabited coral reefs sporadically, but again was of no importance for reef stabilization (Leinfelder and Werner, 1993). The most important stabilization in Jurassic reefs were microbial films and mats, which calcified as typical microbolite crust fabrics (Leinfelder *et al.,* 1993b). Microbial calcification, resulting in comparable types, also is important in modern reefs, but is largely restricted to the cavity and cave environments, probably because of competition with coralline algae (Reitner, 1993; Reitner *et al.,* 1996; Montaggioni and Camoin, 1993).

2.3.4a. Jurassic Reefal Microbolites. Jurassic, and similarly other, microbolites should be categorized under a macroscopic, mesoscopic, and microscopic scale (Schmid, 1996). A combination of these allows not only for a straightforward descriptive classification but also for genetic clues (Schmid, 1996; Leinfelder *et al.,* 1996) (Fig. 8).

The occurrence of Jurassic microbolites with similar thrombolitic fabrics at different water depths, including deep shelf settings probably about 400 m

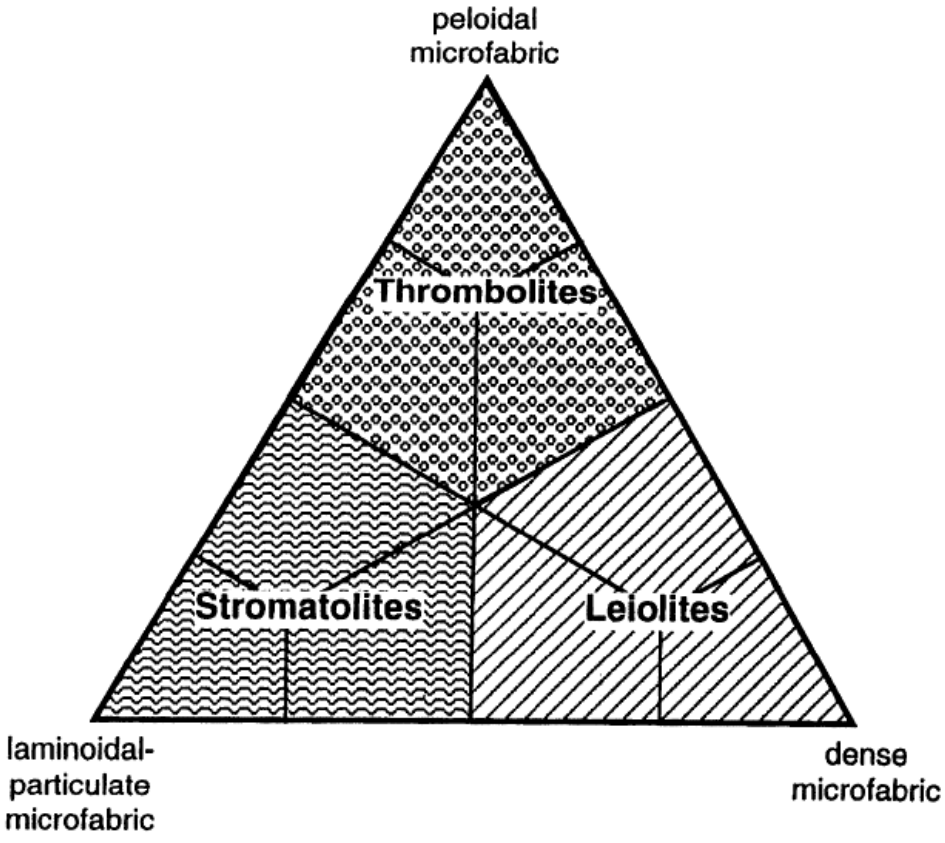


FIGURE 8. Classification of Jurassic microbolites according to their fabric. (Simplified after Schmid, 1995, and Leinfelder *et al.*, 1996.)

deep (Jansa *et al.,* 1989; Dromart *et al.,* 1994) as well as their frequent and prolific development in Jurassic reef caves (Schmid, 1995), shows that microbolites were potentially aphotic, and hence are not related solely to cyanobacterial origin. This does not necessarily mean that cyanobacterial were not involved; they may even have dominated in shallow settings. The conclusion is that microbial films and mats composed of cyanobacteria and/or eubacteria, possibly even diatoms, can result in the same typical clotted peloidal microfabric that triggers a thrombolitic mesofabric. Such microbes often produce similar polysaccaroid macromolecules that fix calcium ions and act as an organic catalyst for calcification (Reitner, 1993). Thrombolitic types are frequent from shallow to deep water, whereas stromatolitic types are largely though not exclusively related to shallow water, probably because diurnal changes of light intensities are reflected by a dominance of motile oscillatorian cyanobacteria. If occurring in deeper water, other regular changes such as background sedimentation or nutrient availability might have caused a similar though less pronounced laminated fabric (Leinfelder and Schmid, 2000).

Reduced sedimentation is the most important prerequisite for the development of microbial crusts. Microbial films also may grow under elevated background sedimentation but then trap and baffle sediment rather than calcify in the typical clotted peloidal fashion (Fig. 9). This process is obvious by the development of laminoidal fenestral intertidal fabrics (loferites), which also were frequent during the Jurassic. An example is the coral reef-rimmed Kimmeridgian Ota Platform of central Portugal, where such loferites developed vastly in back reef position (Leinfelder, 1992, 1994b). Loferites may be pure carbonate mudstones or even intraclastic grainstones, and the frequent occurrence of microbial mats is only indicated by laminoidal fenestral fabrics. In other settings with similar background sedimentation but greater water depth the occurrence of microbial mats would not be documented at all because diagenesis would be too slow to ,,shock frost“ laminoidally arranged gas bubbles of decaying microbial material (Leinfelder and Keupp, 1995). As a conclusion, the occurrence of distinct microbolite fabrics such as thrombolites or stromatolites with a clotted peloidal microfabric is diagnostic of low sedimentation rates, a fact that is corroborated by the frequent occurrence of microbolites at hiatuses and condensation levels. However, sedimentation rates can vary, and given that they are below a critical threshold, microbial fabrics reflect these changes. Arborescent, digitate microbial mesofabrics indicate elevated (but still fairly low) background sedimentation rates. Consequently, occurrence and fabric patterns of microbolite crusts are a useful tool for sequence stratigraphic interpretation (Leinfelder, 1993b; Nose, 1995; see Section 2.4.2).

Kempe (1990), Kempe and Kazmierczak (1994), and Kempe *et al.* (1996) argued that vast development of microbolites during Earth history should be indicative of strongly increased seawater alkalinity, which in turn may be associated with ecosystem collapses and mass appearances of calcareous microbolites. During the Precambrian, this was thought to be due to the sodic nature of the oceans, whereas during the Phanerozoic alkalinity could be

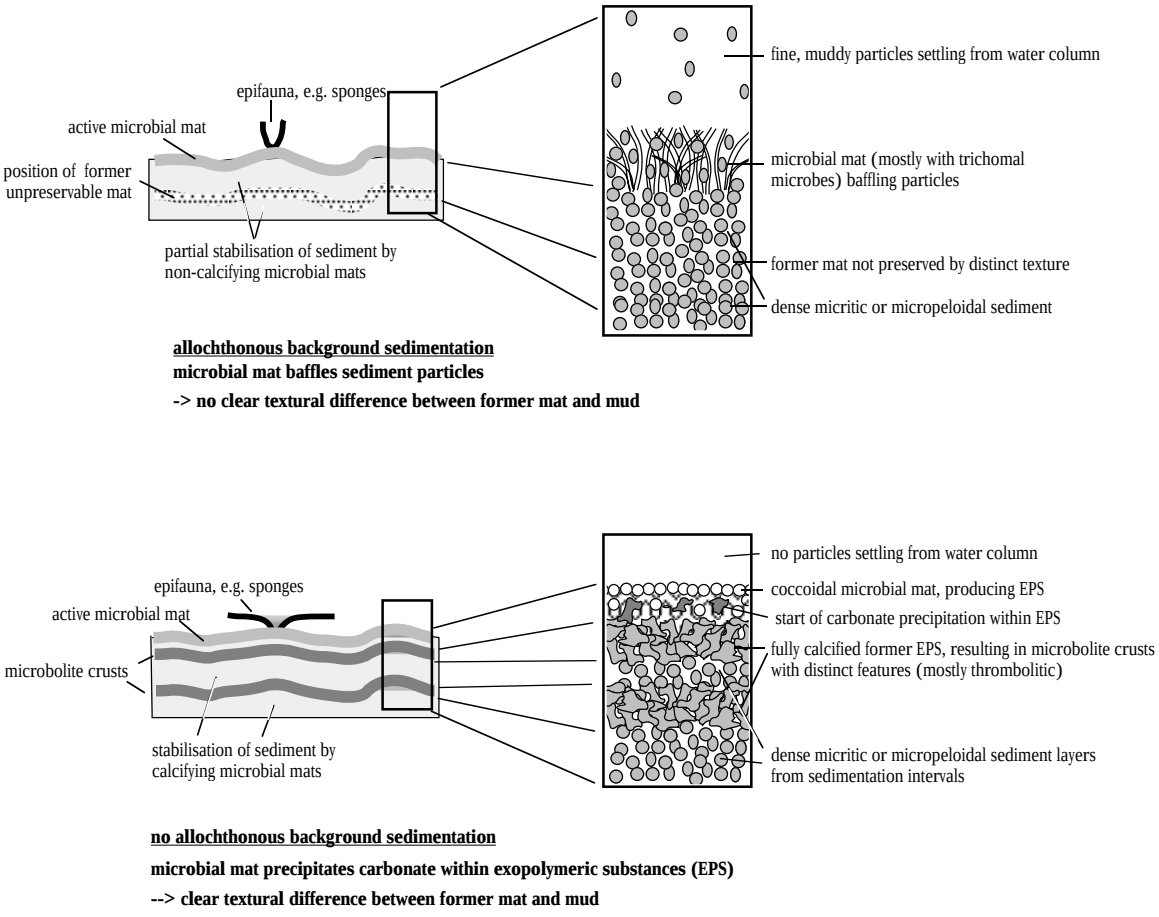


FIGURE 9. Preservation of Jurassic microbial mats. Mats may grow with or without background sedimentation. Under slow sedimentation, mat microbes were probably dominated by trichomal cyanobacteria-trapping sediment particles. Distinct microbolite structures did not develop. Under strongly reduced to zero sedimentation microbes produced large amounts of exopolymeric substances (EPS), which largely are polysaccharoids and some proteins. EPS may act as catalyst for calcification in distinct, mostly thrombolitic, microbolite patterns.

(Note Figure is originally in landscape format, it was turned here 90° for better readability of this online-copy)

regionally increased by stagnant basins via the H_2S alkalinity pump or by increased influx of sialic weathering products. Probably Jurassic seas had a slightly higher alkalinity than today, which might have facilitated the formation of microbolite precipitation. However, the alkalinity model alone cannot explain the co-occurrence of pure thrombolite reefs and macrofauna-rich reefs at certain time intervals (see Section 2.4.4).

Microbolites also occur as a typical element of Jurassic coral reefs, ranging presumably from oligotrophic to mesotrophic, so in general, microbolite development was largely eurytrophic. However, it appears plausible and there are several supporting arguments that microbolite development was enhanced whenever nutrient levels increased. In eastern Spain, a unique but widespread Oxfordian low-diversity association of hexactinosan sponges thrived under zero background sedimentation in a very oligotrophic setting, which was possible by the adaptations discussed earlier (see Section 2.3.2). Normally, the very reduced sedimentation rate should be favorable for extensive development of microbolites. However, in this special case, nutrient values were apparently so low that they only allowed for impoverished development of microbolites, making this example an exception to the reliability of microbolites that characteristically occur whenever sedimentation rates are very low. Another argument for the positive influence of nutrients on microbolite development is that reefal microbolite crusts are often better developed in areas with very reduced though noticeable terrigeneous influx relative to pure carbonate settings. Finally, the exclusion of reefal macrofauna for distinct time intervals in certain areas probably is often due to strong eutrophication that excluded the reef organisms. However, this can only be proven in cases where oxygen impoverishment occurred, which is highlighted by an association of pure microbolite reefs, bacterial framboidal pyrite, richness in authigenic glauconite, and the occurrence of dysaerobic or poikiloaerobic pectinid bivalves (Leinfelder, 1993a; Leinfelder *et al.,* 1996). In principle, oxygen depletion might not necessarily be related to eutrophication but could be solely caused by lack of water exchange. Actually, slightly impoverished oxygenation under oligotrophic conditions is indicated by the before-mentioned sponge associations of eastern Spain, but as discussed earlier, vast microbolite development was not possible because of the lack of nutrients. In conclusion, pure microbolite development is interpreted here as directly indicative of eutrophication, which in some cases might even have resulted in discernable, occasional oxygen depletion. Black shales and bituminous sediments did not develop due to the lack of rapid burial from low sedimentation rates. This makes pure microbolite development perfect indicators of eutrophication— oxygen depletion in low sedimentation regimes, at least for water depths where other limiting factors such as very high water energy or salinity fluctuations can be ruled out. Microbolites therefore are important tools for paleoceanographic reconstructions (see Section 2.4.4).

2.3.4b. Living on Microbolite Crusts. A wealth of other encrusting organisms lived on the surfaces of Jurassic microbolite crusts. Many of these were

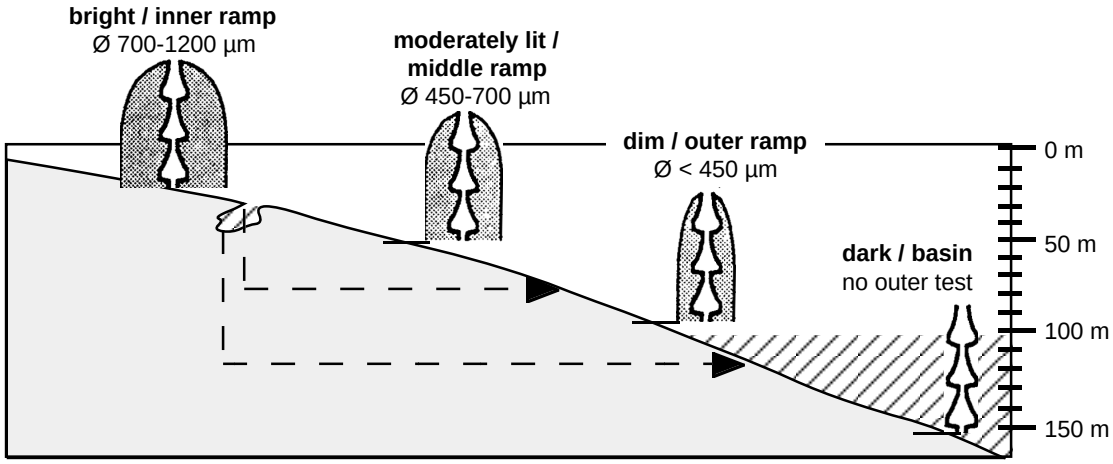


FIGURE 10. *Tubipliytes inorronensis,* interpreted by Schmid (1995) as a miliolid foraminifer with a twofold test, occurs across a broad bathymetric range in Jurassic coral. sponge, and microbial reefs. The thickness of its outer test is correlated with illumination and can be used as a relative bathymetric dipstick, provided reef cave dwelling is recognized. (After Schmid, 1995, and Leinfelder *et al.,* 1996, simplified.)

considered earlier as enigmatic, alga-type organisms, but are now in part interpreted as foraminifers (Leinfelder, 1986; Schmid, 1995, 1996; Schmid and Leinfelder, 1996). Some of these, such as the loftusiid foraminifer *Lithocodium aggregatum,* the miliolid foraminifer *Tubiphytes morronensis,* or the enigmatic organism *Bacinella irregularis,* in some cases may actually contribute to binding and construction of reefs, whereas like the other microencrusters (e.g., the enigmatic *Koscinobullina socialis,* bryozoans, serpulids) they are normally just accessory organisms. However, they often are perfect indicators of environmental factors, particularly water depth: *Lithocodium* and *Bacinella* both are restricted to shallow settings; *Girvanella minuta* is frequent in coastal settings; and *Tubiphytes,* though eurybathic, is nevertheless a good indicator (Fig. 10), since the thickness of its outer wall changes with light availability, although low-light but shallow cave settings must be taken into consideration (Schmid, 1996; Leinfelder and Schmid, 2000). Using microencruster associations rather than indicator species, allows for a very refined paleobathymetric interpretation (Fig. 11).

2.3.5. Other Organisms and Infrastructure Jobs

Sponges are assisted in water filtering by an enormous crowd of other organisms. However, it would be beyond the scope of this chapter to discuss them all. Among the most common are pectinid, ostracean, and pteriacean bivalves, serpulids, crinoids, bryozoans, and brachiopods. Deeper sponge mounds also might contain burrowing bivalves, including rare nuculids and pholadomyids, Pparts of which were sediment feeders.

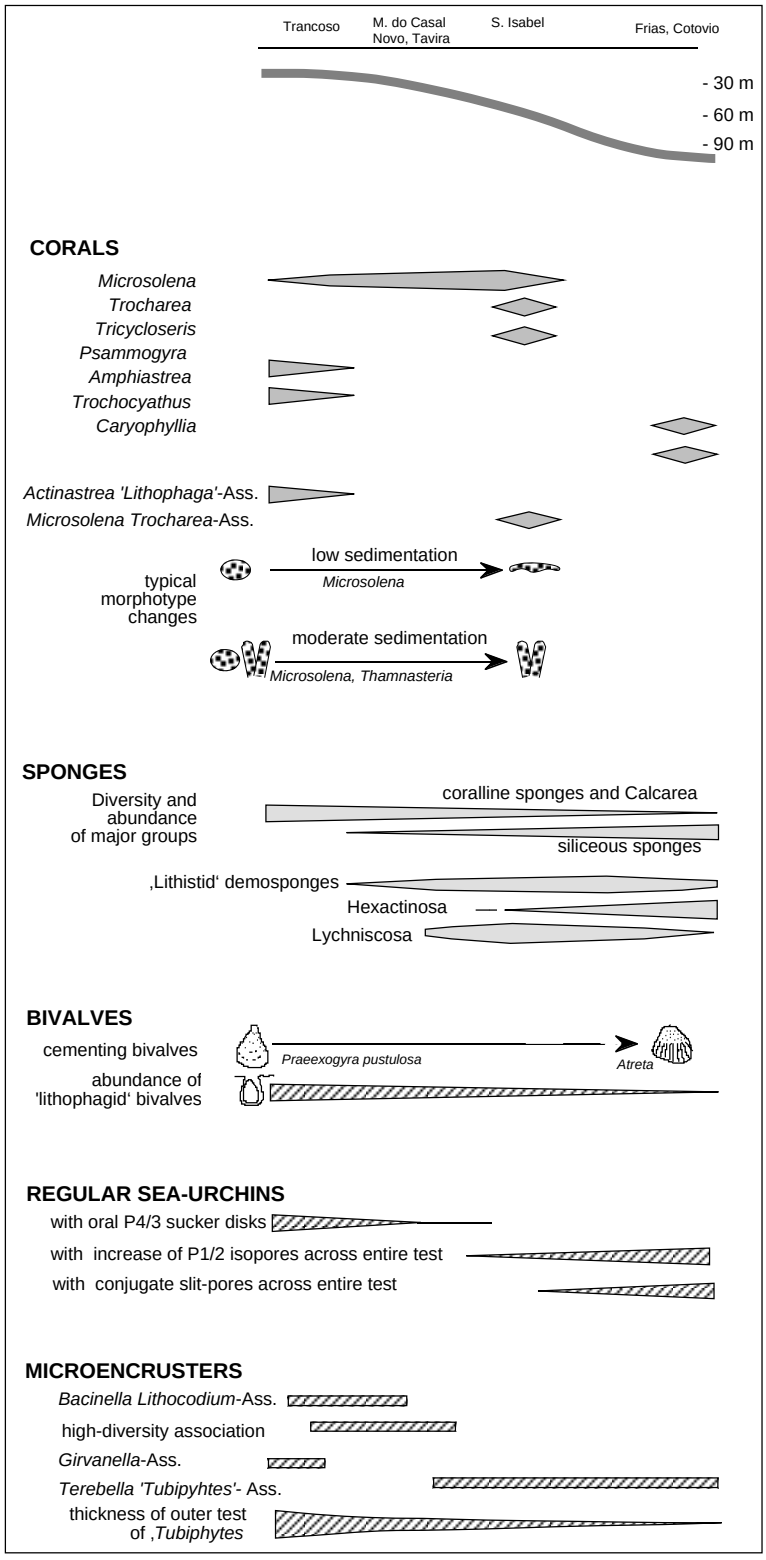


FIGURE 11. Bathymetric distribution and comparative paleoecology of Upper Jurassic reef organisms and associatons from lberia. (Modified and expanded after Leinfelder *et ei.,* 1993a,b, and Werner *et al.,* 1994).

Gastropods, including nerineids, also are widespread, but their life habit is largely unknown. Belemnite and ammonoid taxa, belonging to the predators and possibly scavengers, were frequent in sponge reefs and several taxa definitely lived within the reefs. Crustaceans, many of which belong to the ,,litter recycling brigade", certainly were also frequent in Upper Jurassic reef systems but are rarely preserved. A high number of taxa, however, are known from the Solnhofen, Nusplingen, and other lithographic limestones of southern Germany, which developed in close association with Upper Jurassic coral and sponge reefs. Among the vertebrates are spectacularly preserved organisms of Upper Jurassic reef ecosystems, such as ,,parrot-fish-like" chondrostean *Gyrodus,* which probably fed on valved benthos and corals, as well as sharks and rays, reptiles, and even *Archaeopteryx,* the first bird that lived on island in the Upper Jurassic coral - seas of southern Germany (for recent findings, see, e.g., Röper *et al.,* 1996; Renesto and Viohl, 1997; Dietl *et al.,* 1997). Many of these organisms provide additional clues to the special settings of Jurassic ecosystems. Cementing bivalve taxa change along a water depth gradient (Werner *et al.,* 1994), burrowing bivalves allow for the recognition of soft muds within reef systems, crinoid types may indicate energy levels, and the general abundance of filter feeders and sediment feeders gives insight into the trophic situation. Comparative paleoecological analysis allows evaluation of differences in these patterns. It is very obvious, for example, that the general occurrence of ,,true" (i.e., noncyanobacterial) calcareous algae, such as dasycladaceans, occur in shallow-water coral reef settings rather than in sponge reefs. Additionally, certain taxa of dasycladaceans, foraminifers, nerineids, and ammonoids allow for paleotemperature analysis, biogeographic comparison, or biostratigraphic correlation.

2.4. Controlling Factors of Jurassic Reef Ecosystems: The Comparative Approach

Above I have discussed the role of Jurassic organisms in the reef ecosystem and highlighted some examples where functional autecological interpretation and general considerations about the biology of reef organisms give clues to many environmental parameters. This knowledge is important when interpreting qualitative and quantitative patterns of co-occurrence of organisms. Modern reef settings are best characterized by diagnostic reef associations that particularly reflect water depth and energy levels but also other factors such as nutrient availability or sedimentation rate. This approach is particularly useful in the Atlantic—Caribbean realm where general reef diversity is lower than in the Indopacific and dominance of certain taxa under given environmental parameters is obvious. Examples of useful reef associations are the *Acropora palmata* association, the *Montastrea annularis* association, the *Porites porites* association, or the *A. cervicornis* association, among many others (e.g., Geister, 1983, 1992; Greb *et al.,* 1996), all of which reflect different energy levels and water depths. Slightly elevated background sedimentation

rates can be reflected in different ratios of key taxa abundance, such as *Montastrea cavernosa* versus *Montastrea annularis* (Greb *et al.,* 1996), or in the occurrence of robust associations as, for instance, in the strongly terrigeneously influenced reefs off Brazil (Leão and Ginsburg, 1997).

Although reef associations may appear already distinct in a qualitative manner, it is particularly important to use quantitative or at least semiquantitative criteria on abundance of taxa (whenever possible at the species level) in order to decipher environmental parameters in a reliable fashion. A lot of quantitative and semiquantitative faunal and floral analyses of many Upper Jurassic reefs are now available, besides new qualitative data on reef faunas, with possibly the best examples from Portuguese and Spanish coral reefs (Errenst, 1990a,b; Rosendahl, 1985; Leinfelder, 1986, 1994b; Nose, 1995; Schmid, 1996; Aurell and Bádenas, 1997; Nose and Leinfelder, 1997). A very useful method for comparative studies is the establishment of coral fauna diversities based on the „trophic nucleus“ concept and the Shannon Index (Kauffman and Scott, 1976; Odum, 1983; Werner, 1986). The trophic nucleus is composed of the minimum number of species whose individuals amount to at least 80% of the entire individual number. It is plausible to use volume percent (which can be done by image analysis or by applying volume factors to percentages based on numbers of individuals). Good taxonomic data on the species level also are available from northern Germany (Bertling, 1993). Many new data also are available from the Lorraine and Swiss coral reefs (Insalaco, 1996a; Insalaco *et al.,* 1997), but taxonomic resolution mostly is only on the generic level, except for a few studies (Geister and Lathuiliére, 1991; B. Lathuiliére, personal communication; Laternser, 2000). As for the siliceous sponge facies, the Iberian Upper Jurassic examples are well studied (Leinfelder *et al.,* 1993a; Werner *et al.,* 1994; Krautter, 1995, 1997; M. Krautter, personal communication) down to the species level, and many new results on sponge reefs are available from the French, Swiss, German, Polish, and Rumanian Jurassic (Gaillard, 1983; Herrmann, 1996; Matyszkiewicz, 1996, 1997; Keupp *et al.,* 1996; Koch, 1996; Koch *et al.,* 1994; Pisera, 1997), although distinct sponge associations based on representative populations could only be established occasionally (Werner *et al.,* 1994; Krautter, 1995, 1997).

2.4.1. Paleoecological Gradients and Their Interplay

Leinfelder (1993a) and Leinfelder *et al.* (1993a,b) recognized the strong control of physical environmental parameters on the establishment and composition of Upper Jurassic reefs based on paleoecological, sedimentological, and sequential analysis. They stated that water depth, sedimentation rate, and nutrient-oxygen fluctuations were the dominant controlling mechanisms besides water energy, temperature, substrate, and salinity. They demonstrated (Fig. 12) that reef growth is only possible if background sedimentation drops below a critical threshold, allowing for improvement in diversity and formation of microbial crusts when substantially lowered. This is true for shallow water and deeper shelf reef types, which change along the bathymetrical

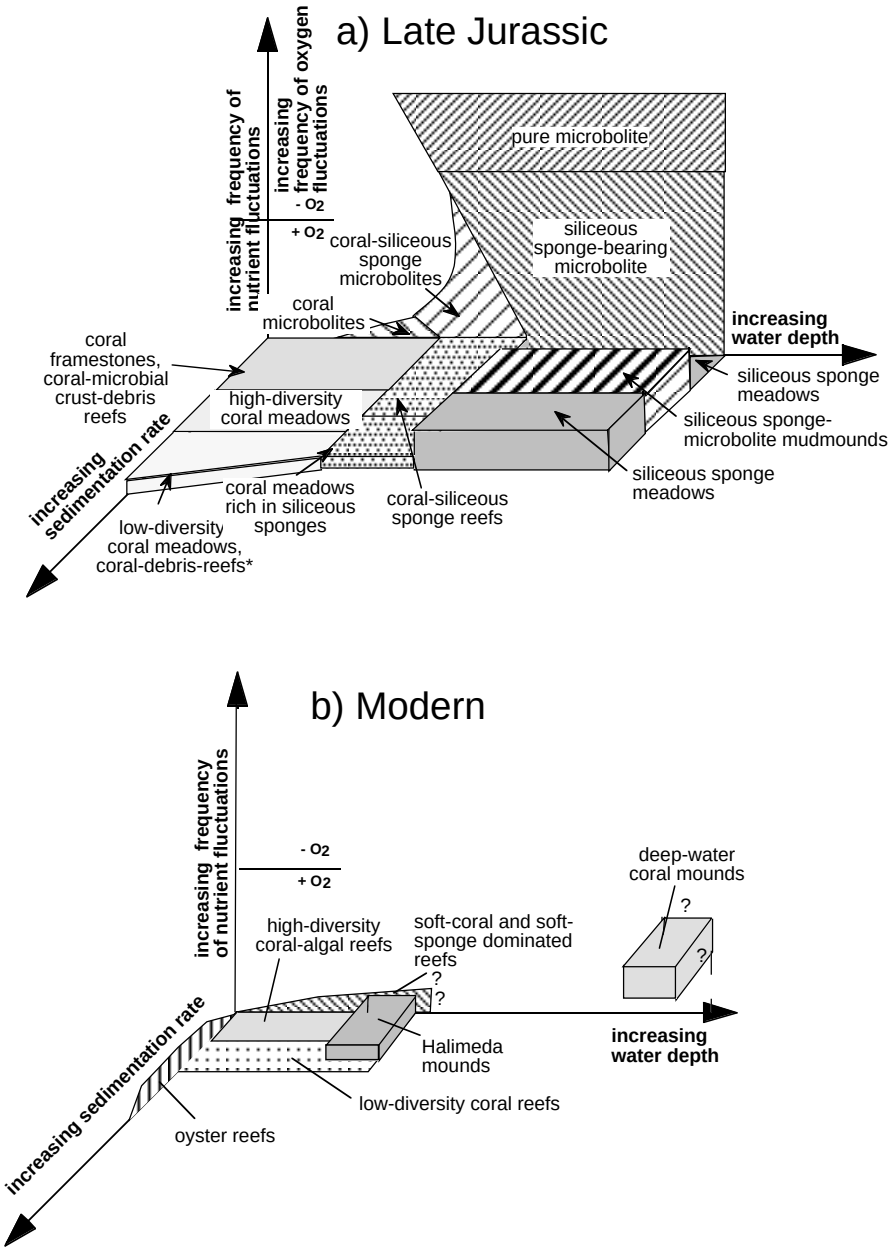


FIGURE 12. (a) The triple factor model of Upper Jurassic reefs in Comparison with (b) a similar tentative model for modern reefs. Differences in background sedimentation rate, bathymetry, nutrients, and oxygen concentrations largely determines the occurrence and composition of Jurassic reefs. Environmental tolerances are much smaller in modern reefs. Note that modern deepwater coral mounds show an offset distribution, appearing in a separate ‚reef window" (cf. 20). See text for further explanation. (Modified after Leinfelder, 1993a, Leinfelder *et al.*, 1996**,** and Leinfelder and Nose, 1999**.).**

gradient from coral associations to mixed coral-siliceous sponge to pure siliceous sponge associations. Bathymetry by itself is no single factor, but relates to a variety of factors such as illumination, abundance of plankton, temperature, and atmospheric pressure. Sedimentation rate not only moderates diversity, but also the development of mudmounds, which need a reduced but noticeable background sedimentation rate for their development. Resedimentation also is the critical factor in high-energy settings, preventing microbolite development unless the physically generated debris material can be exported and internal sedimentation and resedimentation is reduced. One Upper Jurassic coral association was even adapted to reduced salinities, whereas the rest was fully marine (Leinfelder *et al.,* 1996).

Another critical factor is the concentration of nutrients, which often is coupled with terrigeneous background sedimentation. it appears that elevated oligotrophic conditions could be tolerated only by specialized hexactinellid sponges, whereas moderately oligotrophic to slightly mesotrophic conditions were the more favorable settings for most Jurassic reefs. If nutrient concentrations were strongly raised and eventually even accompanied by bottom-water oxygen depletion, growth of macrofauna was possible only during the normal episodes, whereas microbolites could develop in either situation. Depending on the frequency of eutrophication-dysoxygenation pulses, macrofauna was restricted to distinct levels or even was excluded from reef development, so it eventually gave rise to pure microbolite reefs (Fig. 12). This concept was further developed and applied by Leinfelder *et al.* (1994, 1996), Nose (1995), Schmid (1996), and Insalaco *et al.* (1997). Leinfelder and Nose (1999). compared reef windows and general environmental gradients from Jurassic and modern reefs, stating that modern coral reef growth has narrower environmental tolerances than Jurassic coral reefs, owing to increasing specialization of reef organisms and complexity of reef structure (Fig. 12).

Water depth, sedimentation rate, nutrient concentrations, and oxygen values themselves are strongly governed by sea-level state and geotectonic structure. Therefore, the actual position of a given reef within these gradients eventually reflects the geotectonic, paleogeographic, and paleoceanographic setting, which makes reef analysis a powerful tool to decipher the Jurassic regional and global ecology as well as and geotectonic and sequential development (Leinfelder, 1994a).

2.4.2. Control of Ecological Gradients by Sea-Level Fluctuations

A general sequence stratigraphic model has been developed for Jurassic reefs influenced by terrigeneous input (Fig. 13). Reef growth generally occurred in the company of third-order sea-level rises that widely reduced the terrigeneous influx across the shelf. Independent analysis of growth rates for reefs, based on coral and microbolite growth rates (Schmid, 1996), however, revealed that most Iberian reefs did not grow across an entire transgressive third-order cycle but occurred only during additional environmental improvement along with fourth- or fifth-order sea-level rise that eventually opened the

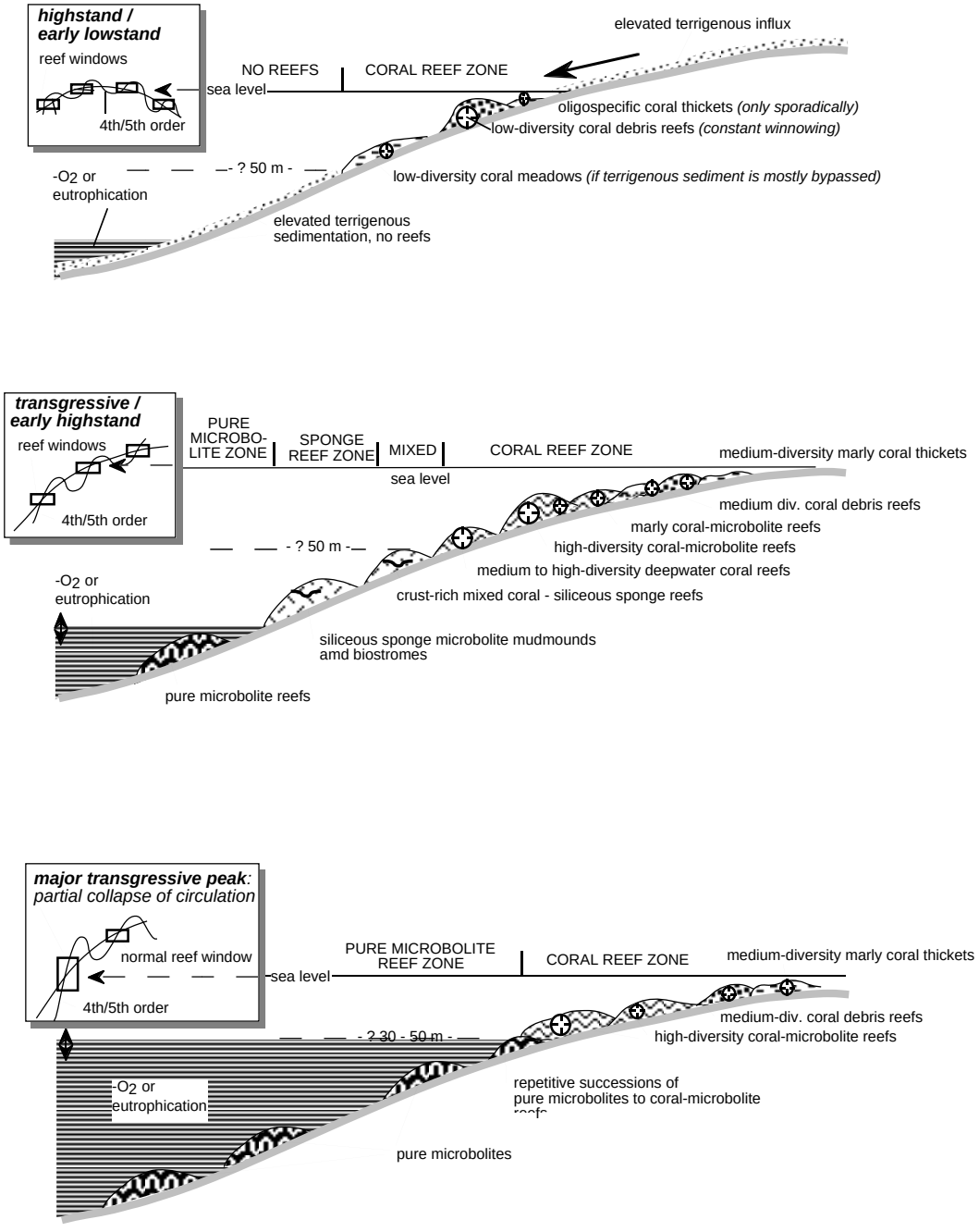


FIGURE 13. Simplified sequence stratigraphic model for Upper Jurassic reefs in terrigeneously influenced settings. During highstand and early lowstand reefs, sedimentation is elevated across the shelf so that reefs may only occur in the constantly wave-washed zone, giving rise to the typical coral-debris reefs. Low-diversity marly coral meadows also may occur sporadically. During sea-level rise, reefs of various types expand widely across the shelf. Due to very reduced sedimentation, reefs often contain a high-diversity fauna and are rich in microbolite crusts, resulting in distinct reef bodies, commonly with pronounced relief. Sea-level rise, however, might also lead to a partial collapse of shelf circulation due to additional climatic equilibration, giving rise to atrophic or oxygen-depleted settings with pure microbolite reefs occurring up to fairly shallow waters. Most reefs grew only during fourth- and fifth-order floodings within a third-order framework.

„reef window“ (Fig. 13). Leinfelder (1993a) and Leinfelder *et al.* (1994) pointed out that in areas distant to siliciclastic hinterland, such as the sponge mudmounds of southern Germany, general reef growth may persist across several third-order cycles but does show lateral waxing and waning correlatable with sea-level fluctuations. This illustrates that variations of background sedimentation due to sea-level oscillations do have pronounced and determining effects of reef growth even in these cases, an example of which is discussed in Section 2.4.4b. Highstand and lowstand reefs are rarer and are either of the constantly winnowed high-energy type or show very impoverished diversities (Fig. 13).

2.4.3. Control of Ecological Gradients by Shelf Configuration

Shelf structure not only determines bathymetry, but influences sedimentation and resedimentation in addition to sea-level fluctuations (Fig. 14). On low-angle ramps, reefs of the high-energy zone have problems exporting the biologically and wave-generated debris that continuously resediments. Reefs

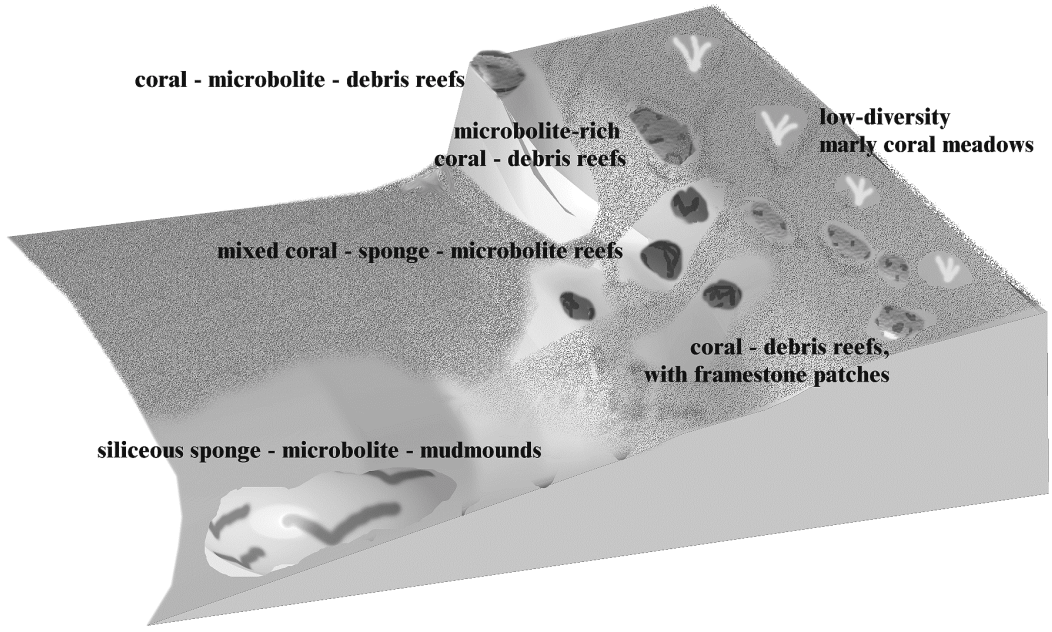


FIGURE 14. Jurassic reef types differ according to different shelf configurations and positions. Some characteristic examples are given. Homoclinal ramps (foreground) show characteristic coral—debris reefs in agitated water and siliceous sponge mounds or biostromes in the lower mid to outer ramp. Steepened ramps and rimmed shelves may suppress sponge mound development in deeper waters because of proximity to mud and sand-exporting. shallow-water carbonate factories. Steepened depositional slopes are the preferred site for crust-rich reefs of moderately deep water, whereas coral—microbolite--debris reefs are indicative of a position in dose proximity to a bypass margin. enabling enhanced gravitational export of surplus calciclastics generated within the reefs.

are therefore crust-free and short-lived, since they normally are suffocated in their own debris. Such reefs must have been among the most widespread but are often overlooked since their relics are taken as allochthonous reef debris of other nonpreserved reefs. Large relics of isolated massive corals or even relics of the original framework are indicative of the existence of the reefs (coral—debris reef type). A good example of a partially preserved reef are some Oxfordian reefs at St. Ursanne, Switzerland (Takacs, unpublished results) or many reefs in lberia, such as reef bodies of the Amaral formation (Nose, 1995).

If a slope break existed, a large proportion of the debris could be exported, giving rise to the development of coral—microbial—debris reefs. These were reefs that grew at slope edge in the constantly wave-washed zone, and hence are rich in fragments of corals and other reef organisms. Contrasting the coral— debris of high-energy ramps, these reefs contain a lot of microbial crusts, stabilizing and cementing the loose, wave-generated material. This was only possible due to facilitated winnowing and gravitational export over a steep depositional or bypass margin so that microbolite crusts could stabilize the remaining material. A case study for this type are the shelf-edge reefs of the narrow Ota platform of central Portugal (Leinfelder, 1992, 1994b), but comparable reefs occur elsewhere (e.g., Schmid and Jonischkeit, 1995).

Export of sediment across a steepened slope prevented the growth of deeper shelf sponge reefs, and it is only at the steep slopes that microbial crust-rich reefs may have developed due to the given bypass possibilities. Consequently, coral-microbial reefs and coral-sponge-microbial reefs are characteristic of very reduced sediment influx, and as such are often indicative of steepened slopes. They may, however, also occur during sea-level rise on homoclinal ramps below the fair weather wave base as a consequence of reduced sedimentation. If on a slope setting, such reefs are accompanied by allochthonous sediments, such as turbidites and debrites, or canyon development. Well-studied examples originate from central and southern Portugal and Spain (Leinfelder *et al.,* 1993a; Nose, 1995; Schmid, 1996; Baumgärtner and Reyle, 1995). The coral-microbolite-debris reef type mentioned above, however, is always diagnostic for steep slopes, even without additional sedimentological criteria, such as allochthonous sediments.

Siliceous sponge mudmounds are largely confined to lower mid to outer, often homoclinal, ramp settings that are distant from shallow-water carbonate factories, because in this position they receive suitable amounts of allochthonous muddy material for their growth. In cases where shallow-water carbonate factories are lacking and terrigeneous sediment also is not imported, no mounds can grow due to both lack of allochthonous material and superoligotrophic conditions, the latter of which prevents the pervasive growth of microbolites (Leinfelder, 1994a; Leinfelder *et al.,* 1996). Under these conditions, low-diversity sponge biostromes with enormous individual numbers may develop (Krautter, 1997; Section 2.4.4c). If influx of carbonate mud is too high for the growth of sponge mounds, sponge biostromes may still develop, which in this case are mud-rich and often contain lower numbers and different siliceous sponge morph types than low-sedimentation biostromes. If

carbonate factories were too near because of steep shelf slopes, neither biostromes nor bioherms could develop.

Given suitable conditions, growth of sponge mounds may be pervasive, such as on the broad shelf sea of southern Germany. Mounds have the tendency to amalgamate vertically, and thus may create strong submarine relief if sponge reef growth is not interrupted by longer periods of sedimentation. During the late Kimmeridgian, mounds with submarine relief of more than 50 m are known (Gwinner, 1976). These gave rise to the punctuated occurrence of coral reefs on the highest mounds. Most of these reefs are of the coral-debris type and the coral-microbolite-debris type (unpublished results, cf. Paulsen, 1964). In this example, the homoclinal, nearly level-bottom initial outer ramp configuration was suitable for extensive growth of sponge-microbial mudmounds from the Late Oxfordian onward, which in turn changed the configuration of the shelf, and hence the controlling factors of reef growth, such as bathymetry, water energy, and sedimentation-resedimentation patterns. Similar, partially intrinsic change of reef composition and accompanying controlling factors occurred on the wide and shallow, coral-dominated Oxfordian shelf of eastern France. Here, shallowing was accompanied by reduction in terrigeneous influx which allowed for the establishment of uniform microsolenid associations substituting for each other before autodifferentiation of communities changed the entire setting (unpublished results, cf. Geister and Lathuilière, 1991; Insalaco *et al.*, 1997).

2.4.4. The Interplay of Control Mechanisms: Selected Examples

A few examples should illustrate the interplay of processes and models outlined above.

2.4.4a. Example 1. *Bathymetry and sedimentation rates as major controllers of coral associations from the central Lusitanian Basin, Portugal.* Figure 15 shows the principal coral associations from the Kimmeridgian of the central Lusitanian Basin, which were analyzed in a semiquantitative to quantitative manner using image analysis and counts-per-area data. The reefs occur at different positions within a generally prograding succession shallowing upward from basinal and prodelta marls and clays with intercalated turbiditic sandstones to inner ramp oolitic and coraliferous carbonates (Nose, 1995). Seismic data support the interpretation of a prograding slope system and give additional bathymetric control (Leinfelder and Wilson, 1989). Similar to modern Caribbean associations these reef associations can be arranged along a bathymetric gradient using dominant coral morphologies, microencruster associations, and depth-diagnostic cementing bivalve taxa, as well as the position of associations within a shallowing upward succession and their lateral interfingering with high- or low-energy sediments (oolitic and bioclastic grainstones vs. lime wackestones and clayey muds). The deepest coral associations are dominated by platy microsolenid corals and already show a high proportion of lithistid sponges. Figure 15, however, also shows that although

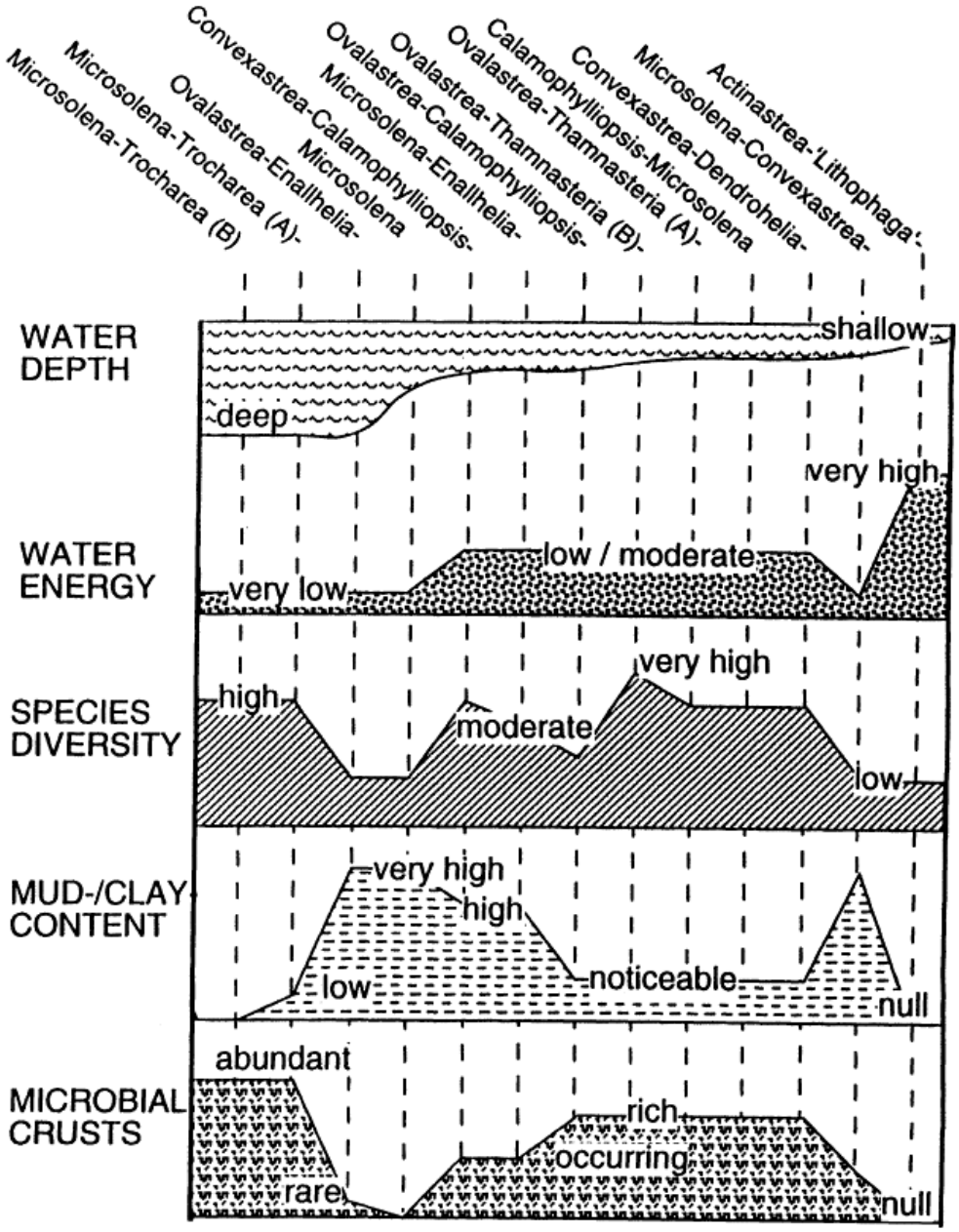


FIGURE 15. Coral associations of Portugal change along a bathymetric gradient. Relative bathymetric calibration and interpretation of water energy is possible by occurrence of reef associations within shallowing-upward succession, by sedimentological features, by morphotype interpretation of diagnostic corals, and by associated fauna (compare with 11). Note that species diversity does not change uniformly along with bathymetry, but mostly is negatively correlated with terrigeneous clay content in the ground mass and positively correlated with the amount of microbial crusts, pointing to sedimentation rate as the major modifier of diversity. Highest diversities occur, however, in associations with a low but noticeable clay content, indicating the importance of nutrient availability for Jurassic reef corals (see text for further explanation). (After Nose, 1995, and Nose and Leinfelder, 1997**,** modified.)

coral associations are easily lined up along a bathymetric trend, diversities are highly variable, with high diversities being found not only in shallow but also in deeper settings. The presented example shows that high diversities correlate well with a high amount of microbolite in the reefs and a reduced amount of sedimentary material which indicates strongly reduced sedimentation. It also shows that a very reduced and probably intermittent influx of terrigeneous clay correlates with especially high diversities, which is an expression of the preference for lower mesotrophic settings in Upper Jurassic coral associations. On a smaller scale, however, shallowing is not fully unidirectional but punctuated by flooding surfaces and short-term regressions, allowing interpretation of reef growth in a sequence stratigraphic context (Leinfelder, 1993b; Nose, 1995; Leinfelder and Wilson, 1998). Reefs mostly grew during third- and fourth-order transgressions but could occasionally persist during highstand or early lowstand, though in different composition (see Fig. 13).

Characteristics of transgressive coral reefs are:

- Widely developed across the shelf, dominating the sedimentation.
- Pure carbonate.
- Rich in microbial crusts, demonstrating low background sedimentation.
- High species diversity, low dominance.
- Mostly of the low-energy type.

Features of highstand and early lowstand coral reefs are:

- Generally rare, with only punctuated occurrence.
- Mostly of low diversity, microbolite free types, often with a clayey or silty groundmass.
- Crust-free debris type reefs in the constantly wave-washed zone.

2.4.4b. Example 2. *Shelf-configuration and sea-level-driven variability of sedimentation rates as motor for the development of major sponge mound complexes:* The Oxfordian *Gosheim reef of Southwestern Germany.* In a simplified manner, Upper Jurassic siliceous sponge mounds are composed chiefly of microbial crusts, carbonate muds, and siliceous sponges in various proportions. Other fauna occurs in variable proportions and allows for bathymetric evaluation (Fig. 16**).** From the late Oxfordian to the early Tithonian time, southern Germany was characterized by particularly intense sponge mudmound formation. This is due to the fact that allochthonous sedimentation derived from shallow-water carbonate factories to the north, east, and northwest was low enough to allow mound formation. In the Swiss Jurassic and particularly the south Portuguese Algarve Basin, carbonate factories were much closer to the suitable depth provinces of the outer ramp due to the steepened character of the ramps, which did not or only occasionally allow for mound formation. On the other hand, a certain amount of allochthonous calcareous muds were necessary to helping a mound accumulate (Leinfelder and Keupp, 1995).

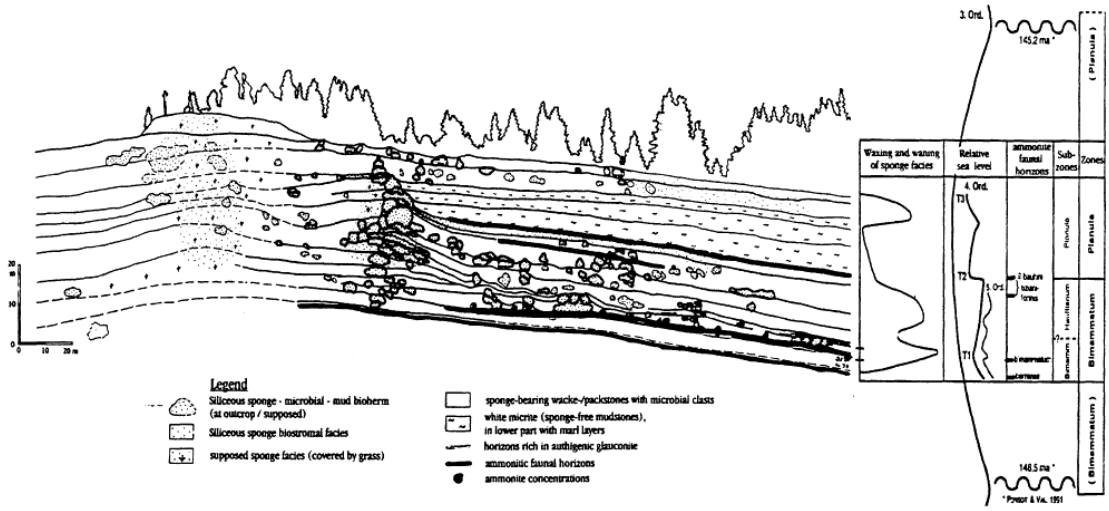


FIGURE 16. Architecture and sequential interpretation of a major composite—siliceous sponge—microbolite mudmound complex of the western Swabian Alb, southern Germany. Growth of the entire complex is related to reduction of sediment influx during a third-order sea-level rise. Episodes of lateral expansion of the composite complex are correlative with fourth- and fifth-order floodings. The (late?) highstand of T3 stopped the growth of the entire complex due to raised import of allochthonous calcarous mud from shallow-water carbonate factories. See text for details.

(Note Figure is originally in landscape format, it was turned here 90° for better readability of this online-copy)

In southern Germany many mounds thicker than about 10 m are intensely recrystallized, dolomitized, or dedolomitized, and hence do not show any clues as to their exact origin. Oxfordian mounds are generally better preserved, which is probably due to the fact that intermittent clayey terrigeneous sedimentation prevented later diagenetic neomorphosis. The Oxfordian mound structure at Gosheim, western Swabian Alb, is remarkable in various ways. It is one of the few mounds where base, top and lateral margins are all observed in outcrop. It shows all internal architectural and sedimentological features and is constrained by a high-resolution ammonite stratigraphic framework. Figure 16 shows the prominent features of the mound. The mound is a composite structure composed of clustered and amalgamated small bioherms of meter-size. The bioherms are very rich in thrombolitic microbial crust (in some cases up to 80%) and contain dense micrite and siliceous sponges in variable amounts. Siliceous sponges are composed of a fairly high-diversity fauna, with 88% of the sponges belonging to the Hexactinellida and only **12%** to the lithistid demosponges, which may reflect both a fairly deep setting and frequent though reduced background sedimentation. All shapes and sizes of sponge morphologies occur, with tube-, vase-, and dish-shaped sponges measuring up to **2** m in diameter or height. Accompanying fauna is rich as welt, with occasional burrowing bivalves, which indicate soft grounds. Hard substrates, particularly the microbial crusts, were inhabited by microencrusters of the *Tubiphytes* association, including large terebellid worm tubes, and by a great variety of brachiopods and epibenthic, mostly pectinid, bivalves. Belemnites and ammonoids are frequent but often enriched to several levels, with some small forms such as *Glochiceras* certainly representing bottomrelated mound dwellers.

The lateral extension of the entire mound structure reaches its maximum at its base, giving the entire mound grossly a pyramidal shape with a basal lateral extension of about 200 m and a height of nearly 50 m (Fig. 16). The basal mounds are arranged in a string-of-pearl fashion, positioned directly above a bed rich in ammonoids, belemnites, oxydized pyrite nodules, authigenic glauconite, and *Chondrites* burrows, which provide evidence of the cessation of sedimentation and possibly even slight oxygen depletion, at least in the topmost seafloor. The basal muds are particularly rich in microbolite crusts and the largest sponges of the entire complex also appear in this level, evidencing favorable conditions over at least many hundreds to thousands of years. Following this basal megabiostrome, composed of individual small bioherms, mound development was restricted to a narrow area to again expand laterally several times. Figure 16 shows that the fractal pattern of mound development is caused by the superposition of sea-level cycles of different magnitude, which modulated sediment influx. The entire structure can be referred to a third-order sea-level rise and it actually correlates with the transgressive system tract of the Ponsot and Vail (1991) depositional system between 146.5 Ma and 145.2 Ma. Based on the Leinfelder and Keupp (1995) model this transgression both reduced terrigeneous influx as well as carbonate mud export from the remote shallow-water carbonate factory, which increased

again during highstand, causing burial of the mound structure by allochthonous carbonate muds (highstand shedding). This correlation suggests that the Oxfordian deep shelf sediments were largely of allochthonous origin rather than representing hemipelagic planktic ooze. Actually, relics of coccoliths are extremely rare, which possibly does not represent preservational bias. Establishment as well as pulses of lateral expansion of the mound structures correlate with ammonoid concentrations and formation of authigenic glauconite relatable to fourth- and higher-order flooding events.

The Gosheim mound thus is a key example for analyzing the origin of Jurassic sponge-rich mudmounds. It highlights the importance of strongly reduced but noticeable intermittent influx of allochthonous sedimentation. There was no obvious structural control. This also appears true for most if not all other sponge mounds in southern Germany. The lateral interfingering with bedded muddy limestones is evidence of the composite character of the mound that despite its cumulative height of about 50 m never rose above the seafloor more than a couple of meters. A composite analysis of biostratigraphic data, maturity analysis of authigenic glauconites, and independent growth rate measurements of microbolites from measurable coral reefs indicates that mound growth was around 1 mm/year, but preservation potential was only 15 to 20%.

2.4.4c. Example 3. *Low-diversity sponge biostromes as indicators of starved oligotrophic shelves.* In eastern Spain, more than 70,000 km^2 is covered by a unique and extremely uniform association of siliceous sponges of Mid-Oxfordian age. This association was recently described in detail by Krautter (1995, 1997). The laterally extensive biostromal unit is only a couple of meters thick but nevertheless spans several ammonite zones (maximum cordatum to planula zone, hence six ammonite zones). Except for a very few exceptions no relief is formed and the unit is composed almost solely of dish-shaped sponges comprising up to 90% of rock volume. Despite astronomical individual numbers, the fauna is of low diversity. Ninety percent of the fauna are represented by hexactinosan sponges comprising 24 species. Nearly all these species are known from other sponge reef localities, but the accompanying taxa are missing and three genera strongly dominate. Eighty percent of all sponges are of the dish shape. The rarity of encrusting organisms on sponges, such as serpulids, bryozoans, or oysters, is remarkable, although these forms occur sporadically. The only other elements worth mentioning are terebratulid bryozoans and the regular echinoid *Rhabdocidaris rhodani,* which is indicative of diminished oxygen availability. Similarly, levels of *Chondrites* burrows also indicate that sediment was occasionally depleted in oxygen. Judging from the long time span involved and the frequent iron oxide crusts with hardgrounds, no background sedimentation existed. Interestingly, microbolitic bioherms did not develop, although microbolitic crusts occur as thin layers. The peculiar sponge fauna of this reef was adapted to very oligotrophic conditions that relate to the lack of terrigeneous influx. Lack of nutrients kept microbolite development at a low pace, and together with the lack of allochthonous sedimentation helps explain why bioherms did not develop.

2.4.4d. Example 4. *Oceanographic changes during the hypselocyclum-divisum transgression.* One of the most puzzling features of Upper Jurassic reef development is the development of pure microbolite reefs related to eutrophication and/or oxygen depletion (see Section 2.4.1). Many of these reefs have been described in detail elsewhere (Leinfelder *et al.,* 1993a,b; Nose, 1995; Schmid, 1996). Coral and sponge reefs can be very rich in microbial crust, which here is not considered a pure microbolite reef because macroorganisms and microbolite crusts strongly interfinger. However, there are reefs composed nearly completely of pure thrombolitic microbolite or of a reef structure with upward alternation of pure microbolite and coral-microbolite. Above it was stated that pure microbolite development might be due to a variety of nonbiological factors, such as increased or decreased salinity or intertidal position. We focus here only on examples where such mechanisms can be excluded and where criteria for oxygen depletion, such as clusters of dysaerobic epibenthic bivalves, authigenic glauconite, framboidal pyrite, or secondary gypsum are available. The most interesting episode was that of the late Hypselocyclum-early Divisum zones. Here such reefs developed widely in Iberia and correlate elsewhere with other peculiar reefs. This time was characterized by a strong transgression (Haq *et al.,* 1988; Hantzpergue, 1988; Ponsot and Vail, 1991; Leinfelder, 1993b) promoting vigorous reef growth, despite the fact that in many areas the Lower Kimmeridgian and early Upper Kimmeridgian stages were dominated by terrigeneous deposits. However, many Iberian shelf sections do not show normal trends for reefs like during the major Oxfordian or late Kimmeridgian transgressions. Shallow water coral reefs were not accompanied by deeper-water sponge mounds but rather by pure microbolites. The pure microbolites occasionally exhibit thin horizons of siliceous sponges. These microbolites occurred both in considerably deep waters as well as in moderately deep slope settings. The clusters of meter-scaled club-shaped microbolites at Cotovio (Oxfordian) or the 30-m thick Lower Kimmeridgian Rocha thrombolitic of southeastern Portugal (Fig. 17d) are good examples (Leinfelder *et al.,* 1993a). However, even coral reef growth in some examples became interrupted by pure microbolite growth showing characteristics of oxygen depletion. Examples are the Tormon reef of eastern Spain (Fig. 17a) or the Serra Isabel reefs of central Portugal (Fig. 17c) (Leinfelder *et al.,* 1993a,b; Werner *et al.,* 1994). Outside Iberia, reefs also may show peculiarities during this time interval of the late Early Kimmeridgian (Hypselocyclum-Divisum chrons). Coeval coral-microbolite reefs at La Rochelle, which recently were studied by Taylor and Palmer (1994), Schmid (1996), and Werner (personal communication), grew in slightly deeper water, as evidenced by the microencruster association. The microbolite development is unusually thick and largely substitutes coral growth in the late stages of reef growth, which together with a high individual number of nutrient-loving epifauna (serpulids, large oysters) hints at fairly elevated nutrient availability, although dysaerobic pulses are not directly documented here (Fig. 17b). In southwestern Germany, the same transgression gave rise to the partial interruption of terrigeneous sedimentation and to the development of peculiar

small sponge-brachiopod reefs known as ,,lacunosa-Stotzen.“ Hexactinellid dominance and microencrusters indicate that these reefs certainly were positioned in waters not shallower than about 60 to 80 m, but nutrient increase might be indicated by the dominance of rhynchonellid brachiopods.

Since the bathymetry of these reefs can be assessed by the faunal characteristics of the oxic parts of reef development, the minimum position of a nutricline, which at least in Iberia was associated with an oxycline, can be roughly outlined (Fig. 18). It was strongly fluctuating but reached waters as shallow as about 30 m in central Portugal, 40 m in southwestern France, 60 m in southern Portugal, and possibly 80 m in southwestern Germany. However, such shallowness of the nutricline was largely restricted to the Hypselocyclum-Divisum transgression and is evidence of strong reduction in ocean water circulation which might be an effect of the climatic equilibration of a strongly rising sea level (Leinfelder, 1994a).

2.4.4e. Other Examples. *Reefs as indicators of basin structure und tectonic activity.* There are many other studied examples demonstrating the role of the general tectonic and paleogeographic setting on reef development. The Lusitanian Basin of Portugal provides many examples were reefs are indicative of basin configuration, tectonic setting, water circulation, and sea-level development. Among the examples are reef growth within siliciclastic fan deltas shed into strike-slip basins as indicators of tectonic quiescence, platform development as indicators of rising salt pillows, and patterns of contemporaneous reef and siliciclastic sedimentation indicative of longshore current systems (Leinfelder, 1994b, 1997). Examples from France, Switzerland, and Germany are in preparation for publication.

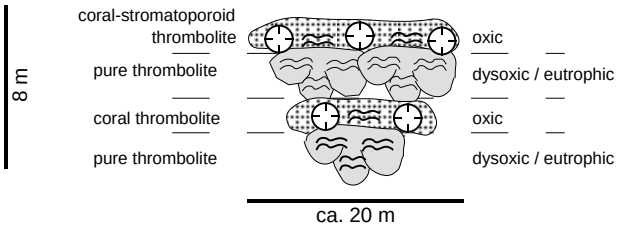
3. Intrajurassic Reef Development: Faunistic Evolution or Environmental Change?

Leinfelder (1994a) discussed the temporal evolution of reefs throughout the Jurassic period and stressed the fact that the abundance of reefs generally has increased with time, although there exist considerable differences in the trend between sponge and coral reefs and differences between the northern and southern Tethys shelf. Based on this compilation and some new data, a brief summary is given here.

3.1. Evolutionary Aspects of Reef Organisms

Siliceous sponge associations and siliceous sponge reefs are known from all three epochs of the Jurassic. On the northern Tethyan shelf, they strongly increase in abundance during the Mid- and Late Jurassic time, whereas on the southern Tethyan shelf, they occurred more widely during Early Jurassic time. With the exception of the lychniskid sponges, known since the later part of

a) Coral thrombolite at Tormón, Celtiberian Basin, eastern Spain



b) Typical coral-microbolite reef at La Rochelle, sw. France

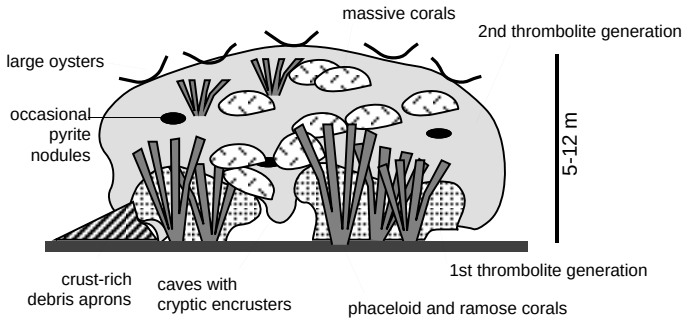
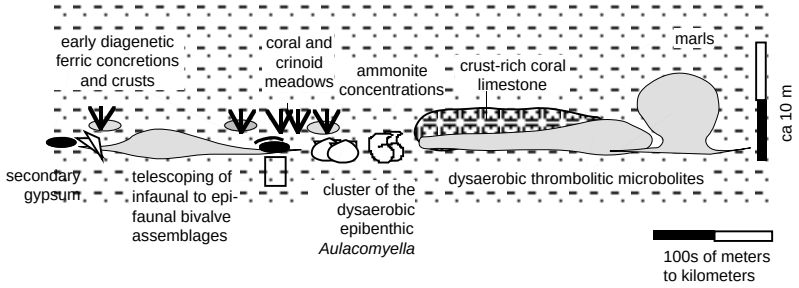


FIGURE 17. Examples of microbolite reefs from the late Early Jurassic (Hypselocyclum—Divisum chron) of southwestern Europe. (a) Repetitive succession of coral—microbolite to pure microbolite reef growth. (b) Coral reef with upward, outward, and downward increasing participation of microbolite crusts. (c) Lateral variability of a condensed level, partly with telescoped successions of dysaerobic and oxygenated reef facies. (d) Thick complex of largely pure microbolite. Siliceous sponges may occur but are refined to distinct leveis.

Mid-Jurassic time, all other groups of these ultraconservative organisms existed prior to the Jurassic (Mehl, 1992). Although exact numbers of taxa are not available to date, the occurrence of lower Jurassic siliceous sponge mounds demonstrates that the general possibility of sponge reef formation existed throughout the entire Jurassic period. A certain evolutionary increase of sponge taxa therefore was caused by increasing availability of sponge reef habitats rather than vicce versa.

Corals suffered a severe extinction at the Triassic-Jurassic boundary (see Chapter 7, this volume), and therefore are extremely rare in the early part of the Early Jurassic. Elmi (1987) mentions a small coral reef occurrence of

c) Lateral variability of the Serra Isabel unit, Lusitanian Basin, central Portugal



d) The Rocha microbolite reef, eastern Algarve, Portugal

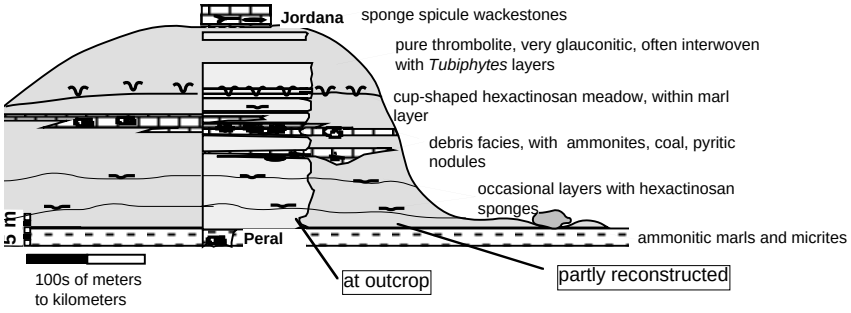


FIGURE 17. *Continued*

Hettangian age in France, but it is still awaiting closer inspection. Besides this enigmatic Hettangian example, earliest coral reef occurrences are from the Sinemurian and are all situated on exotic terranes later accreted to the western margin of North America (Stanley and McRoberts, 1993), which was interpreted by Stanley and Beauvais (1994) and Stanley (1996) as an expression of long-term isolation of corals, surviving from Triassic time, while inhabiting exotic islands of the paleo-Pacific. From the Pliensbachian and particularly Toarcian onward, coral reefs became more frequent and it is since that time that available coral taxa were sufficient to form variable types of coral reefs. Numbers of generic taxa, as compiled from the literature (references in Leinfelder, 1994a), yield about 60 genera for the Early Jurassic with all important major groups still existing. About 100 genera were available during the Mid-Jurassic with about 130 genera in the Late Jurassic (data from various sources, compiled in Leinfelder, 1994a). Despite the fact that Jurassic corals

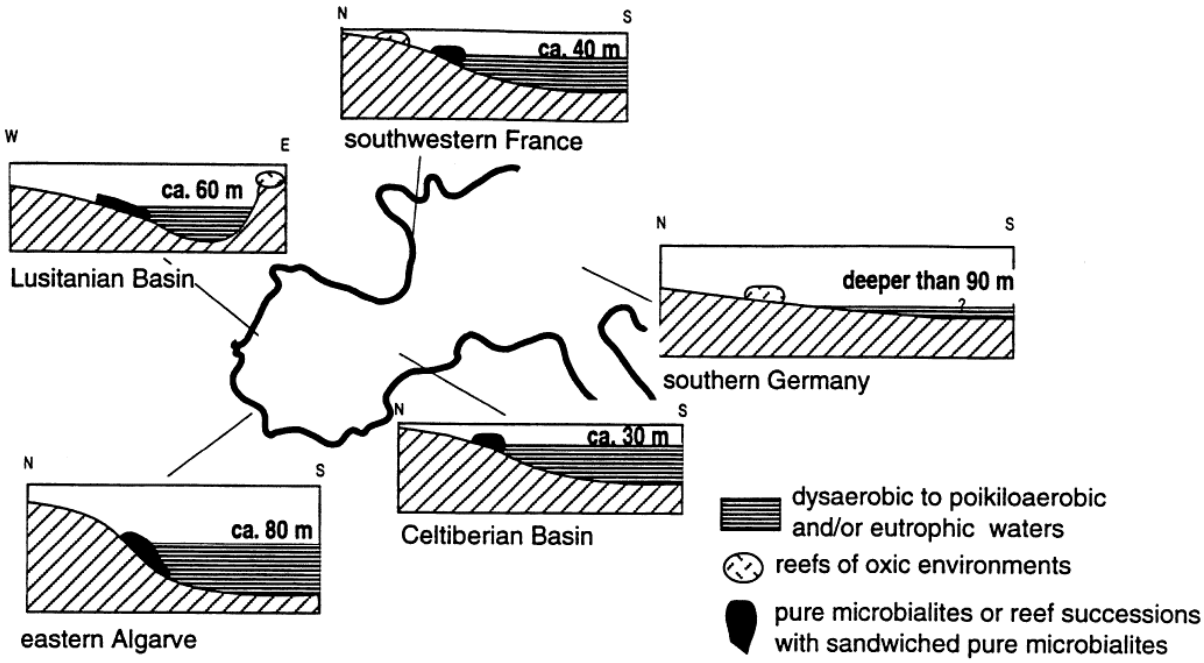


FIGURE 18. The contemporaneous reefs shown in Fig. 17 are interpreted as reflecting eutrophication pulses that were frequently accompanied by oxygen depletion. Aerobic parts of the reefs allowed for bathymetric interpretation and depth mapping of a nutricline-oxycline that occasionally were as shallow as 30 to 40 m in same examples.

(Note Figure is originally in landscape format, it was turned here 90° for better readability of this online-copy)

urgently need taxonomic revision, it is obvious again that the increase in coral reef abundance need not necessarily be due to an adaptive radiation of corals. Nevertheless, the coral fauna diversified and the development of specialized taxa such as very morphovariable species or brackish water specialists allowed for the conquest of previously hostile environments, and this was a positive evolutionary feedback on the size of the ,,reef window“ (see Section 4).

3.2. Sea-Level Development

The expansion of sponge reefs and coral reefs on the northern Tethys shelf correlates considerably well with general sea-level rise (Fig. 19). During Early Jurassic time there was considerable terrigeneous influx of clastics, permitting reef growth only in more or less protected, wide platform areas such as central Portugal (new discovery of sponge facies: Duarte and Krautter, 1998) and southern France (coral reefs). Southern Germany still was dominated by terrigeneous sediments derived from the Vindelician basement uplift and this prevented reef growth. Sea level kept rising well into Late Jurassic time, increasingly improving the environmental conditions suitable for the growth of both coral and sponge reefs by further reducing terrigeneous influx. Only during Late Jurassic time were the shelf areas flooded widely enough to provide suitable carbonate-dominated outer ramp settings on a large scale, where siliceous sponge mounds would develop in a more than 7000 km wide belt extending from Rumania to Texas. Productivity of these carbonate shelves was higher than the increase of accommodation by the general sea-level rise so that a generally shallowing succession developed. The peak of reef formation during the Oxfordian did not coincide with the peak in sea-level rise that occurred later, at the Kimmeridgian—Tithonian boundary (Haq *et al.,* 1988). The relative retreat of reefs already during the Kimmeridgian was caused by tectonic reactivation. Rift tectonics in the northern Atlantic graben systems also resulted in renewed terrigeneous sedimentation and uplifts elsewhere. However, this tectonically and possibly climatically induced general retreat of reefs was punctuated by flooding events of higher order. In many areas, these short-termed events brought back episodical reef growth, particularly during the Hypselocyclum—Divisum, Eudoxus, and Beckeri chrons.

3.3.Tectonic Control

Reef developrnent along the northern Tethys shelf was strongly contrasted by the pattern of reef growth on the southern Tethys shelf, which cannot be correlated with the general sea-level development. Reefs are much rarer, which is particularly true of the Late Jurassic, at least for the western part of the Tethys. During the Early Jurassic, ramps or enechelon grabens still existed yet were rare (Stanley, 1988). They provided environments for coral and sponge reef development on the shallow and deeper shelf. Tectonic but not

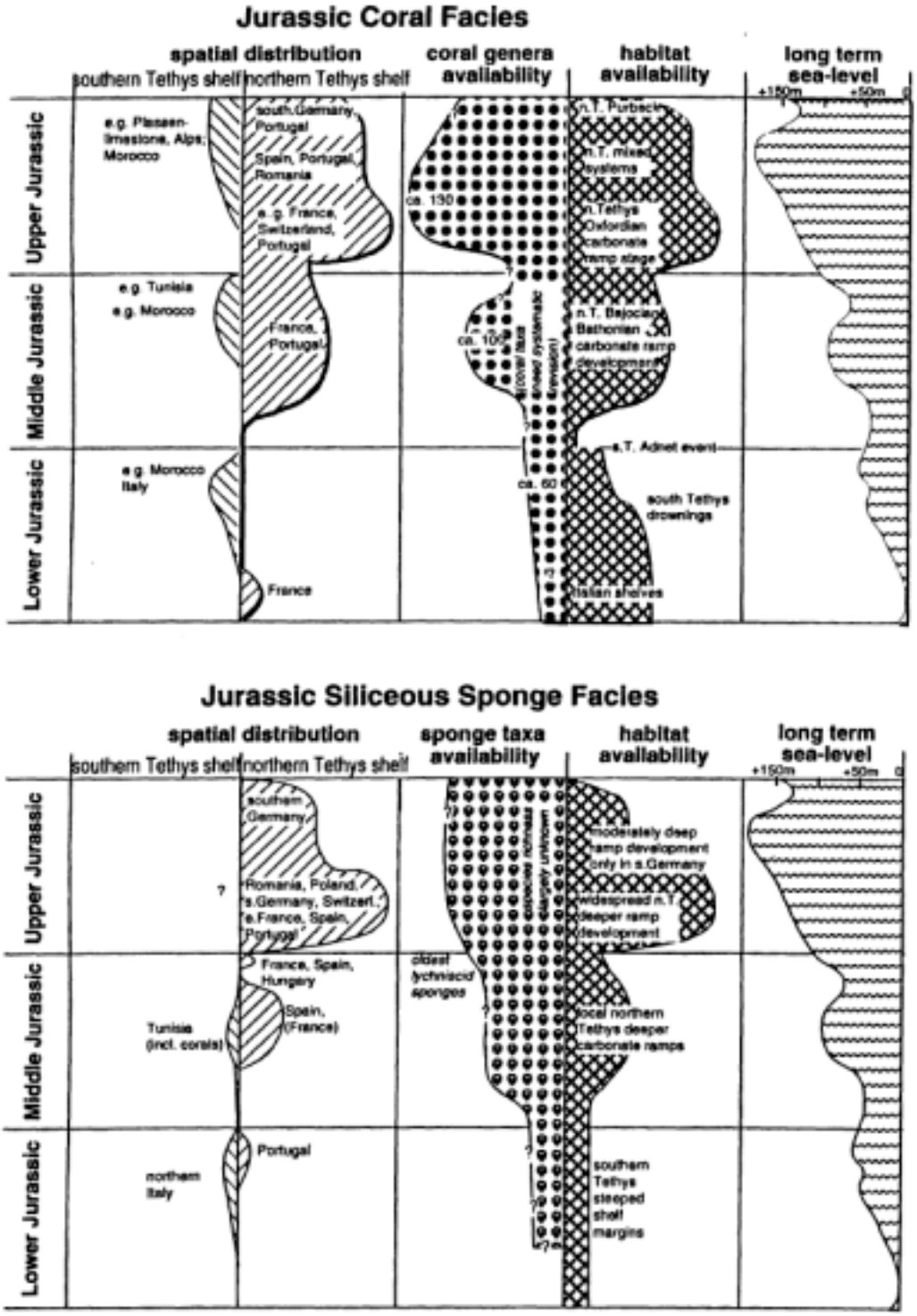


FIGURE 19. Distribution of Jurassic coral and sponge reefs at both margins of the Tethys. Along the northern Tethys shelf, increasing proliferation of reefs is related largely to the raising sea level, whereas along the southern Tethys shelf, the tectonic style of the shelf determines distribution and frequency of reefs. See text for details. (After Leinfelder, 1994a, modified.)

contemporaneous drowning of many of these areas made these potential reef habitats disappear during the Early and Mid-Jurassic. Only at the margins of rare, steeply bound, probably transpressional horst structures could coral reefs occasionally grow still during the Late Jurassic (e.g. Plassen limestone and Italian examples, for references see Section 2.1). Hence, tectonic influence on reef development and reef distribution is particularly obvious on the southern Tethys shelf, but also in the Lusitanian Basin of central Portugal which is an Atlantic rift basin (Wilson *et al.*, 1989). Another interesting feature is that Upper Jurassic coral reefs of the southern Tethys shelf appear to exhibit much less microbolite crusts and only moderate to low diversities, although detailed studies are necessary to prove this qualitative impression. If true, this might be due to strongly oligotrophic conditions, which during the Jurassic did not yet allow maximum diversities (see Section 2.3.1).

4. Conclusions

Starting from a limited stock of surviving reef fauna after the Triassic/ Jurassic mass extinction, Jurassic reefs became increasingly numerous during the course of the Jurassic, and reefs from the Late Jurassic represent one of the major peaks in reef evolution in Earth history. Jurassic reefs were not yet as specialized as modern reefs for highly oligotrophic settings but instead covered a broad array of reefal environments, ranging from shallow, high-energy down to several hundred meters depth, from zero sedimentation to considerably elevated sedimentation rates, from fully marine to brackish, and from mildly oligotrophic to eutrophic and even dysaerobic. However, these very different settings were not occupied by one single reef type, but were characterized by very different reef types, with end member groups consisting of coral reefs, siliceous sponge reefs, and pure microbolite reefs. The many reef types and subtypes were not only statically related to the existence of distinct environments, but could also respond, and to some degree adapt themselves, to environmental change. Besides sedimentological analysis, it is, specifically, the interpretation of physiological abilities of Jurassic reef organisms by constructional morphologic analysis and semiquantitative to quantitative assessments of the trophic and diversity structure of reef associations which allows such conclusions.

This makes Jurassic reefs a most valuable tool for paleoenvironmental, including paleoclimatic, paleooceanographic, sea-level as well as paleostructural analysis. A particular feature in Jurassic reef analysis is the possibility of detecting eutrophic and dysaerobic episodes from development of pure microbolites in regimes of strongly reduced sedimentation, which normally prevents development of black shales. Lateral arrangement of coeval, but different reef types allows for interpretation of general shelf type as well as small-scale differences of submarine morphology. The development of classical sponge mounds was particularly characteristic for homoclinal outer ramps, whereas

coral-siliceous sponge—microbolite reefs may be characteristic for steepened slopes. Reefs of the coral—debris type are largely restricted to fiat ramps or at the shallow shelf break of mildly inclined depositional margins. These debris-pile reefs express problems with the large amounts of calciclastic material produced by wave action and bioerosion (Leinfelder, 1992). This makes them perfect targets for oil exploration provided primary porosity is partially preserved or secondary vuggy leaching porosity developed. If developing along a shelf break in direct proximity of a steep bypass margin, high-energy coral-debris reefs can export large amounts of generated calciclastic material, which enables microbial mats to stabilize the remainder of the debris. This gives rise to easily recognizable coral—microbolite—debris reefs (Leinfelder, 1992).

An important theme is the restriction or proliferation of reefs during sea-level change. Major reef episodes are correlated with third-order rises and highstands, but individual reefs normally grew during forth, fifth, or even higher order. This is particularly true of coral reefs on terrigeneously influenced ramps. Sponge mounds may show composite, cluster-type architecture, with individual, stacked reef bodies also being related to fourth- and fifth-order fioodings or early highstands.

In comparing the structure of modern and Jurassic reefs, similarities and differences exist. The calcareous siliceous sponge—microbolite mudmounds of Jurassic time to the present knowledge are unparalleled by modern analogues, although some siliciclastic cold-water sponge—microbial mats or mounds and some tropical deep-water lithistid associations share certain similarities. Within the Jurassic sponge facies, a wide variety of types and settings occurred. Environmental parameters for these reefs are resolved by a combined approach of paleoecological and sedimentological analysis. The controversial bathymetry of Jurassic siliceous sponge reefs is partly caused by the lack of differentiating sponge reef types. Lithistid-dominated reefs were generally but not necessarily more shallow than hexactinellid-dominated reefs. Siliceous sponge reefs can be transitional with the lower part of the coral reef zone, but are normally below the coral reef zone and possibly deeper than about 50 m. The lower distribution boundary of hexactinosan reefs might well be down to more than 100 m, with the lower limit probably defined by the existence of oxygen-depleted bottom waters or sediment accumulations. The wide distribution of Upper Jurassic sponge reefs especially along the northern Tethys shelf seas is a reflection of the high sea level. Modern shelves are rugged in the preferred depth zone of Jurassic sponge reef growth, due to glacial sea-level fluctuations that make the environment too variable for the development of sponge mounds. Also, the low sea-level of today causes stronger terrigeneous influx, which may bypass shallow-water coral reefs but may suppress reef growth in the deeper water.

Coral reefs and pure microbolite reefs existed both during the Jurassic and today. Just like their Jurassic counterparts, modern microbolite reefs are restricted to extreme settings, such as hypersaline, intertidal, or freshwater ponds or highly abrasive settings. However, the eutrophic—dysaerobic pure

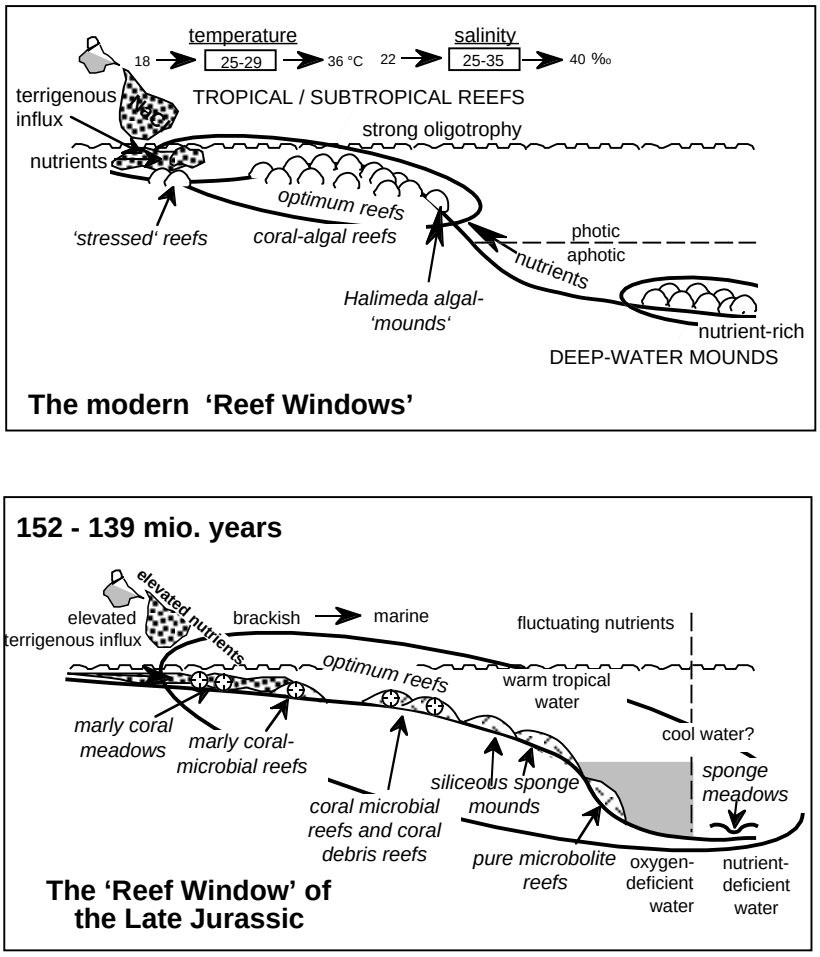


FIGURE 20. The Upper Jurassic and the modern „reef windows," showing generalized reef types and their environmental conditions. (Modern window after James and Bourque, 1992, modifled). Note that the Upper Jurassic reef window was much larger than the modern tropical—subtropical one, due to both better habitat availability (higher sea level) and lesser specialization or reefs. Deep-water coral mounds also are present in modern settings but occur in a distinct window separated from the tropical—subtropical reef window. The optimum for Upper Jurassic coral reefs (as reflected by maximum diversities and pronounced reef growth) was slightly deeper and closer to coastlines than for modern coral reefs. (After Leinfelder and Nose, 1999.)

microbolite type of Early and Late Jurassic of southwest Europe and the Atlantic has no direct modern counterpart, save for the microbolite reefs of some hyperalkaline lakes with anoxic bottom waters such as the Satonda Lake (Kempe and Kazmierczak, 1993). The fairly frequent occurrence of pure microbolite reefs, particularly during some time episodes of the Late Jurassic, is an expression of the greenhouse-type climate of that time, causing tempor

ary collapse of shelf water circulation, a process that is only known today as an effect of hot summers in very marginal seas such as the North Sea or the Adriatic Sea. Jurassic coral reefs were nearly as complex as modern reefs, but lacked one particular element: the coralline red algae (Leinfelder and Nose, 1999). These algae are especially important in Caribbean and Atlantic reefs but also are a prominent feature in Indopacific reefs. Microbolites could anticipate binding and construction in Jurassic reefs as performed by modern coral—red algal reefs, but they normally were unable to develop into the very high-energy zone, giving Jurassic windward shallow-water reefs a distinct debris pile aspect. Also, corals grew more slowly than today, probably because the photosymbiotic relation, though existing, was not yet as flexible and effective. Many Jurassic photosymbiotic corals were apparently still more dependent on heterotrophic nutrition. Consequently, Jurassic coral reefs are more frequently found in terrigeneously influenced, mesotrophic settings than today (Fig. 20).

ACKNOWLEDGMENTS: This chapter benefited from fruitful discussions with many colleagues, especially within my own working group: In particular I owe thanks to Martin Nose (Munich), Manfred Krautter (Stuttgart), Dieter Schmid (Munich), Winfried Werner (Munich), and Martin Takacs (Stuttgart). George Stanley, Jr., and Jeannette Yarnell are thanked for critically commenting on an early draft of this chapter and for improving my English. Long-term financial support by the German Research Foundation (DFG-project Le 580/4) is gratefully acknowledged.

References

Ali, 0. E., 1983, Microsolenid corals as rock-formers in the Corallian (Upper Jurassic) rocks of England, *Geol. Mag.* **120**:375—380.

Allison, N., Tudhope, A. W., and Fallick, A. E., 1996, Factors influencing the stable carbon and oxygen isotopic composition of Porites lutea coral skeletons from Phuket, South Thailand, *Coral Reefs* **15**:43—57.

Aurell, M., and Bádenas, B., 1997, The pinnacle reefs of Jabaloyas (Late Kimmeridgian, NE Spain, Vertical zonation and associated facies related to sea level changes, *Cuad. Geol. Ibérica,* **22**:37—64.

Baria, L. R., Stoudt, D. L., Harris, P. M., and d, P. D., 1982, Upper Jurassic reefs of Smackover Formation, United States GuIf Coast, *Am. Assoc. Petrol. Geol. Bull.* **66**:1449—1482.

Baumeister, J., 1997, Funktionsmorphologie und Paläoökologie regulärer jurassischer Echinoiden des nordwestlichen Tethys-Schelfs, unpublished dissertation (Dr. rer. nat.), Faculty of Geoand Biosciences, University of Stuttgart.

Baumeister, J. G., and Leinfelder, R. R., 1998, Constructional morphology of three Upper Jurassic echinoids, *Paloeontology* **42**(2):203—2 19.

Baumgärtner. M., and Reyle, M., 1995, Oberjurassische Rampenentwicklung in der Region von Jabaloyas und Arroyo Cerezo (Keltiberikum; Spanien), *Profil* **6**:339—361.

Bertling, M., 1993, Ecology and distribution of the Late Jurassic Scleractinian *Thamnasteria concinna* (Goldfuss) in Europe, *Paloeogeogr. Paloeocliniatol. Paloeoecol.* **105**:311—335.

Bertling, M., 1997a, Bioerosion of Late Jurassic reef corals—Implications for reef evolution, *Proc. 8th Int. Coral Reef Sym.* **2**:1663—1668.

Bertling, M., 1997b, Structure and function of coral associations under extreme siltation stress—A case study from the northern German Upper Jurassic, *Proc. 8th Int. Coral Reef Sym.,* **2**:1749 -1754.

Brachert, T., 1992, Sequence stratigraphy and paleo-oceanography of an open-marine mixed carbonate/siliciclastic succession, Late Jurassic; South Germany, *Facies* **27**:179—216.

Buddemeier, R. W., and Kinzie, R. A., 1976, Coral growth, *Oceonogr. Mar. Biol. Annu. Rev.* **14**:183—225.

Coates, G. A., and Jackson, J. B. C., 1987, Clonal growth, algal symbiosis, and reef formation by corals, *Paleobiology* **13:** 363—378.

Conway, K. W., and Barrie, J. V., 1997, Modern Hexactinellid sponge reefs on the western Canadian continental margin, l8th lAS Reg. Europ. Meeting, Heidelberg, 1997, Abstracts, *Gaea heidelbergensis* **3**:105.

Conway, K. W., Barrie, J. V., Austin, W. C., and Luternauer, J. L., 1991, Holocene sponge bioherms on the western Canadian continental shelf, *Continenta1 Shelf Res.* **11**: 771—790.

Crevello, P., and Harns, P., 1984, Depositional models for Jurassic reefal buildups, in: *The Jurassic of the Gulf Rim* (W. P. S. Ventress, D. G. Bebout, B. F. Perkins, and C. H. Moore, eds.), SEPM GuIf Coast Section, Proceedings of the 3rd Annual Research Conference, Tulsa, OK, pp. 57—102.

Dayton, P. K., Mordida, B. J., and Bacon, F., 1994, Polar marine communities, *Am. Zool.* **34**:90—99.

Deusch, M., Friebe, A., and Krautter, M. 1991, Spongiolithic facies in the Middle and Upper Jurassic of Spain, in: *Fossil and Recent Sponges* (J. Reitner and H. Keupp, eds.), Springer, New York, pp. 498—505.

Dietl, G., Dietl, 0., Kapitzke, M., Rieter, M., Schweigert, G., Ilg, A., and Hugger, R., 1996, Der Nusplinger Plattenkalk (Weißer Jura)—Grabungskampagne 1996, *Jh. Ges. Naturk.. Württemberg* **153**:185—203.

Helm, C., 1997, Faunistische Untersuchungen an einem Fleckenriff des Oberjura (florigemmaBank; Süntel, unpublished diploma Thesis, Fachbereich Geowissenschaften, University of Hannover.

Draganescu, A., 1976, Constructional to corpuscular sponge—algal, algal and coralalgal facies in the Upper Jurassic carbonate formation of central Dobrogea (the Casimcea Formation), in: *Carbonate Rocks* ond *Evaporites* (D. Patrullius *et al.,* eds.), Internat. Coll. Carb. Rocks/Evapor. Roumania, Guidebook Series, Vol. **15,** pp. 3—43.

Dromart, G., Gaillard, C., and Jansa, L. F., 1994, Deep-marine microbial structures in the Upper Jurassic of Western Tethys, in: *Phanerozoic Stromotolites II* (J. Bertrand-Sarfati and C. Monty, eds.), Kluwer, Dordrecht, pp. 295—318.

Duarte, L. V., and Krautter, M., 1998, Siliceous sponge mud mounds from the Toarcian of the Lusitanian Basin, Portugal: Facies, stratigraphy and sequential evolution, Abstr. Jurassic Symposium, Vancouver, 1998.

Ellis, P. M., Wilson, R. C. L., and Leinfelder, R. R., 1990, Controls on Upper Jurassic carbonate buildup development in the Lusitanian Basin, Portugal, in: *Carbonate Platforms. Facies, Sequences and Evolution* (M. E. Tucker, J. L. Wilson, P. D. Crevello, J. R. Sarg, and J. F. Read, eds.), *Int. Assoc. Sediment. Spec. Publ.* **9**:169—202.

Elmi, 5., 1987, Le Jurassique inférieur du Bas Vivarais (sud-est) de la France (avec la collaboration de R. Mouterde, C. Ruget, Y. Almeras, and G. Naud), 2ième Colloqu. Centr. Internat. Etudes du Lias (C.l.E.L.), Lyon, 27—3t) Mai 1986, *Cah. Inst. Cathol.. Lyon Sér. Sci.* **1**:63—189.

Errenst, C., 1990a, Das korallenführende Kimmeridgium der nordwestlichen Iberischen Ketten und angrenzender Gebiete (Fazies, Paläogeographie und Beschreibung der Korallenfauna), Teil 1, *Polaeontographica Abt. A* **214**:121—207.

Errenst, C., 1990b, Das korallenführende Kimmeridgium der nordwestlichen Iberischen Ketten und angrenzender Gebiete (Fazies, Paläogeographie und Beschreibung der Korallenfauna), Teil 2, *Palaeontograhica Abt. A* **215:**1—42.

Fagerstrom, J. A., 1987, *The Evolution of Reef Communities,* Wiley, New York.

Fezer, R., 1988, Die oberjurassische karbonatische Regressionsfazies im südwestlichen Keltiberikum zwischen Griegos und Aras de Alpuente (Prov. Teruel, Cuenca, Valencia; Spanien), *Arb. Inst. Geol. Paläont.. Univ. Stuttgart N.F.* **84**:1—119.

Flügel, E., Alt, T., Joachimski, M., Riemann, V., and Scheller, J., 1993. Korallen-Kalke im oberen MaIm (Unter-Tithon) der Südlichen Frankenalb (Laisacker, Marching. Mikrofazies-Merkmale und Fazies-Interpretation, *Geo. Bl. NO-Bayern* **43**:33—56.

Fürsich, F. T., 1981, Salinity-controlled benthic associations from the Upper Jurassic of Portugal, *Lethaia* **14**:203—223.

Fürsich, F. T., and Werner, W., 1986, Benthic associations and their environmental significance in the Lusitanian Basin (Upper Jurassic, Portugal), *N. Jb. Geol. Palaont. Abh.* **172**:271—329.

Fürsich, F. T., and Werner, W., 1991, Palaeoecology of coralline sponge—coral meadows from the Upper Jurassic of Portugal, *Paläont. Z.* **65**:35—69.

Gaillard, C., 1983, Les biohermes à spongiaires et leur environnement dans l'Oxfordien du Jura méridional, *Docum. Lab. Géol. Lyon* **90**:1—515.

Geister, J., 1983, Holozäne westindische Korallenriffe: Geomorphologie, Ökologie und Fazies, *Facies* **9**:173—284.

Geister, J., 1992, Modern reef development and Cenozoic evolution of an oceanic island/reef complex: Isla de Providencia (Western Carribean Sea, Colombia), *Facies* **27**:1—70.

Geister, J., and Lathuilière, B., 1991, Jurassic coral reefs of the northeastern Paris basin (Luxembourg and Lorraine), Excursion A 3, Excursion-Guidebook, VI. Int. Sympos. on Fossil Cnidaria, Münster.

Ginsburg, R. N., 1997, Coral reefs are cities under the sea. Transparencies and teachers notes to introduce coral reefs to students and adults, (manuscript), Project Miami RARE., The Hachette Filipacchi Foundation.

Greb, L., Saric, B., Seyfried, H., Broszonn, T., Brauch, 5., Gugau, G., Wiltschko, C., and Leinfelder, R., 1996, Ökologie und Sedimentologie eines rezenten Rampensystems an der Karibikküste von Panamá, *Profil* **10**:1—168.

Gwinner, M. P., 1976, Origin of the Upper Jurassic limestones of the Swabian Alb (Southwest Germany), *Contr. Sedimentol.* **5**:1—75.

Gygi, R. A., and Persoz, F. 1986, Mineralostratigraphy, litho- and biostratigraphy combined in correlation of the Oxfordian of the Swiss Jura range, *Eclogae geol. Helv.* **79**:455—491.

Hantzpergue, P., 1988, *Les Plates-Formes Recifales du Jurassique Nord-Aquitain.* Livret-Guide Excursion GFEJ, Poitiers.

Haq, B. U., Hardenbol, J., and Vail, P. R., 1988, Mesozoic and Cenozoic chronostratigraphy and cycles of sea level change, *SEPM, Spec. Publ.* **42**:71—108.

Henrich, R., Hartmann, M., Reitner, J., Schäfer, P., Freiwald, A., Steinmetz, S., Dietrich, P., and Thiede, J.. 1992, Facies belts and communities of the Arctic Vesterisbanken Seamount (Central Greenland Sea), *Facies* **27**:71—104.

Henrich, R., Freiwald, A., Wahrmann, A., Schäfer, P., Samtleben, C., and Zankl, H., 1996, Nordic cold-water carbonates: Occurrences and controls, in: *Global and Regional Controls on Biogenic Sedimentation.I. Reef Evolution* (J. Reitner, F. Neuweilar, and F. Gunkel, eds.), research reports. *Göttinger Arb. Geol. Palaeont.* Sb 2: 35—52.

Herrmann, R., 1996, Entwicklung einer oberjurassischen Karbonatplattform: Biofazies, Riffe und Sedimentologie im Oxfordium der Zentralen Dobrogea (Ost-Rumänien), *Berliner geowiss. Abb. E* **19**:1—101.

Highsmith. R. C.. 1979, Coral growth rates and the environmental control of density banding, *J. Exp. Mar. Biol. Ecol.* **37**:105—125.

Hobbie, J. E., Holm-Hansen, 0., Packard, T. T., Pomeroy, L. R., Sheldon, R. W., Homas, J. P. and Wiebe, W. J., 1972, A study of the distribution and activity of microorganisms in the ocean water, *Limnol. Oceanogr.* **17**:544—555.

Hubbard, J. A., and Pocock, Y. P., 1972, Sediment rejection by scleractinian corals: a key to palaeo-environmental reconstruction, *Geol.Rundschau* **61**:598—626.

Insalaco, E., 1996a, Upper Jurassic microsolenid biostromes of northern and central Europe: Facies and depositional environment, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **121**:169—194.

lnsalaco, E., 1996b, The use of Late Jurassic coral growth bands as palaeoenvironmental indicators, *Palaeontology* 39:413—431.

Insalaco, E., Hallam, A., and Rosen, B., 1997, Oxfordian (Upper Jurassic) coral reefs in Western Europe: Reef types and conceptual depositional model, *Sedimentology* 44:707—734.

James, N. P., 1983, Reef environments, in: *Carbonate Depositional Environments* (P.A. Scholle, D. G. Bebout, and C. H. Moore, eds.), *Am. Assoc. Petrol. Geol., Mem.* **33**:345—440.

James, N. P., and Bourque. P., 1992, Reefs and mounds, in: *Facies Models. Response to Sea Level Change* (R. G. Walker and N. P. James, eds.), Geological Association of Canada, Waterloo, pp. 323—347.

Jansa, L. F., Pratt, B. R., and Dromart, G., 1989, Deep water thrombolite mounds from the Upper Jurassic of offshore Nova Scotia, in: *Reefs, Canada and Adjacent Areas* (H. H. J. Geldsetzer, N. P. James, and G. E. Tebbutt, eds.), Can. *Soc. Petroleum Geol. Mem.* **13**:725—735.

Kauffman, E. G., and Scott, R. W., 1976, Basic concepts of community ecology and paleoecology, in: *Structure and Classification of Paleocommunities* (R. W. Scott and R. R. West, eds.), Dowden, Hutchinson, and Ross, Stroudsburg, pp. 1—28.

Kempe, S., 1990, Alkalinity: The link between anaerobic basins and shallow water carbonates? *Naturwissenschaften* **77**:426—427.

Kempe, S., and Kazmierczak, J., 1993, Satonda Grater Lake, Indonesia: Hydrogeochemsistry and biocarbonates, *Facies* **29**:1—32.

Kempe, S, and Kazinierczak, J., 1994, The role of alkalinity in the evolution of ocean chemistry, organisation of living systems and biocalcification processes, in: *Past and Present Biomineralization Processes. Considerations about the Carbonate Cycle* (F. Doumenge, ed.), IUCN-COE Workshop, Monaco, 1993, *Bull. Inst. Oceanogr. Monaco No. Spéc.* **13**:61—117.

Kempe, S., Kazmierczak, J., Reimer, A., Landmann, G., and Reitner, J., 1996, Microbialites and hydrochemistry of the Crater Lake of Satonda—a status report, in: *Global and Regional Controls on Biogenic Sedimentation. 1. Reef Evolution. Research Reports* (J. Reitner, F. Neuweiler, and F. Gunkel, eds.), *Göttinger Arb. Geol. Paläont.* Sb**2**:59—63.

Keupp, H., Brugger, H., Galling. U., Hefter, J., Herrmann, R., Jenisch, A., Kempe, S.. Michaelis, W., Seifert, R., and Thiel, V., 1990, Paleobiological controls of Jurassic spongiolites, in: *Global and Regional Controls on Biogenic Sedimentation. 1. Reef Evolution. Research Reports* (J. Reitner, F. Neuweiler, and F. Gunkel, eds.), *Göttinger Arb. Geol. Paläont.* Sb**2**:209—214.

Koch, R., 1996, Paleogeography, microfacies and diagenesis of Upper Jurassic (Malm) "Reef"-limestones in the Geislingen-Eybtal area (Swabian Alb), in: *Global and Regional Controls on Biogenic Sedimentation. 1. Reef Evolution. Research Reports* (J, Reitner, F. Neuweiler, and F. Gunkel, eds.), *Göttinger Arb. Geol. Paläont.* Sb**2**:215—220.

Koch, R., Senowbari-Daryan, B., and Strauss, H., 1994, The Late Jurassic Massenkalk Fazies of Southern Germany: Calcareous sand piles rather than organic reefs, *Facies* **31**:179—208.

Krautter, M., 1994, Observations on *Eudea clavata* Lamouroux (Calcarea) from the Upper Jurassic of Portugal, in: *Proceedings of the 4th International Porifera Gongress ‚Sponges in Time and Space" Amsterdam 1993* (R. W. M. van Soest, T. M. *G.* van Kempen, and J. C. Braekman, eds.), Balkema, Amsterdam, pp. 29—34.

Krautter, M., 1995, Kieselschwämme als potentielle Indikatoren für Sedimentationsrate und Nährstoffangebot am Beispiel der Oxford-Schwammkalke von Spanien, *Profil* **8**:281—304.

Krautter, M., 1996, Kieselschwämme aus dem unterjurassischen Misonekalk der Trento-Plattform (Südalpen, Taxonomie und phylogenetische Relevanz, *Paläont. Z.* **70**:301—313.

Krautter, M., 1997, Aspekte zur Paläükologie postpaläozoischer Kieselschwämme, *Profil* **11**:199—324.

Laternser, R., 2000, Oberjurassische Korallenriffe von Nordostfrankreich (Lothringen) und Südwestdeutschland — unpublished dissertation, University of Stuttgart.

Leão, Z. M. A. N., and Ginsburg, R. N., 1997, Living reefs surrounded by siliciclastic sediments:

The Abrolhos coastal reefs, Bahia, Brazil, *Proc. 8th Int. Coral Reef Sym.* **2**:1767—1772.

Legarreta, L., 1991, Evolution of a Callovian—Oxfordian carbonate margin in the Neuquén Basin of west-central Argentina: Facies, architecture, depositional sequences and global sea-level changes, *Sediment. Geol.* **70**:209—240.

Leinfelder, R. R., 1986, Facies, stratigraphy and paleogeographic analysis ofUpper? Kimmeridgian to Upper Portlandian sediments in the environs of Arruda dos Vinhos, Estremadura, Portugal, *Münchn. Geowiss. Abh.* A**7**:1—215.

Leinfelder, R. R., 1992, A modern-type Kimmeridgian reef (Ota Limestone, Portugal, Implications for Jurassic reef models, *Facies* **26**:11—34.

Leinfelder, R. R., 1993a, Upper Jurassic reef types and controlling factors.—A preliminary report, *Profil* **5**:1—45.

Leinfelder, R. R., 1993b, A sequence stratigraphic approach to the Upper Jurassic mixed carbonate—siliciclastic succession of the central Lusitanian Basin, Portugal, *Profil* **5**:119—140.

Leinfelder, R. R., 1994a, Distribution of Jurassic reef types: A mirror of structural and environmental changes during breakup of Pangea, in: *Pangea: Global Environments and Resources* (B. Beauchamp, A. F. Embry, and D. Glass, eds.), *Can. Soc. Petrol. Geol. Mem.* **17**:677—700.

Leinfelder, R. R., 1994b, Karhonatplattformen und Korallenriffe innerhalb siliziklastischer Sedimentationsbereiche (Oberjura, Lusitanisches Becken, Portugal). *Profil* **6**:1—207.

Leinfelder, R. R., 1997, Coral reefs and carbonate platforms within a siliciclastic setting: General aspects and examples from the Late Jurassic of Portugal: *Proc. 8th Int. Coral Reef Sym,* Panama City, V.Z., p. 1737—1742, Smithsonian Tropical Research Institute, Balboa, Panama.

Leinfelder, R. R., and Ginsburg, R. N., 1998, Städte unter Wasser—Gibt es so etwas? in:
Riffe—Ein faszinierendes Thema für den Schulunterricht. Materialien für die Fächer Biologie, Erdkunde und Geologie (R. R. Leinfelder, U. Kull, and F. Brümmer, eds.), *Profil* **13**:105—116.

Leinfelder, R. R., and Keupp, H., 1995, Upper Jurassic mud mounds: Allochthonous sedimentation versus autochthonous carbonate production, in: *Mud Mounds: A Polygenetic Spectrum of Fine-grained Carbonate Buildups* (J. Reitner and F. Neuweiler, coord.), *Facies* **32:**17—26.

Leinfelder, R. R., and Nose, M., 1999, Increasing complexity—decreasing flexibility. A different perspective of reef evolution through time, *Profil* **17**:135—147.

Leinfelder, R. R., and Nose, M., submitted for publication, Physical and geological controls of Upper Jurassic reef growth, in: *Reef Systems in Earth History* (E. Flügel and H. Zankl, eds.), Springer. Heidelberg—Berlin.

Leinfelder, R. R., and Schmid, D. U., 2000, Mesozoic reefal thrombolites and other microbolites, in: *Microbial Sediments* (R. Riding, ed.), Springer, Berlin, pp. 289—294.

Leinfelder, R. R., and Werner, W., 1993, The systematic position and palaeoecology of the alga *Marinella lugeoni* Pfender, *Zitteliana* 20:105—122.

Leinfelder, R. R., and Wilson, R. C. L., 1989, Seismic and sedimentologic features of Oxfordian—Kimmeridgian syn-rift sediments at the eastern margin of the Lusitanian Basin, Portugal, *Geol. Rundschau* **78:**81—104.

Leinfelder, R. R., and Wilson, R. C. L., 1998, Third- order sequences in an Upper Jurassic rift-related second-order sequence, central Lusitanian Basin, Portugal, in: *Mesozoic and Cenozoic Sequence Stratigraphy of European Basins* (P--C. de Graciansky, J. Hardenbol, T. Jacquin, and P. R. Vail, eds.), SEPM Spec. Publ. Vol. **60**, pp. 507—525.

Leinfelder, R. R., Krautter, M., Nose, M., Ramalho, M. M., and Werner, W., 1993a, Siliceous sponge facies from the Upper Jurassic of Portugal, *N. Jb. Geol. Paläont. Abh.* **189**:199—254.

Leinfelder, R. R., Nose, M., Schmid, D. U., and Werner, W., 1993b, Microbial crusts of the Late Jurassic: Composition, palaeoecological significance and importance in reef construction, *Facies* **29**:195—230.

Leinfelder, R. R., Krautter, M., Laternser, R., Nose, M., Schmid, D. U., Schweigert, G., Werner, W., Keupp, H., Brugger, H., Herrmann, R., Rehfeld-Kiefer, U., Schroeder, J. H., Reinhold, C., Koch, R., Zeiss, A., Schweizer, V., Christmann, H., Menges, G., and Luterbacher, H., 1994, The origin of Jurassic reefs: Current research developments and results, *Facies* **31**:1—56.

Leinfelder, R. R., Werner, W., Nose, M., Schmid, D. U., Krautter, M., Laternser, R., Takacs, M., and Hartmann, D., 1996, Palaeoecology, growth parameters and dynamics of coral, sponge and microbolite reefs from the Late Jurassic in: *Global and Regional Controls on Biogenic Sedimentation. 1. Reef Evolution. Research Reports* (J. Reitner, F. Neuweiler, and F. Gunkel, eds.), *GöttingerArb. Geol. Paläont.* Sb**2**:227—248.

Lévi, C., and Lévi, P., 1988, Nouveaux spongiaire Lithistides bathyaux à affinités crétacées de la Nouvelle CaIédonie, *Bull. Mus. Nat. d'Histoire Naturelle Paris* **10**(A2):241—263.

Mackie, G. 0., Lawn, 1. D., and Pavans de Ceccatty, M., 1983, Studies on hexactinellid sponges. II. Excitability, conduction and coordination of responses in *Rhabdocalyptus dawsoni* (Lambe, 1873), *Phil. Trans. Royal Soc. London B Biol. Sci.* **301**:401—418.

Matheos, S. D.,and Morsch, S M., 1990, Geochemistry and paleoecological aspects of coralbearing limestones from the late Jurassic at the southern end of the Sierra da la Vaca Muerta, Nenquén Basin, Argentina. *N.Jb. Geol. Polöont. Abh.* **181**:159—169.

Matyszkiewicz, J., 1996, The significance of Saccocoma—calciturbidites for the analysis of the Polish epicontinental Late Jurassic basin: an example from the southern Cracow—Wielun Upland. Poland), *Facies* **34**:23 40.

Matyszkiewicz, J., 1997, Microfacies, sedimentation and some aspects of diagenesis of Upper Jurassic sediments from the elevated part of the Northern peri-Tethyan shelf: A comparative study on the Lochen area (Schwäbische Alb) and the Cracow area (Cracow—Wielun Upland, Polen), *Berlin. Geowiss. Abb. (E)* **21**:1—111.

Mehl, D., 1992, Die Entwicklung der Hexactinellida seit dem Mesozoikum—Paläobiologie, Phylogenie und Evolutionsökologie, *Berliner Geowiss. Abh. (E)* **2**:1—164.

Meyer, R. K. F., and Schmidt-Kaler, H., 1989, Paläogeographischer Atlas des süddeutschen Oberjura (Malm), *Geol. Jb. A* **115**:3—77.

Montaggioni, L. F., and Camoin, G. F., 1993, Stromatolites associated with coralgal communities in the Holocene high-energy reefs, *Geology* **21**:149 -152.

Montgomery, S. L, 1993, Cotton Valley Lime of East Texas: New pinnacle reef play in the Late Jurassic, in: *Petroleum Frontiers (Petroleum Information Gorp.),* Vol. **10**, pp. 1—55.

Montgornery, S. L., 1996, Cotton Valley Lime pinnacle reef play: Branton Field, AAPG *Bull.* **80**:617-629.

Morsch, S. M., 1989, Scleractinian corals from the Oxfordian La Manga Formation in the Neuquén Basin, Argentina, *Mem. Assoc. Australas. Palaeontols.* **8**:303—306.

Nose, M., 1995. Vergleichende Faziesanalyse uiid Palökologie korallenreicher Verflachungsabfolgen des iberischen Oberjura, *Profil* **8**:1 —237.

Nose, M., submitted for publication, The modern (sub)tropical reef window, in: *Reef Systems in Earth Histoiy* (E. Flügel and H. Zankl, eds.), Springer, Heidelberg—Berlin.

Nose, M., and Leinfelder, R., 1997, Upper Jurassic coral communities within siliciclastic settings (Lusitanan Basin, Portugal, Implications for symbiotic and nutrient strategies), *Proc. 8th Int. Coral Reef Symp.* **2**:1755—1760.

Nose, M., and Leinfelder, R. R., submitted for publication, The Upper Jurassic (sub)tropical reef window, in: *Reef Systems in Earth History* (E. Flügel and H. Zankl, eds.), Springer, Heidelberg Berlin.

Odum, E. P., 1983, *Grundlagen der Ökologie,* Thieme, Stuttgart.

Palmer, T. J., and Fürsich, F. T., 1981, Ecology of sponge reefs from the middle Jurassic of Normandy, *Paloeontology* 24:1—23.

Paulsen, S., 1964, Aufbau und Petrographie des Riffkomplexes von Arnegg im höheren Weißen Jura der Schwäbischen Alb (Württemberg), *Arbeiten aus dem Institut für Geologie und Paläontologie der Universität Stuttgart, NE.* **42**:1—98.

Pisera, A., 1997, Upper Jurassic siliceous sponges from the Swabian Alb: Taxonomy and Paleoecology, *Palaeontol. Polonica* **57**:1—216.

Pittet, B., Strasser, A., and Dupraz, C., 1995, Palaeoecology, palaeoclimatology and cyclostratigraphy of shallow-water carbonate - siliciclastic transitions in the Oxfordian of the Swiss Jura. IAS-l6th Regional Meeting of Sedimentology— 5ième Congrès Fran~ais de Sédimentologie, *ASF, Field Trip Guide Book, Publication ASF, Paris* **23**:225-254.

Ponsot, C. M., and Vail, P. R., 1991, Sequence stratigraphy of the Jurassic: New data from the Paris-London Basin, EUG VI-Congress, Strasbourg, *Terra Cognita* **28**:48.

Pümpin, V. F., 1965, Riffsedimentologische Untersuchungen im Rauracien von St. Ursanne und Umgehung (Zentraler Schweizer Jura), *Eclogae geol. HeIvetiae* **58**:799—876.

Ramalho, M., 1988, Sur Ia découverte de biohermes stromatolithiques à spongiaires siliceux dans le Kimméridgien de l'Algarve (Portugal), *Comun. Serv. Geol. Portugal* **74**:41—55.

Reid, R. E. H., 1968, Bathymetric distribution of Calcarea and Hexactinellida in the present and the past, *Geol. Mag.* **105**:546 -559.

Reiswig, H. M., and Mackie, G. 0. 1963, Studies on Hexactinellid Sponges. III. The taxonomic status of Hexactinellida within the Porifera, *Phil. Trans. Royal Soc. London B Biol. Sci.* **301**:419—428.

Reitner, J., 1993, Modern cryptic microbialite/metazoan facies from Lizard Island (Great Barrier Reef, Australia)—Formation and concepts, *Facies* **29**:3—40.

Reitner, J., and Keupp, H., 1991, The fossil record of the haplosclerid excavating sponge Aka de Laubenfels, in: *Fossil and Recent Sponges* (J. Reitner and H. Keupp, eds.), Springer, Berlin, pp. 102—120.

Reitner, J., Wörheide, G., Thiel, V., and Gautret, P., 1996, Reef caves and cryptic habitats of lndo-Pacific reefs—Distribution patterns of coralline sponges and microbialites, in: *Global and Regional Controls on Biogenic Sedimentation. 1. Reef Evolution. Research Reports* (J. Reitner, F. Neuweiler, and F. Gunkel, eds.), *Göttinger Arb. Geol. Paläont.* Sb**2**:91—100.

Renesto, S., and Viohl, G., 1997, A sphenodontid (Reptilia, Diapsida) from the Late Kimmeridgian of Scharnhaupten (southern Franconian Alb, Bavaria, Germany), *Archaeopteryx* **15**:27—46.

Rheinheimer, G., 1980, *Aquatic Microbiology,* 2 ed., Wiley and Sons, New York.

Riegl. B., 1995, Effects of sand deposition on scleractinian and alcyonacean corals, *Mar. Biol.* **121**:517—526.

Rogers, C. 5., 1990, Response of coral reefs and reef organisms to sedimentation, *Mar. Ecol. Prog. Ser.* **62**:185—202.

Röper, M., Rothgaenger, M., and Rothgaenger, K., 1996, *Die Plattenkalke von Brunn (Landkreis Regensburg). Sensationelle Fossilien aus dem Oberpfälzer Jura,* Eichendorf Verlag, Eichendorf.

Rosendahl, S., 1985, Die oberjurassische Korallenfazies von Algarve (Südportugal), *Arb. Inst. Geol. Paläont. Univ. Stuttgart NE.* **82:**1-125.

Roux, M., Bouchet, P., Bourseau J. P., Gaillard, C., Grandperrin, R., Guille, A. Q.**,** Laurin, B., Monniao, C., Richer de Forges, B., Rio, M., Segonzac, M., Vacelet, J., and Zibrorius, H., 1991, L'étagement du benthos bathyal observe à l'aide da la soucoupe CYANA, in: *L'Environements Carbonate Bathyal en Nouvelle—Calédonie* (B. Lambert and M. Roux, eds.), *Doc. Travaux Inst. Géol. Albert-de-Lapparent* **15**:151—165.

Sartorio, D., 1989, Reef and open episodes on a carbanate platform margin from Malm to Cenomanian: The Cansiglio example (Southern Alps), *Mem. Soc. Geol. Ital.* **40**:91—97.

Schlichter, D., 1992, A perforated gastrovascular cavity in the symbiotic deep water coral *Leptoseris fragilis:* A new strategy to optimize heterotrophic nutrition, *Helgoländer Wissenschaftliche Meeresuntersuchungen* **45**:423—443.

Schmid, D. U., 1995, *‚Tubiphytes" morronensis*—Eine fakultativ inkrustierende Faraminifere mit endosymbiantischen Algen, *Profil* **8**:305—317.

Schmid, D. U., 1996, Marine Mikrobolithe und Mikroinkrustierer aus dem Oberjura, *Profil* **9**:101—251.

Schmid, D. U., and Jonischkeit, A., 1995, The Upper Jurassic São Romão limestone (Algarve, Portugal, An isolated carbonate ramp, *Profil* **8**:319—337.

Schmid, D. U., and Leinfelder, R. R., 1996, The Jurassic *Lithocodium aggregatum—Troglotella incrustans* foraminiferal consortium, *Palaeontology* **39**:21—52.

Schuhmacher, H., 1976, *Korallenriffe. Verbreitung, Tierwelt, Ökologie,* BLV Verlagsgesallschaft. München.

Scotese, C. R., Walsh, D. B., Kraus, J. U., and Bocharova, N. Y., 1993, Plate evolution of Pangae from the Late Paleozoic to the Jurassic. Pangea Conference (Can. Soc. Petrol. Geol.), August 15—19, 1993, Calgary, book of abstracts, p. 274, and PALEOMAP Project, International Lithosphere Program,

Scott, R. W., 1988, Evolution of Late Jurassic and Early Cretaceous reef biotas, *Palaios* **3**:184—193.

Stanley, G. D. jr., 1988; The history of Early Mesozoic reef communities: A three step process, *Palaios* **3**:170—183.

Stanley, G. D. Jr., 1996, Recovery of reef communities after the Triassic mass extinction, *Paleont. Soc. Sp. Publ.* **8**:370.

Stanley, G. D., Jr., and Beauvais, L., 1994, Corals from an Early Jurassic coral reef in British Columbia: Refuge on an oceanic island reef, *Lethaia* **27:**35—47.

Stanley, *G.* D., Jr., and McRoberts, C. A., 1993, A coral reef in the Telkwa Range, British Columbia: the Earliest Jurasic example, *Can. J. Earth Sci.* **30**:819—831.

Stanley, G. D., Jr., and Swart, P., 1995, Evolution of the coral—zooxanthellae symbiosis during the Triassic: A geochemical approach, *Paleobiology* **21**:179—199.

Steiger, T., 1981, Kalkturbidite im Obarjura dar Nördlichen Kalkalpen (Barmsteinkalke, Salzburg, Österreich), *Facies* **4**:215—348.

Steiger, T., and Jansa, L. F., 1984, Jurassic limestones of the seaward edge of the Mazagan Carbonate Platform, Northwest African continental margin, Morocco, *Initial Reports, DSDP* **79**:449—491.

Steiger, T., and Wurm, D., 1980, Faziesmuster oberjurassischer Plattformkarbonate (Plassenkalke, Steiermark), *Facies* **2**:241—284.

Takacs, M., in prep., Vergleichende Analyse zeitgleicher oberjurassischer Korallen- und Kieselschwammriffe aus dem Schweizer Jura, unpublished dissertation, University of Stuttgart.

Taylor, P. D., and Palmer, T. J., 1994, Submarine cavas in a Jurassic reef (La Rochelle, France) and the evolution of cave biotas, *Naturwissenschaften* **81**:357—360.

Trammer, J., 1988, Ecalogic history of the Oxfordian sponge assamblage in the Polish Jura Chain, *Berliner Geowiss. Abh. A* **100**:44—45.

Turnsek, D., Buser, S., and Ogorelev, B., 1981, An Upper Jurassic reef complax from Slovenia, Yugaslavia, in: *European Fossil Ree fModels* (D. F. Toomey, ed.), *Soc. Econ. Paleont. Mineral. Sp. P.* 3**0**:361—369.

Wagenplast, P., 1972, Ökologische Untersuchung der Fauna aus Bank- und Schwammfazias des Weißen Jura der Schwäbischen Alb, *Arb. Inst. Geol. Paläont. Univ. Stuttgart N.F.* **67**:1—99.

Walker, K. R., and Alberstadt, L. P., 1975, Ecological succession as an aspect of structure in fossil communities, *Paleobiology* **1**:238— 257.

Warme, J. E., Burke, R. B., Crevello, P. D., Halliwell-Haziett, B., and Letsch, D. K., 1988, Evolution of the Jurassic High Atlas Rift, Morocco: Transtension, structural and eustatic controls on carbonate facies: *Am. Assoc. Petrol Geol. Mediterranean Basins Conf. Nice, Sept. 1988, Fieldtrip 9. Guidebook.*

Werner, W., 1986, Palökalogische und biofazialle Analyse des Kimmaridge (Oberjura) von Consalação, Mittelportugal, *Zitteliana* **13**:1—109.

Werner, W., Leinfelder, R. R., Fürsich, F. T., and Krautter, M., 1994, Comparative palaaoecology of marly coralline sponge-bearing reefal associations from the Kimmeridgian (Upper Jurassic) of Portugal and Southwestern Germany. *Cour. Forsch. Inst. Senckenb.* **172**:381—397.

Wiedenmayer, F., 1980, Spicules and sponges in the lower Jurassic of the western Tethys, *Sedimenta* **8**:135—145.

Wilkinson, C. R., and Evans, E., 1989, Sponge distribution across Davies Reef, Great Barriar Reef, relative to location, depth, and water movament, *Coral Reefs* **8**:1—7.

Wilkinson, C. R., and Trott, L. A., 1985, Light as a factor determining the distribution of sponges across the central Great Barrier Raaf, *Proc. 5th Int. Coral Reef Congr. Tahiti* **5**:125—130.

Wilson, R. C. L., Hiscott, R. N., Willis, M. G., and Gradstein, F. M., 1989, The Lusitanian Basin of west central Portugal: Mesozoic and Tertiary tectonic, stratigraphy and subsidence history, in: *Extensional Tectonics and Stratigraphy of the North Atlantic Margins* (A. J. Tankard, and H. Balkwill, eds.), *AAPG Mem.* **46:**341—361.

TOPICS IN GEOBIOLOGY

Series Editors: Neu H. Landman, American Museum of Natural History, New York, NY
Douglas 5. Jones, Univarsity of Florida, Gainasvilla, FL

Current volumes in this series

Volume 4 THE GREAT AMERICAN BIOTIC INTERCHANGE Edited by Francis G. Stehli and S. David Webb

Volume 5 MAGNETITE BIOMINERALIZATION AND MAGNETOREGEPTION IN ORGANISMS
A New Biomagnetism
Edited by Joseph L. Kirschvink, Dauglas 5. Jonas, and Bruce J. McFadden

Volume 6 *NA UTILUS*
The Biology and Paleobiology of a Living Fossil
Edited by W. Bruce Saunders and Neil H. Landman

Volume 7 HETEROCHRONY IN EVOLUTION
A Multidisciplinary Approach
Editad by Michael L. McKinney

Valume 8 GALAPAGOS MARINE INVERTEBRATES
Taxonomy, Biogeography, and Evolution in Darwin‘s Islands
Edited by Matthaw J. James

Volume 9 TAPHONOMY
Releasing the Data Locked in the Fossil Record
Edited by Peter A. Allison and Derek E. G. Briggs

Volume 10 ORIGIN AND EARLY EVOLUTION OF THE METAZOAN
Edited by Jere H. Lipps and Philip W. Signor

Volume 11 ORGANIG GEOCHEMISTRY
Principles and Applications
Edited by Michael H. Engel and Stephan A. Macko

Volume 12 THE TERTIARY RECORD OF RODENTS IN NORTH AMERICA
William Korth

Volume 13 AMMONOID PALEOBIOGRAPHY
Edited by Neil H. Landman, Kazushige Tanabe. and Richard Arnold Davis

Volume 14 NEOGENE PALEONTOLOGY OF THE MANONGA VALLEY, TANZANIA
A Window into the Evolutionary History of East Africa
Edited by Terry Harrison

Volume 15 ENVIRONMENTAL MICROPALEONTOLOGY
The Application of Microfossils to Environmental Geology
Edited by Ronald E. Martin

Volume 16 PALEOBIOGEOGRAPHY
Bruce S. Lieberman

Volume 17 THE HISTORY AND SEDIMENTOLOGY OF ANCIENT REEF SYSTEMS
Edited by George D. Stanley, Jr.

Volume 18 EOCENE BIODIVERSITY
Unusual Occurrences and Rarely Sampled Habitats
Edited by Gregg F. Gunnell

A Continuation Order Plan is available for this series. A continuation order will bring delivery of each new volume immediately upon publication. Volumes are billed only upon actual shipment. For further information please contact the publisher.

Important note:

This is an informal digital reprint of the below paper provided for your personal use, since no more reprints are available by the author.
Text and figures are identical with the original paper. However, some figure patterns might be rendered slightly different to the original paper and landscape sized figures are turned 90° for better online readability. Also, there might be some additional spelling mistakes (owing to OCR-recogition). Line feed returns can also be different to the original text but page feed returns are identical with the original. A few spelling mistakes of the original paper were corrected (but the original version was kept as crossed-out word) **OK, click for first page of paper**

Reinhold R. Leinfelder

Institute for Paleontology and Historical Geology, University of München, Richard-Wagner-Str. 10, D-80333 München, Germany

Jurassic Reef Ecosystems

in:

The History and Sedimentology of Ancient Reef Systems

Edited by

George D. Stanley, Jr.
University ofMontana
Missoula, Montana

Kluwer Academic /Plenum Publishers New York, Boston, Dordrecht, London, Moscow

---
Leinfelder, R.R. (2002): Jurassic Reef Ecosystems.- In: Stanley, G.D.Jr. (ed.), The History and Sedimentology of Ancient Reef Systems, pp. 251-309, Kluwer Academic/Plenum Publishers, New York.