

Increasing complexity - decreasing flexibility. A different perspective of reef evolution through time

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Abstract

The evolution of reef systems is dependent on a great variety of factors. Evolution, adaptive radiation, and extinction of reef organisms provide the reef building potential whereas plate tectonics, sea-level changes and oceanographic conditions define where and when reefs actually develop. However, two additional important trends superimpose this pattern. These are (1) the evolution of reef building blocks and (2) the variable width of the global reef window.

In terms of ecological structure and carbonate productivity, reefs are composed of different reef building blocks which define the modular complexity of a reef. Such basic building blocks include microbial, parazoan, metazoan, photosymbiotic and red algal modules. These building blocks successively developed throughout the evolution of the System Earth, and are still all available in modern reef systems (REITNER 1997).

The unidirectional increase in modular complexity is partly modified, partly paralleled by the variable environmental sets of physicochemical conditions which reef organisms demanded and were adapted to. Until the base of the Cenozoic, such global 'reef windows' mostly widened, due to new adaptational strategies of reef organisms (e.g., photoautotrophy, baffling, aphotosymbiotic and photosymbiotic reef building). The reef windows of the Late Jurassic to Cretaceous were possibly the widest ever. Subsequently, the modular complexity of reefs and the interdependence of reef biota increased with the improvement of the photosymbiotic relation, the appearance of fast growing corals, new synecologic strategies, and the radiation of encrusting coralline algae. This resulted in a distinct narrowing of the tropical reef window and, consequently, the separation of a new, distinct, deep-water coral mound window.

Reef systems existed nearly throughout the entire Earth history. However, reef evolution was punctuated by global reef crises. Extinction events were rapid, but recovery times were very slow. In the light of possible extinction of modern coral reefs by human impact, Earth history provides two major lessons: The high modular complexity of modern reefs which includes Archaean, Proterozoic, Phanerozoic, Mesozoic, and Cenozoic building blocks makes it likely that some robust reef types such as microbial reefs, *Halimeda*-mounds or low-diversity coral meadows might survive. However, lag time for the reestablishment of complex systems, thus for modern coral reefs, are extremely large, often spanning millions of years and hence extending far beyond human time scales.

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INTRODUCTION

Reef systems have accompanied and modified the System Earth since its earliest stages. The oldest reef-type bodies are nearly as old as the oldest Archaean crust (e.g. North Pole, Australia, 3.5 billion years, LOWE 1980). Despite this longevity, reef systems are not at all a conservative element but have changed and evolved drastically through time. Many different reef organisms have played important geobiological roles throughout the evolution of the Earth, producing oxygen during the Proterozoic, removing toxic calcium at the end of the Precambrian, shaping shelves and influencing the carbon cycle during the Phanerozoic, establishing strong compartmentalization of shelf systems even in high-energy settings during the Tertiary, and today assuring existence for billions of people by providing coastline protection, food, pharmaceutical substances, and touristic economic value (cf. LEINFELDER & BRÜMMER 1998, REITNER 1998, STEININGER & MARONDE 1997).

Like any other ecosystem, reef systems are particularly driven by the available energy input and the removal of noxious by-products. In reef systems, adaptation to these basic requirements was refined to great perfection. In modern reefs, efficiency in the energy consumption is nearly perfect due to different nutrition strategies, including photosymbiosis. Removal of noxious matter is maintained both by recycling of phosphates and nitrates via endosymbionts, and by enzymatic neutralization, leading to mineralic deposition such as removal of surplus calcium by calcareous skeletons (cf. KEMPE et al. 1989). These strategies eventually resulted in the establishment of a largely independent, self-sustaining system, which is a stable system within its environmental boundaries, but is very vulnerable, if the amplitude or frequency of physicochemical disturbance extends beyond these limits.

Comparing Ancient reefs with modern reefs has to take processes of reef evolution into account. Maximum complexity of reefs has increased continuously through time, which implies that the environmental flexibility of reef systems was different during earlier stages in the evolution of the System Earth. Trophic, structural and productive aspects of the reef system can be differentiated in a modular set of reef building blocks. These different modules appeared one after the other in the course of Earth history and remained available in all subsequent reefs (REITNER 1998; Fig. 1). Energy management has not always been as perfect as it is today. The modern, nearly closed-circuit system, which is mainly dependent on the easily available energy

from light, developed in the course of reef evolution, optimizing recycling and depository strategies. This was possible only by adaptive evolution and adaptive breakthroughs in the autecology and synecology of reef organisms. As a consequence, general reef variability first increased with the development of new building blocks, but later decreased due to increasing specialization and interdependence of reef organisms, which evoked narrowing of environmental tolerances for the entire system. In each time slice, the physiological and synecological demands and abilities of available reef organisms define the boundary conditions for reef growth. The ecospace between these multifactorial boundary conditions can be termed the global 'reef window' of a given time-slice (cf. JAMES & BOURQUE 1992, LEINFELDER 1997, LEINFELDER & NOSE in prep., NOSE & LEINFELDER in prep.). As a consequence of reef evolution and available habitats, the width of the reef window was matter of fluctuations, accompanied by a pronounced decrease from the Cenozoic onward (see below).

A widely held view of reef evolution through time is that the many reef crises during Earth history have had dramatical impacts on the evolution of the reef system. Actually, some global extinctions (end-Permian, Cretaceous/Tertiary boundary) had a strong influence on the biotic composition of subsequent reef systems. Other crises particularly affected reef biota much more than other biota (such as the intra-Late Devonian and end-Triassic reef crises). Reef extinction events were apparently rapid, but lag times for complete re-establishment of reef systems were enormous. After the intra-Late Devonian reef crisis it took more than 100 million years for major shallow-water coral reefs to fully recover, although other reef types were partially filling this gap. After the end-Permian extinction it took about five million years for the first reefs to reappear (FLÜGEL 1997), after the reef crisis at the base of the Jurassic there is another considerable, though debated, lag time (LEINFELDER 1994). However, once re-established, reefs gained, and increased, their previous modular complexity almost instantly. This shows that extinction events and reef crises mostly had an impact on the type and frequency of reefs by reducing the diversity of important reef organisms (such as corals) or even eliminating some major taxa (e.g. archaeocyathids, rictohofeniid brachiopods, rudistid bivalves), but not generally on the modular complexity of reefs when seen in terms of building blocks. As a whole, reef crises had therefore little impact on the general evolution of the reef ecosystem through time, except for causing large lag times.

The scope of this paper is to outline a modern view of reef evolution through time by combining the concept of increasing modular complexity with the concept of waxing and waning of reef windows through time, both of which are discussed in more detail in the following chapters.

THE FIRST MEGATREND: INCREASE OF REEF BUILDING BLOCKS

Microbial calcification

Recently, REITNER (1998) has introduced the concept of modularity in reef systems. This concept is reviewed, discussed, and enlarged here (Fig. 1). In a broad manner, reefs represent preservable carbonate bodies produced, or induced, by epibenthic organisms. This definition does not include any specific water depth or relief. In this broad sense, reefs existed since the earliest Archaean. Stromatolite-like bodies are as old as 3.5 billion years (LOWE 1980, WALTER 1983). Simple stromatolitic microbialite reefs proliferated from about two billion years onward, and greatly contributed to the origin of hydrospheric and atmospheric oxygen. The microbialites of the Archaean were probably mostly built of chemolithotrophic and heterotrophic anaerobic bacteria (*RBB 1: Anaerobic Microbolite Reef Building Block*), whereas energy input has changed to solar energy at least since the early Proterozoic by the development of autotrophic cyanobacteria, later accompanied by unicellular algae (*RBB 2: Photoautotrophic Microbolite Reef Building Block*). Stromatolitic reefs, composed of RBB 1-2, were, from the base of the Phanerozoic onward, accompanied by many other reef types dominated, or characterized, by 'parazoans' (sponges) or 'true' metazoans. Probably due to this competition, stromatolites had to withdraw to extreme environments not suitable for other reef organisms. Such settings include hypersaline ponds, deep-water settings, intratidal and supratidal flats, or freshwater environments, where pure microbialites can still be found today. Though often overlooked, microbial carbonates were, nevertheless, of variable importance in most other Phanerozoic reef types, including present tropical coral reefs (LEINFELDER et al. 1993b, MONTAGGIONI & CAMOIN 1993, SCHMID 1996).

Microbial - soft sponge consortium

The next event in the evolution of the reef ecosystem was the rise of epibenthic 'parazoans' and their indirect contribution to reef formation. Soft sponges and siliceous sponges are often intimately

related to bacterial films, probably sharing energy flow in a symbiotic relation (cf. REITNER 1993, SCHUMANN-KINDEL et al. 1996). This results in preferred non-enzymatic, microbially induced calcification of sponge-containing microbialites (auto-micrite formation sensu REITNER et al. 1995). Availability of soft and siliceous sponges probably also increased the capacity to baffle allochthonous calcareous muds and enlarged the upward-facing area of reefs due to formation of irregular surfaces. Contribution of sponges ('parazoans') in reefs may have arisen in Middle to Late Proterozoic times (*RBB 3: Soft/Siliceous Sponge Reef Building Block*). Sponge-microbial reefs composed of RBB 1-3 accompanied major parts of Earth history (see Fig. 1).

Onset of enzymatic calcification

The next reef building block to develop was the invention of enzymatic calcification in epibenthic 'parazoans' (*RBB 4: Calcareous Sponge Reef Building Block*). This was invented by the enigmatic *Claudina*-organisms in the Neoproterozoic, about 600 Mio years ago (REITNER 1998), then refined by the 'calcareous' sponges in the Early Cambrian (archaeocyathid reefs), and further developed both by the stromatoporoids (now mostly considered as demospongid 'coralline sclerosponges'), which flourished particularly in Mid-Paleozoic reef systems, and the *Calcarea* sponge group. Coralline sponges directly contributed to the formation of reef bodies with their skeletons, and were also able to baffle sediments. All four RBBs mentioned were of importance in many different reef types during Earth History and so they are still today, where these bacteria-sponge related modules particularly develop in caves and cavities of modern tropical coral reefs (cf. REITNER 1993).

Carbonate production by higher metazoans

The next step to increasing the modular complexity of the reef ecosystems was the occurrence of calcareous sessile 'true' metazoans, chiefly Paleozoic heterotrophic corals, which fed on sources different from those for the sponges. Sponges are largely bacteria-filterers and bacteria-cultivators, as well as osmotrophic feeders (KRAUTTER 1997), whereas corals, among many other ways of nutrition feed on zooplankton and small nekton, hence using an alternative energy source (*RBB 5: Metazoan Reef Building Block*).

Enhancement of modular complexity by autophototrophic symbiosis

The development of autophototrophic symbiotic relations in reef metazoans was a major event in reef evolution, allowing their hosts to directly control primary organic and skeletal production

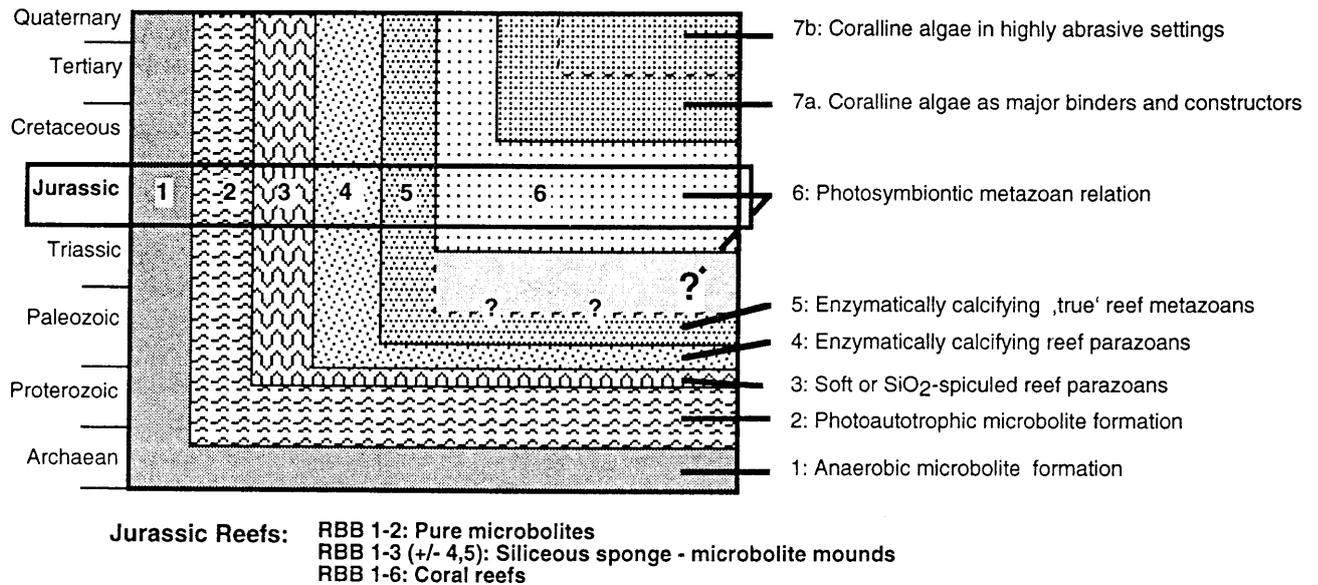


Fig. 1. The development of reef building blocks (RBBs) throughout Earth history (after REITNER 1998, modified). Modular complexity in ecological structure and carbonate productivity increases towards modern reefs. Time not to scale. Note that all reef building modules have survived and are functional until today. Most of the Precambrian to Paleozoic modules today are present in the cavity system of modern reefs. At a given time slice, individual reefs need not have maximum potential modular complexity. This is exemplified by the Jurassic time slice (black frame). Jurassic reefs comprise at least three basic reef groups which differ by their modular complexity.

(RBB 6: *Metazoan Photosymbiosis Reef Building Block*). It is unclear as to which time interval photosymbiosis first developed. Many modern calcareous sponges have photosymbionts, and based on fairly rapid growth rates of Paleozoic stromatopoids (COWEN 1988, KERSHAW 1998), it may be guessed that quite some of them already possessed photosymbionts. As to corals it is widely debated whether or not Paleozoic forms had photosymbionts (COWEN 1988, NUDDS & DAY 1997, ROSEN et al. 1991, SCRUTTON 1998). Certainly, photosymbiotic relations were invented various times independently from each other. It is also unclear, from which time onward the modern group of corals, the scleractinians, have developed photosymbiotic forms. There is good evidence that at least since the Jurassic, and probably starting in Late Triassic time (STANLEY & SWART 1995), scleractinians possessed symbiotic algae, although the efficiency of the symbiotic system was certainly lower than today, making many Jurassic corals still strongly dependent on heterotrophic uptake of food (LEINFELDER et al. 1996, NOSE & LEINFELDER 1997). Also, for several other extinct reef organisms, such as some groups of the rudistid bivalves, photosymbiosis is plausible but difficult to prove (COWEN 1988, KAUFMANN & JOHNSON 1988). STEUBER (1997, 1998)

and GILI et al. (1995), among others, give arguments against photosymbiosis in rudistids.

The impact of coralline algae

The last major event in reef evolution was the participation of encrusting coralline red algae in reef formation (*RBB 7: Coralline Algae Reef Building Block*). Red algae of various groups were present but, apart from several exceptions, not structurally important for reef formation prior to Late Cretaceous and Tertiary times. Some, but probably not all phylloid algae of Palaeozoic reefs might actually also represent red algae (RIDING & GUO 1992), but they were sediment baffler rather than encrusters. The first alga of coralline algal affinity, *Marinella lugeoni*, arose during the Late Jurassic (LEINFELDER & WERNER 1993). Although occasionally occurring in rock-forming quantities in other environments, the taxon was only a marginal element in reef settings. It was only from the later part of the Cretaceous onward that encrusting coralline algae were of major importance in reefs. Only since that time were the microbial binders (RBB 1,2) generally accompanied by very effective binding and cementing organisms. It should be noted that the importance of coralline algae in modern reefs is discussed controversially (MACINTYRE

1997), but there is no doubt that in modern reefs pathogen-related lack of corallines changes the reef system considerably (LITTLER & LITTLER 1997). Quite some modern coral reef examples are even dominated by corallines (LEÃO & GINSBURG 1997, TESTA 1997). Doubtless, high-energy reef crest formation is only possible by means of corallines (MACINTYRE 1997), leading to strong compartmentalization of reef zones and adjacent environments.

General aspects in the development of reef building blocks

Several strategies in the evolution of reef building blocks should be emphasized:

(1) Despite the fact that many extinctions had strong impacts on reef organisms (see above), the general increase in modular complexity is largely unidirectional. For most of the Phanerozoic time, reef ecosystems were composed of up to six RBBs (Fig. 1). However, the intra-Late Devonian collapse of the stromatoporoid-coral reef system pushed back the quantitative importance of RBB 5 (calcified metazoans) and, if already existing at that time, possibly eliminated most of RBB 6 (metazoan photosymbiosis) which probably was reinvented in reef systems only in the Triassic. The gap was filled by widespread and better developed RBB 4 (sponge calcification RBB), which gave rise to Late Paleozoic and, again, Mid-Triassic reef types rich in calcareous sponges and microbial carbonate. Nevertheless, reefs including RBB 5 (calcified metazoans) were widespread, although they did not form large structures. As an example, Upper Permian calcisponge-dominated reefs such as the Capitan-Massive may be huge, but roughly coeval reefs rich in rugosan corals or richthofeniid brachiopods remained small (WEIDLICH 1997, FLAJS et al. 1997). The end-Permian extinction brought an enormous reduction in reef occurrences and a subsequent lag time of reef development, but did not alter modular reef complexity trends. The end-Cretaceous extinction eliminated a major reef building group, the rudistid bivalves, but again, modular complexity trends did not suffer (Fig. 1).

(2) Not all reefs of a given time had the potential maximum modular complexity in reef building blocks. For instance, the mid-Paleozoic stromatoporoid-coral reefs composed of RBBs 1-5 or even 1-6 were accompanied by sponge reef mounds composed of RBBs 1-3 only. The same is true of Jurassic reefs which include pure microbolites (RRB 1-2) and sponge mounds (RRB 1-3), as well as light-dependent coral reefs (RRB 1-6) (Fig. 1, 2). Pure microbolite reefs (RBBs 1-2) even persisted

throughout the entire Earth history in settings unsuitable for the development of higher reef building blocks.

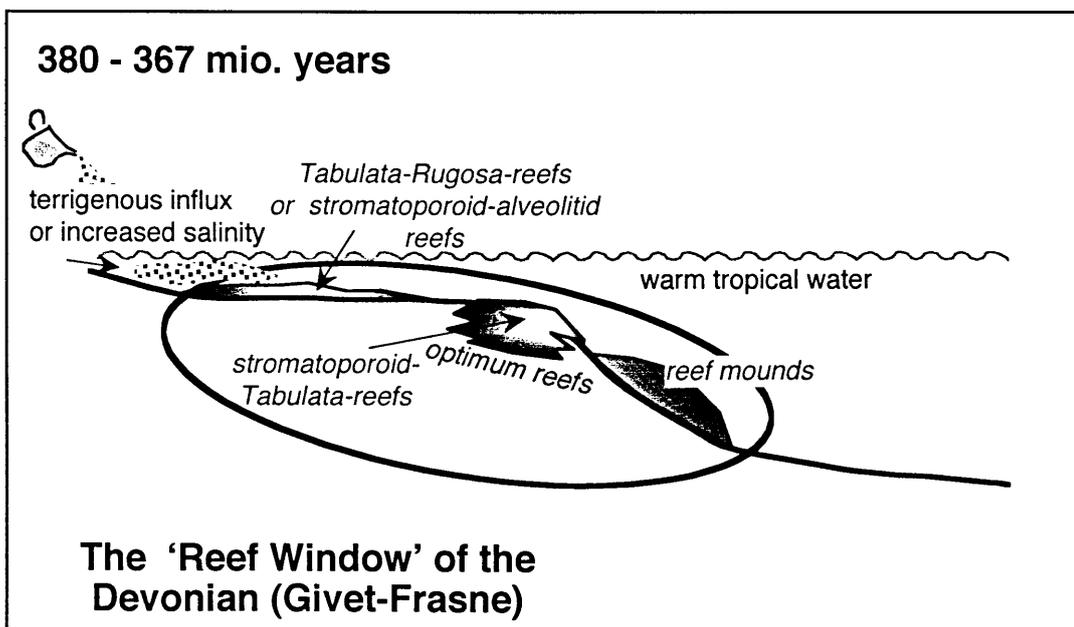
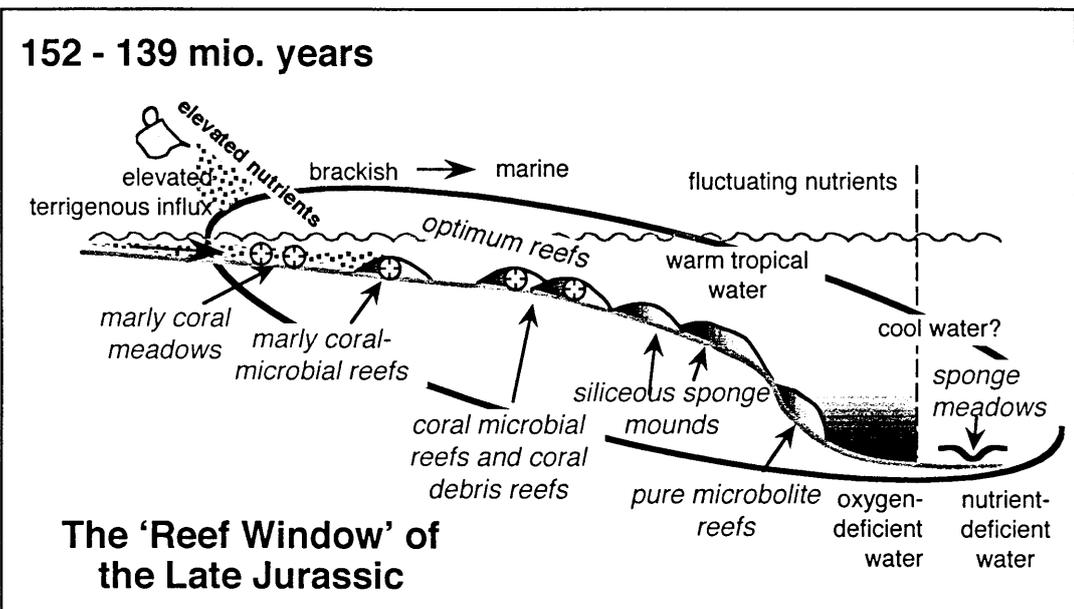
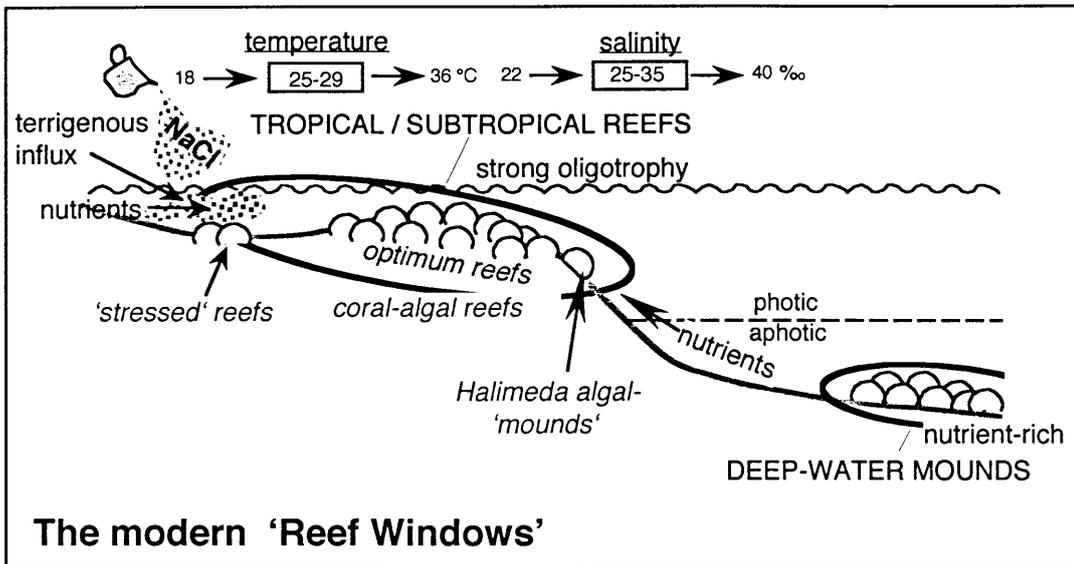
(3) Our present-day tropical reefs have the highest complexity regarding reef building blocks (RBB 1-7b). It is noticeable that no building block of earlier reef systems was abandoned, highlighting the long, *grosso modo*, unidirectional evolutionary history of reef ecosystem structure. Only reefs containing RBBs 1-7 should be considered having structure similar to modern reefs.

THE SECOND MEGATREND - WIDENING AND NARROWING OF THE REEF WINDOW

In general, increasing modular complexity of reefs was paralleled by increasing adaptation and synecological interdependence of reef organisms. However, similar modular complexity does not necessarily indicate similar environmental demands. Provided rudistid bivalves were photosymbiotic, they had a RBB-structure identical to modern reefs but nevertheless probably mostly lived in different environmental settings (see below). Moreover, the fact that earlier reef building blocks were not abandoned allowed a more or less wide variability of reefs with different modular complexity within a given time slice. It is mainly the environmental demands and adaptations of the available parazoan and metazoan reef taxa that define the physicochemical setting a given reef is adapted to. Besides this, general availability of suitable reef habitats is another crucial factor in determining whether or not certain reef types can develop. General reef habitat availability is largely controlled by plate tectonics, sea-level development and oceanographic patterns (LEINFELDER 1994).

Archaeon to Triassic global reef windows

The environmental demands for the first bacterial reefs in the Archaeon are unknown but were possibly well defined; controlling factors might have been availability of organic matter or inorganic methane as well as calcium and carbonate/bicarbonate ions, suitable water temperatures, alkalinity and pH-values, and strongly reduced sedimentation rates. A suitable set of these factors was probably only rarely achieved, making Archaeon reef bodies rare. With the development of cyanobacteria and the cooling of Precambrian oceans, stromatolites expanded vastly into many photic environments, although low illumination



is sufficient for such simple organisms. With the onset of 'parazoan' and 'true' metazoan development, reef ecosystems were more widely defined. New energy sources were opened by new feeding strategies of reef organisms. Moreover, the ability to tolerate certain sedimentation rates, owing to the baffling and binding activities of the reef organisms, lifted them more rapidly to higher feeding levels. Dependence upon light diminished due to heterotrophic feeding strategies. With the development of photosymbiosis, additional energy sources were introduced, without abandoning reef settings on the deeper shelf. Increased growth rates of photosymbiotic 'parazoans' and metazoans also helped tolerating higher background sedimentation and more frequent fragmentation by high-energy events, respectively. During the Paleozoic, the reef window was fairly wide in the Mid and early Late Devonian (Fig. 2) (NOSE & LEINFELDER in prep.), to become cut off in its shallow/high-energy part owing to the extinction, or decimation, of high-energy reef organisms part at the intra-Late Devonian reef crisis. Famennian to Lower Carboniferous coral facies is largely restricted to deep settings (e.g. GISCHLER 1996). Nevertheless, the margins of the subsequent reef windows, though strongly fluctuating and punctuated by reef gaps, remained moderately wide, with very different types of reefs developing during the Late Paleozoic and into the Triassic.

Jurassic reef window

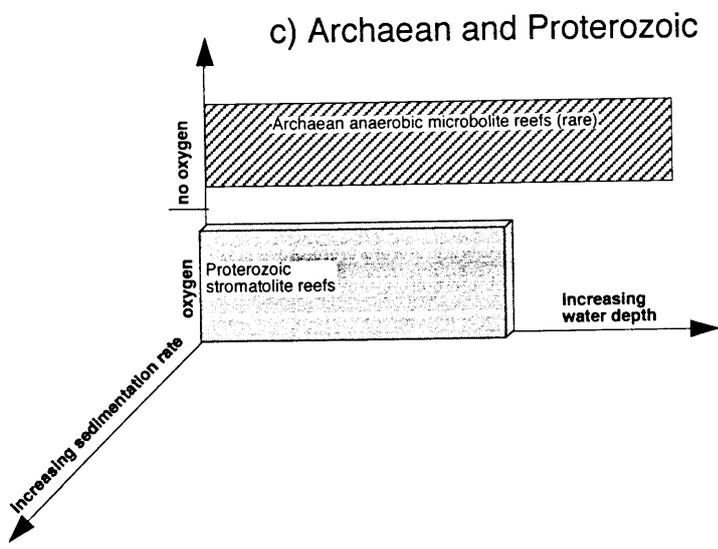
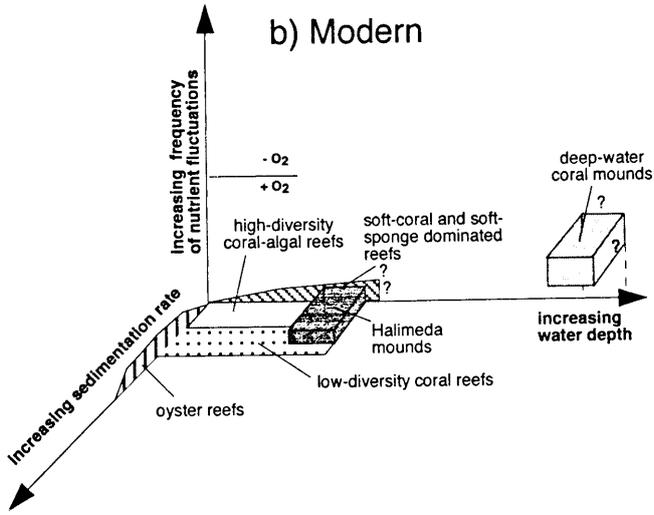
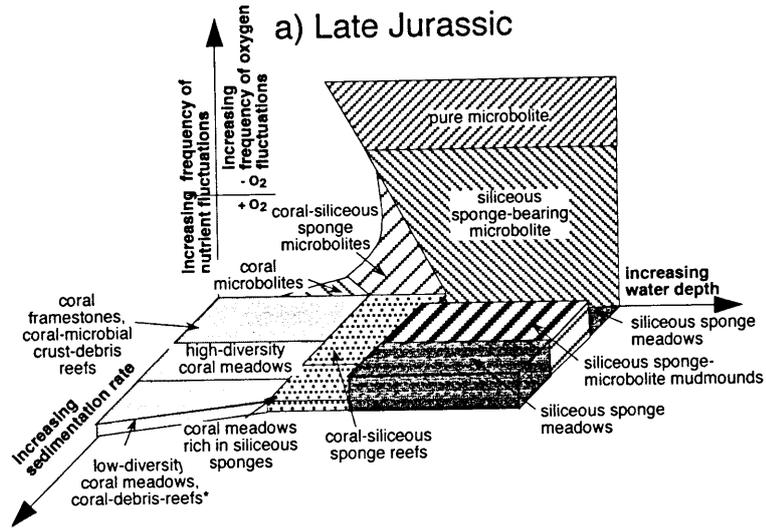
The Jurassic reef examples demonstrate that the reef window was very wide, which mostly is

due to its transitional situation. Many marginal, 'stressed' reefs (siliciclastic reefs, brackish water reefs, various deep shelf reefs, dysaerobic reefs) existed, owing to the widespread occurrence of the 'conservative' reef organisms (sponges, microbionites) together with the newly established adaptive strategies, particularly within corals. It was the time of change towards photic algal symbiosis in scleractinian corals, with corals thriving both in mesotrophic and in increasingly oligotrophic environments (LEINFELDER et al. 1996, NOSE & LEINFELDER 1997, NOSE & LEINFELDER in prep.) (Figs. 2, 3).

Cretaceous reef window

The reef window of the mid to late Cretaceous still remains to be defined, since there is a lot of controversy as to the exact environmental demands of rudistid reefs versus Cretaceous coral reefs (cf. KAUFFMAN & JOHNSON 1988, GILI et al. 1995). In general, the reef window remained at least as large as during the Late Jurassic, although deeper shelf mound reefs became less important, probably due to stratified water bodies. Coral reefs started to change to the coral-coraline algal type which might have resulted in narrowing of their environmental tolerances. Rudists might have taken over in more unstable reef settings such as those involving elevated or fluctuating nutrient concentrations, higher sedimentation rates, or hot water temperatures as a consequence of a super-greenhouse effect (cf. GILI et al. 1995, KAUFFMAN & JOHNSON 1988, 1997, STEUBER 1996, 1997, SCOTT 1995, VOIGT 1995).

Fig. 2. Examples for general reef windows (modified from LEINFELDER 1997 and LEINFELDER & NOSE in prep.. Modern reef window based on JAMES & BOURQUE 1992, modified, Devonian reef window based on MAY & NOSE, in NOSE & LEINFELDER in prep.). Note that the modern tropical/subtropical reef window is smaller than the Devonian and Late Jurassic reef window. Modern reefs occur within two distinct reef windows (tropical/subtropical reefs and deep-water mounds) separated by a bathymetric/nutrient gap. Contrasting, Jurassic reefs occupied a vast potential area across the shelf. Besides the variable size of the reef windows, major differences are the strong oligotrophy and the stronger compartmentalization of modern reefs, as caused by the highly developed photosymbiotic relation and the development of algal reef crests in highly abrasive settings. The position for optimum reefs (as defined by maximum modular complexity and maximum taxon diversity) is also variable through time, depending on the adaptational evolutionary stage of reef organisms. Modern optimum reefs occur in shallow, agitated, strongly oligotrophic waters. Jurassic optimum reefs thrived in slightly deeper, mesotrophic waters. Reefs along the margins of the reef window ('stressed reefs') also differ considerably through time. Modern deep-water coral mounds are offset from the tropical reef window by a nutrient and bathymetric gap, and thus do not belong to the same reef window (see Fig. 3). Jurassic deep-water sponge mounds may grade into coral reefs and consequently occupy the same reef window. See text for further explanation.



Cenozoic to modern reef windows

After the disappearance of the rudistid bivalves during the end-Cretaceous, coral reefs had difficulties to take over all free marginal settings of the reef window, previously inhabited by rudists. After a lag episode of deep-water coral reefs during the Paleocene, coral-coraline algal reefs reconquered shallower environments and, in the Miocene, became adapted to abrasive highest energy settings. This gave rise to the development of algal ridges (STANLEY 1989), which caused strong compartmentalization of reef into environmentally very different zones, such as reef front, reef crest/flat and back reef-lagoonal zones. This has also fundamentally changed the sedimentology within the reefs and the reef surroundings. Reef zonation has existed earlier but complete sheltering of lagoons in highest energy environments normally was not possible prior to the development of algal ridges. It seems that microbially bound high-energy reef crests developed only very exceptionally during earlier times of Earth history (LEINFELDER 1992, NOSE & LEINFELDER in prep.).

Waxing, waning and splitting of reef windows

In conclusion, the development of the reef window dimensions is not parallel with the largely unidirectional development of reef building blocks, but reflects both major global environmental crises and different adaptive strategies of reef organisms. The reef window widened continuously until the intra-Late Devonian reef crisis, and remained more narrow until the Mid-Triassic. From the Late Triassic to the final Cretaceous, it widened, only to

become narrow again after the Cretaceous/Tertiary boundary (Figs. 2, 3). The wide mid-Paleozoic and mid/late Mesozoic reef windows share some similarities (sponge reefs and mudmounds in the deeper waters, differentiated coral and other reef types in the shallow water), but it appears that marginal settings were more widely exploited by reefs in the Mesozoic example (Fig. 2). The narrow Late Paleozoic to Mid-Triassic reef window is quite different from the narrow Mid-Tertiary to modern reef window, because Late Paleozoic to Mid-Triassic reef types were largely confined to somewhat deeper settings, whereas the Cenozoic tropical window is still narrower, and reefs thrive almost exclusively in shallow water. Present deep-water coral associations (FREIWALD et al. 1997, HENRICH et al. 1997) appear not at a marginal position within, but are distinctly separated from the modern tropical/subtropical reef window, thus possessing their own ecological window. Kelp forests are the intermediate shallow-water ecosystem between modern deep-water coral associations and modern tropical reefs (FREIWALD 1993, HENRICH et al. 1997), separating both along a temperature and nutrient gradient (Figs. 2, 3). The only reefs in slightly deeper water, which are not offset from the modern tropical coral reef window, are *Halimeda*-green algal mounds, mostly occurring in water depths less than 20 m (Fig. 2). Hence, they overlap in water depth with coral reefs, but represent areas with slightly higher nutrition (ROBERTS et al. 1987a,b) (Fig. 3). Actually, *Halimeda* may act as a 'pest organism', overgrowing reef scleractinians in polluted reefs (e.g., Caribbean, personal investigation).

Fig. 3. Reef windows are multifactorial systems which can only be graphically presented in a simplified manner. This figure compares the triple factor model of Jurassic reefs (a, after LEINFELDER 1993 and LEINFELDER et al. 1996) with tentative models for modern reefs (b) and Precambrian reefs (c). In relation to the controlling factors 'sediment influx', 'water depth', and 'nutrient and oxygen fluctuations'. Jurassic reefs were quite tolerant, with different reef types being the product of different positions within the reef window. Modern reefs are much more environmentally restricted than Jurassic reefs in terms of the three factors displayed, resulting in a much smaller reef window (cf. Fig. 2). *Halimeda* mounds overlap the depth distribution of tropical coral reefs, and are probably related to elevated nutrient influx. Note that modern deep-water coral mounds are offset by a bathymetric and nutrient gap and thus represent an own ecological window (cf. Fig. 2). The position of this window within the triple factor model is tentative. Archaean reefs also grew within a very limited, though different reef window, but probably extended down to aphotic zones. Due to moderate light dependence, Proterozoic stromatolite reefs had a narrower window, but, unlike Archaean reefs, could probably cope up with subtile sedimentation owing to the development of trichomal cyanobacteria with a small sediment baffling capacity.

CONCLUSIONS

Increase in ecological and productive complexity (modular complexity): Reef systems have existed from Archaean times until today. Despite the fact that reefs suffered various times from global extinction or severe reduction, they have continuously increased their potential maximum modular complexity through time. This is expressed as an increase in number of reef building blocks which are the basic modules for reef growth, and which successively allowed even complex reefs to develop into a largely self-sustaining system with energy input mainly being derived from solar energy.

The reef window concept. Optimum and stressed reefs: Superimposed on the unidirectional increase of available building blocks are the environmental demands and abilities of parazoan, metazoan and floral reef organisms which define the general physicochemical setting for reef growth. These general settings are described here as 'reef windows'. The center of a reef window represents 'optimum' conditions where reefs of maximum modular complexity and maximum diversity develop. The window width defines the tolerance of the global reef system at a given time. The margins of the window are characterized by low-diversity, but not necessarily low-modular complexity, 'stressed' reefs. Modern stressed reefs may exhibit both a low-diversity/low-complexity and low-diversity/high-complexity pattern. Examples are nutrient-stressed *Halimeda* mounds (cf. ROBERTS et al. 1987b), and sediment-stressed coral-algal reefs (GREB et al. 1996, LEÃO & GINSBURG, 1997), respectively.

Variable window dimensions: Global reef window dimensions were considerably variable during Earth history. The width of a reef window defines how optimum reefs are buffered within the global reef system. A wide reef window indicates wide flexibility of the global reef system. For example, the Jurassic global reef system was more flexible than the modern one, with special reef types growing under elevated sediment stress, freshwater influence, elevated nutrient flux, even partial oxygen depletion (LEINFELDER 1993, LEINFELDER et al. 1996). Moreover, the center of the Jurassic reef window (the 'optimum' conditions) was not identical with the center of the modern one. This fact is related to lower efficiency of the newly developed photosymbiotic relation in Jurassic corals and the lack of reef building coralline red algae in Jurassic times (hence resulting in lower maximum modular complexity than today). Consequently, coral reefs have increasingly conquered habitats formerly stressful

or even hostile for reef growth, on costs of their environmental flexibility.

Influence of geological factors: Another important factor influencing the width of a global reef window is the general plate-tectonic, geomorphologic, and oceanographic framework of a given time. Modern reefs grow within a fairly narrow global reef window not only due to the outlined increased modular complexity, but also due to partial lack of other suitable reef settings. Presently, there obviously is an overall lack of habitats for potential mid-ramp reefs, which is related to Cenozoic restructuring of the shelves by frequent sea-level changes, as well as the low sea-level of today (LEINFELDER 1993, 1994). This does not permit growth of reef sponge mounds similar to the Mesozoic or Paleozoic, except for extremely rare, non-reefal occurrences (CONWAY & BARRIE 1997). Partially mirroring Phanerozoic carbonate deep-water mounds are modern deep-water coral mounds (FREIWALD et al. 1997). Unlike Phanerozoic examples, these are, however, offset from the modern tropical reef window by a temperature and bathymetric gap. For example, Jurassic siliceous sponge mounds sometimes shallowed continuously, to transform gradually into coral reefs (LEINFELDER et al. 1993a, LEINFELDER et al. 1994).

The fate of modern reefs: In general, the global reef window widened in the course of the Late Proterozoic, Paleozoic and most parts of the Mesozoic but this trend was matter of frequent fluctuations, particularly from the Devonian to the Mid-Triassic. During this time span the width of the reef window was a sum of evolution, adaptation and extinction of reef organisms, and variable availability of reef habitats. Contrasting, the Cenozoic trend towards further increased complexity of reef building blocks was negatively correlated with rapid narrowing of the reef window, mostly owing to increasing synecological interdependence of reef organisms. This trend reflects the general adaptational strategy towards a self-sustaining, low-oligotrophy, buffered ecological system. If situated in the center of the reef window, modern reefs would be well buffered and robust against perturbances. However, environmental stress, including overfishing, sewage and sediment influx, mass tourism, thinning of the ozone layer, possible global increase of temperatures, as well as increasing frequency and amplitude of El Niño-related bleaching events has already pushed the present coral reefs very close to the margin of the reef window, with many individual coral reefs having already passed the window margin. The fact that all reef building blocks are still available in modern reefs makes it likely that even a possible global extinction of modern coral reefs by the outlined factors will not

completely erase the global reef system. Possibly, microbial reefs or other robust low-complexity reef types, such as oyster reefs, *Halimeda* mounds, or oligospecific coral meadows could survive at places. However, Earth history clearly shows that lag times for reestablishment of even less complex reef types than modern coral reefs are enormous, going far beyond human time scales.

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This contribution is dedicated to the 75th birthday of R.L.'s predecessor and our colleague in office at Stuttgart University, Prof. Dr. O. Geyer. O. Geyer was not only among the first in Germany to establish a successful working group for the study of modern coral reefs (see article by his former student, Prof. Dr. Jörn Geister, this volume), he also had a strong focus on Jurassic coral fauna and sponge reefs, and therefore has considerably influenced the work of the present authors. O. Geyer already warned of negative human impact on modern coral reefs, at times where reef protection was no general topic.

The present article is a short essay on the evolution of reefs in aftermath of the DFG-priority program 'Biogenic sedimentation - Evolution of Reefs'. The article is based on own research projects on Jurassic, Paleozoic and modern reefs, as well as on own experiences in reef protection issues, but it also attempts to integrate different views on reef evolution processes. It is hoped that this article may serve as an outline for future comparative research on modern and ancient reef systems, particularly on analysis of horizontal (ecospace-related) and vertical (time-related) stress in reef ecosystems. The 'reef window concept' presented here is an attempt towards a better understanding of conditions for reef growth. This knowledge is also necessary to successfully minimize human impact on existing coral reefs, to give them a chance for survival.

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REFERENCES

- CONWAY, K.W. & BARRIE, J.V. (1997): Modern Hexactinellid sponge reefs on the western Canadian continental margin, 18th IAS Reg. Europ. Meeting, Heidelberg, 1997, Abstracts.- *Gaea heidelbergensis*, **3**:105.
- COWEN, R. (1988): The Role of Algal Symbiosis in Reefs Through Time.- *Palaios*, **3**, 221-227.
- FLAJS, G., HÜSSNER, H., FENNINGER, A. & HUBMANN, B. (1997): A richthofeniid-microbial-sponge buildup in the Upper Permian of Chios (Greece).- In: REITNER, J., NEUWEILER, F. & GUNKEL, F. (eds.): Global and Regional Controls on Biogenic Sedimentation. I. Reef Evolution. Research Reports.- *Göttinger Arb. Geol. Paläont.*, **Sb2**: 309-312.
- FLÜGEL, E. (1997): Riffe heute und früher. Die Entwicklung eines Ökosystems in der geologischen Zeit.- In: STEININGER, F.F. & MARONDE, D. (Hrsg.): Städte unter Wasser: 2 Milliarden Jahre.- *Kleine Senckenbergreihe*, **24**: 13-18.
- FREIWALD, A. (1993): Coralline Algal Maerl frameworks - Islands within the phaeophytic kelp belt.- *Facies*, **29**: 133-148.
- (1998): Modern nearshore cold-temperate calcareous sediments in the Troms District, Northern Norway.- *Journ. Sedim. Res.*, **68**: 763-776.
- FREIWALD, A., HENRICH, R. & PÄTZOLD, J. (1997): Anatomy of a deep-water coral reef mound from Stjærnsund, West-Finnmark, Northern Norway. In: JAMES, N.P. & CLARKE, J. (eds.): Cool-water carbonates.- *SEPM, Sp. Publ.*, **56**, 141-162.
- GILI, E., MASSE, J.-P. & SKELTON, P.W. (1995): Rudists as gregarious sediment dwellers, not reef-builders, on Cretaceous carbonate platforms.- *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **118**: 245-267.
- GISCHLER, E. (1996): Late Devonian-Early Carboniferous deep-water coral assemblages and sedimentation on a Devonian seamount: Iberg Reef, Harz Mts., Germany.- *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **123**: 297-322.
- GREB, L., SARIC, B., SEYFRIED, H., BROSSONN, T., BRAUCH, S., GUGAU, G., WILTSCHKO, C. & LEINFELDER, R. (1996): Ökologie und Sedimentologie eines rezenten Rampensystems an der Karibikküste von Panamá.- *Profil*, **10**: 1-168.
- HENRICH, R., FREIWALD, A., WEHRMANN, A., SCHÄFER, P., SAMTLEBEN, C. & ZANKL, H. (1997): Nordic cold-water carbonates: Occurrences and controls.- In: REITNER, J., NEUWEILER, F. & GUNKEL, F. (eds.): Global and Regional Controls on Biogenic Sedimentation. I. Reef Evolution. Research Reports.- *Göttinger Arb. Geol. Paläont.*, **Sb2**: 35-52.
- JAMES, N.P. & BOURQUE, P. (1992) Reefs and mounds. In: WALKER, R.G. & JAMES, N.P. (eds.): *Facies models. Response to sea level change*, 323-347, *Geol. Assoc. Canada, Waterloo*.
- KAUFMANN, E.G. & JOHNSON, C.C. (1988): The morphological and ecological evolution of middle and upper Cretaceous reefbuilding rudists.- *Palaios*, **3**: 194-216.
- & -- (1997): Ecological evolution of Jurassic - Cretaceous Caribbean reefs.- *Proc. 8th Int. Coral Reef Symp.*, **2**: 1669-1676, Panama-City.
- KEMPE, S., KAZMIERCZAK, J. & DEGENS, E.T. (1989): The Soda Ocean concept and its bearing on evolution.- In: CRICK, R. E. (ed.), *Origin, evolution and modern aspects of*

- biomineralization in plants and animals, 29-34, Plenum Press, New York.
- KERSHAW, S. (1998): The applications of stromatoporoid palaeobiology in palaeoenvironmental analysis.- *Palaeontology*, **41**: 509-544.
- KRAUTTER, M. (1997): Aspekte zur Paläökologie postpaläozoischer Kieselschwämme.- *Profil*, **11**:199-324.
- LEÃO, Z.M.A.N., & GINSBURG, R.N. (1997): Living reefs surrounded by siliciclastic sediments: The Abrolhos coastal reefs, Bahia, Brazil.- *Proc. 8th Int. Coral Reef Symp.*, **2**: 1767-1772.
- LEINFELDER, R.R. (1992): A modern-type Kimmeridgian reef (Ota Limestone, Portugal): Implications for Jurassic reef models. - *Facies*, **26**: 11-34.
- (1993); Upper Jurassic reef types and controlling factors - A preliminary report.- *Profil*, **5**: 1-45.
- (1994): Distribution of Jurassic reef types: A mirror of structural and environmental changes during breakup of Pangea. In: BEAUCHAMP, B., EMBRY, A.F. & GLASS, D. (eds.): *Pangea: Global Environments and Resources*.- *Can. Soc. Petrol. Geol., Mem.*, **17**: 677-700.
- (1997): Die Korallenriffe der Jurazeit.- In: STEININGER, F.F. & MARONDE, D. (Hrsg.): *Städte unter Wasser: 2 Milliarden Jahre*.- *Kleine Senckenbergreihe*, **24**: 101-112.
- LEINFELDER, R.R. & BRÜMMER, F. (1998): Der Mensch und die Riffe: Bedeutung, Gefährdung, Schutzmaßnahmen. In: LEINFELDER, R., KULL, U. & BRÜMMER, F. (eds.): *Riffe - ein faszinierendes Thema für den Schulunterricht. Materialien für die Fächer Biologie, Erdkunde und Geologie*.- *Profil*, **13**: 21-36.
- LEINFELDER, R. R. & NOSE, M. (in prep.): Physical and geological controls of Upper Jurassic reef growth. In: FLÜGEL, E. & ZANKL, H. (eds.): *Reef systems in Earth history*. Heidelberg - Berlin (Springer).
- LEINFELDER, R.R. & WERNER, W. (1993): The systematic position and palaeoecology of the alga *Marinella lugeoni* Pfender, *Zitteliana*, **20**:105-122.
- LEINFELDER, R.R., KRAUTTER, M., NOSE, M., RAMALHO, M.M. & WERNER, W. (1993a): Siliceous sponge facies from the Upper Jurassic of Portugal.- *N. Jahrb. Geol. Paläont., Abh.*, **189**, 199-254.
- LEINFELDER, R.R., NOSE, M., SCHMID, D.U. & 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., LATERNSE, 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. & LUTERBACHER, H.-P. (1994): The origin of Jurassic reefs. Current research developments and results (ed. & coord. Leinfelder, R.R.)- *Facies*, **31**, 1-56.
- LEINFELDER, R.R., WERNER, W., NOSE, M., SCHMID, D.U., KRAUTTER, M., LATERNSE, R., TAKACS, M. & HARTMANN, D. (1996): Palaeoecology, growth parameters and dynamics of coral, sponge and microbolite reefs from the Late Jurassic. In: REITNER, J., NEUWEILER, F. & GUNKEL, F. (eds.): *Global and Regional Controls on Biogenic Sedimentation. I. Reef Evolution. Research Reports*.- *Göttinger Arb. Geol. Paläont.*, **Sb2**: 227-248.
- LITTLER, M.M. & LITTLER, D.S. (1997): Disease-induced mass mortality of crustose coralline algae on coral reefs provides rationale for the conservation of herbivorous fish stocks.- *Proc. 8th Int. Coral Reef Symp.*, **2**: 719-724, Panama-City.
- LOWE, D.R. (1980): Archaean Sedimentation.- *Annual Review of Earth and Planetary Sciences*, **8**:145-167.
- MACINTYRE, I.G. (1997): Reevaluating the role of crustose coralline algae in the construction of coral reefs.- *Proc. 8th Int. Coral Reef Symp.*, **2**: 725-730.
- MONTAGGIONI, L.F. & CAMOIN, G.F. (1993): Stromatolites associated with coralg communities in the Holocene high-energy reefs- *Geology*, **21**: 149-152.
- NOSE, M. & LEINFELDER, R. (1997): Upper Jurassic coral communities within siliciclastic settings (Lusitanian Basin, Portugal, Implications for symbiotic and nutrient strategies. - *Proc. 8th Int. Coral Reef Symp.*, **2**: 1755-1760.
- & -- (in prep.): The 'reef window' concept. In: FLÜGEL, E. & ZANKL, H. (eds.): *Reef systems in Earth history*. Heidelberg -Berlin (Springer).
- NUDDS, J. & DAY, A. (1997): The effects of clastic sedimentation on a fasciculate rugose coral from the Lower Carboniferous of Northern England.- *Bol. R. Soc. Esp. Hist. Nat. (Sec. Geol.)*, **91**, (1-4), 93-97.
- REITNER, J. (1993): Modern Cryptic Microbialite/Metazoan Macies from Lizard Island (Great Barrier Reef, Australia) - Formation and Concepts.- *Facies*, **29**: 3-40.
- (1998): Entwicklung von Riffsystemen im Laufe der Erdgeschichte. "Städte unter Wasser - 2 Milliarden Jahre Riffe".- *Aufschluss*, **48**: 49-57.
- REITNER, J., GAUTRET, P., MARIN, F. & NEUWEILER, F. (1995): Auto-micrites in a modern marine microbialite Formation model via organic matrices (Lizard Island, Great Barrier Reef).- *Bull. Inst. oceanogr. Monaco*, nr. spéc., **13**: 1p.
- RIDING, R. & GUO, L. (1992): Permian marine calcareous algae.- In: RIDING, R. (ed.): *Calcareous algae and stromatolites*, 452-480, Springer, Berlin.
- ROBERTS, H.H., PHIPPS, C.V. & EFFENDI, L. (1987a): *Halimeda* bioherms of the eastern Java Sea, Indonesia.- *Geology*, **15**: 371-374.
- , --, &-- (1987b): Morphology of large *Halimeda* Bioherms, Eastern Java Sea (Indonesia): A side-scan sonar study.- *Geo-Marine Letters*, **7**: 7-14.
- ROSEN B. R., PAGE, H. A., & PERRIN, M. (1991): In Search of the Invisible Algal Symbiosis in Fossil Corals. — In: VI. International Symposium on Fossil Cnidaria including Archaeocyatha and Porifera, Munster/Westphalia, September 9-14, 1991; Abstracts: **a3**; Münster (Geol.-Paläont. Mus.).
- SCHUMANN-KINDEL, G., BERGBAUER, M. & REITNER, J. (1996): Bacteria associated with mediterranean sponges. In: REITNER, J. NEUWEILER, F. & GUNKEL, F. (eds): *Global and Regional Controls on Biogenic Sedimentation. I. Reef Evolution. Research Reports*. Göttinger Arb. Geol. Paläont., **Sb2**:125-128.
- SCOTT, R.W. (1995): Global environmental controls on Cretaceous reefal ecosystems.- In: PHILIP, J. & SKELTON, P.W. (eds.): *Palaeoenvironmental models for the benthic associations of Cretaceous carbonate platforms in the Tethyan realm*.- *Paleogeogr., Palaeoclimatol., Palaeoecol.*, **119**: 187-199.

- SCRUTTON, C.T. (1998): The Palaeozoic corals, II: structure, variation and palaeoecology.- *Proceed. Yorkshire Geol. Soc.*, 52: 1-57.
- Schmid, D.U. (1996): Marine Mikrobolithe und Mikroinkrustierer aus dem Oberjura.- *Profil*, 9, 101-251.
- STANLEY, G.D. JR. & SWART, P. (1995): Evolution of the coral-zooxanthellae symbiosis during the Triassic: a geochemical approach, *Paleobiology*, 21: 179-199.
- STANLEY, S.M. (1989): *Earth and life through time*.- 2nd ed., 689 pp., Freeman, New York.
- STEININGER, F.F. & MARONDE, D. (eds.) (1997): Städte unter Wasser - 2 Milliarden Jahre.- *Kleine Senckenberg-Reihe*, 24: 1-186.
- STEUER, T. (1996): Stable isotope sclerochronology of Late Cretaceous rudist bivalves.- In: REITNER, J., NEUWEILER, F. & GUNKEL, F. (eds): *Global and Regional Controls on Biogenic Sedimentation. I. Reef Evolution. Research Reports. Göttinger Arb. Geol. Paläont.*, **Sb2**:199-202.
- STEUER, T. (1997): Hippuritid rudist bivalves in siliciclastic settings - functional adaptations, growth rates and strategies.- *Proc. 8. Int. Coral Reef Symp.*, 2: 1761-1766.
- TESTA, V. (1997): Calcareous algae and corals in the inner shelf of Rio Grande do Norte, NE Brazil.- *Proc. 8th Int. Coral Reef Symp.*, 2: 725-730, Panama-City.
- VOIGT, S. (1995): Verbreitung humider und arider Klimate der nördlichen Hemisphäre während der Oberkreide.- *Berliner geowiss. Abh.*, **E16**: 201-205.
- WALTER, M.R. (1983): Archaean stromatolites: Evidence of the Earth's earliest benthos.- In: SCHOFF, J.W. (ed.): *Earth's earliest biosphere. Its origin and evolution*, 187-213, Princeton Univ. Press, Princeton.
- WEIDLICH, O. (1997): Comparative analysis of Late Permian reefal limestones from the Capitan Reef (New Mexico, USA) and the Oman Mountains.- In: REITNER, J., NEUWEILER, F. & GUNKEL, F. (eds.): *Global and Regional Controls on Biogenic Sedimentation. I. Reef Evolution. Research Reports.- Göttinger Arb. Geol. Paläont.*, **Sb2**: 329-332.