

Comparative palaeoecology of marly coralline sponge-bearing reefal associations from the Kimmeridgian (Upper Jurassic) of Portugal and Southwestern Germany

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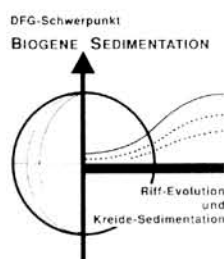
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Abstract: Three marly reefal associations from the Kimmeridgian of Portugal (Alcobaça, Serra Isabel) and southwestern Germany (Faulenhau), which share a high proportion of coralline sponges as a main unifying element, were studied in a comparative manner. The two Portuguese associations are dominated by corals and coralline sponges (Alcobaça), and by crinoids and corals (Serra Isabel), respectively. Both sedimentological and palaeoecological analysis evidence a very shallow environment at Alcobaça and a deeper slope setting at Serra Isabel. The association at Faulenhau, occurring within the sponge mound facies of Southern Germany, is dominated by hexactinellid and lithistid siliceous sponges, but contains an unusually high proportion of coralline sponges.

Comparison of the three associations allows the establishment of bathymetric gradients and enables interpretation of the somehow enigmatic association at Faulenhau. All three associations grew in a fully marine, low-energy, low-sedimentation environment. The compositional differences are due to increasing bathymetry (presumably Alcobaça less than 20 m, Serra Isabel 50-60 m, Faulenhau 70-90 m). This is well reflected only at the generic and species level, where several taxa from various groups (coralline sponges, bivalves, microbes and microproblematica) are stenobath, whereas many others are not. The main trends towards deeper water are decrease in the diversity of corals, coralline sponges and "algae", increase in the diversity of siliceous sponges, change in the composition of encrusting bivalves, and decrease in the activity of boring bivalves. Changes in morphotypes and dominance of guilds occur among corals, sponges and bivalves, but are only partially helpful in discriminating environmental differences.

Bathymetric change is commonly, but not necessarily correlated with a change in nutrient and oxygen levels. Partial decoupling of these factors is obvious at Serra Isabel, where siliceous sponges are, at a cm-scale, replaced upwards by a hermatypic coral-crinoid association. However, the dominance of sponges at Faulenhau cannot be explained solely by slightly increased nutrient levels, since the diversity of coralline sponges is much lower than at Alcobaça and Serra Isabel. It is expected that the bathymetric position of the majority of the Upper Jurassic sponge-crust mounds grew in water deeper than for the Faulenhau example, i.e. below 70-90 m, although siliceous sponge facies could have occurred at lower depths in regions or at times of lowered oxygen contents or slightly increased nutrient levels, e.g. during rapid sea-level rise.

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THE Upper Jurassic of Europe is famous for its richness in both shallow-water and deep-water reefal structures. Reefs are concentrated both along the passive continental margins of the Tethyan Ocean and the incipient North Atlantic Ocean as well as in

the epicontinental seas connecting both areas. The northern Tethyan shelf exhibited a relatively simple and tectonically passive ramp configuration, where down-slope mounds composed of varying amounts of siliceous sponges, microbial crusts and lime mud developed in a belt extending from Rumania to Poland, Southern Germany, Switzerland, SE-France, SE-Spain to southern Portugal (KEUPP et al., 1990). On shallower parts of the northern Tethyan shelf contemporaneously coral meadows and coral reefs thrived (e.g. Switzerland, France, southern Portugal). At the later Atlantic margin, the onset of ocean formation was heralded by the formation of tectonically active marginal basins. A well exposed ex-

ample is the Lusitanian Basin of Central Portugal, where coral-rich reefs and reef meadows occurred in various tectonic and sedimentary settings (ELLIS et al., 1990; LEINFELDER, 1992; LEINFELDER & WILSON, 1989). The shallow epicontinental seas connecting the Tethyan and Atlantic realm, e.g. the Anglo-Paris-Basin were also rich in coral reefs (e.g. HILLY & HAGUENAUER, 1979; GEISTER & LATHUILIERE, 1991).

Nevertheless, bathymetric position and other determining factors for the growth and composition of Upper Jurassic reefs are still a matter of controversial debate (KEUPP et al., 1990; SELG & WAGENPLAST, 1990). Commonly, shallowing-upwards sedimentary successions contain siliceous sponge - microbial crust reefs in their lower parts and coral reefs in their upper parts, pointing to different depth distribution of both reef types (NOSE, et al. 1992). However, siliceous sponge facies can also occur as a "pioneer community" at the base of small coral-rich bioherms (e.g. GINER & BARNOLAS,

1979; NOSE et al., 1992). Some authors even place siliceous sponge reefs in very shallow water (e.g. KOCH & SCHORR, 1986; WIRSING & KOCH, 1986).

We consider the comparative palaeoecological approach as a useful tool for evaluating similarities and contrasts between different reef facies and for discriminating some of the controlling parameters. However, comparisons are only possible, if associations to be compared share some common elements, despite their general dissimilarity. As a first step, we present here three reefal associations from three different environmental settings which nevertheless can be aligned along a gradient from dominance of corals to dominance of siliceous sponges. All associations contain considerable amounts of coralline sponges as the prominent unifying element. Equivalence of palaeoecological comparison is given by (1) the occurrence of all three associations in marly sediments, (2) a semi-quantitative analysis, and (3) by their Kimmeridgian age, the last point excluding faunal differences caused by phylogenetic substitution of elements.

To date, most palaeoecological studies only deal with associations within one environmental setting, with the succession of associations within a single section, or compare associations from one region (e.g. FÜRSICH, 1981; WERNER, 1986; FÜRSICH & WERNER, 1986; OSCHMANN, 1990; HEINZE, 1991). However, chance, endemism and local peculiarities can, to a large part, influence the composition of a given association in a given region, so that comparative palaeoecological analysis of laterally disconnected, even remote regions is a good means to filter out local effects and to more reliably distill primary controlling factors.

Material and methods

Two of the three associations come from the north (Alcobaça) and the centre (Serra Isabel) of the Lusitanian Basin of Portugal, one from the Swabian Alb of Southwestern Germany (Faulenhau) (Fig. 1). Quantitative to semiquantitative faunal collections were made over several years in order to obtain a statistically relevant data base. Since the co-occurring taxa differ considerably in size, number of individuals were corrected for average body size by means of different factors (for details of method see FÜRSICH & WERNER, 1991).

Associations

Alcobaça (Portugal)

Setting and composition: The *Comophyllia polymorpha* - *Crispispongia* cf. *expansa* association has been found

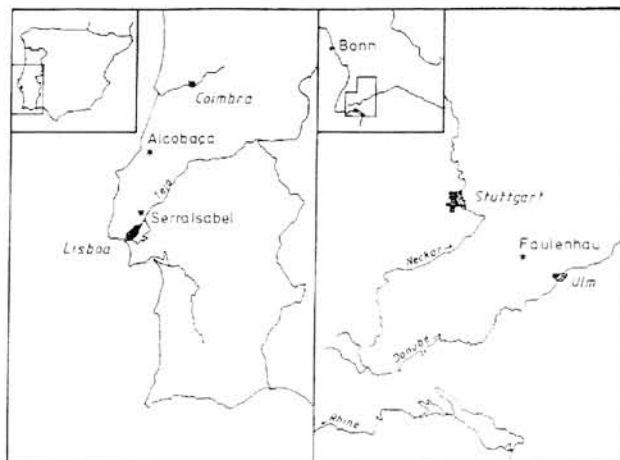


Figure 1. Location of the three Kimmeridgian reefal associations discussed in the text. – Left: The Alcobaça and Serra Isabel localities from the Lusitanian Basin of Portugal. – Right: The Faulenhau Location from the Swabian Alb of southwestern Germany.

within the Alcobaça Formation, which comprises fine- to coarse-grained mixed siliciclastic-carbonate sediments deposited in the northern, shallow part of the Lusitanian Basin (Fig. 1). The association was found at 13 localities at different levels within a 5 to 10 m thick unit in the upper part of the Alcobaça Formation. It occurs within silty marls and is commonly associated with quartz-rich, marly oolites. Only a brief description of the association is given here, since it was already presented in detail by FÜRSICH & WERNER (1991).

Together with a highly diverse coral community, coralline sponges, represented by 19 taxa, are the dominant faunal group. Principal growth forms are cylinders (e.g. *Crispispongia parabolis*, *Corynella quenstedti*) as well as fans (e.g. *Elasmostoma* sp. A, *Crispispongia* cf. *expansa*). Rarely, branched forms such as some specimens of *Eudea* occur. The average size of coralline sponges is about 2–3 cm. Except for one doubtful demosponge found within a microbial crust, no siliceous sponges could be observed. More than 60 taxa of corals are present, whereby flat to inverted cone-shaped growth forms dominate (*Comophyllia polymorpha*, *Meandראה bonanomii*). Commonly, these corals are fixed to the substrate only by a small attachment area. Sizes of massive coral colonies may attain 15 cm.

Bivalves (e.g. the oyster *Praeexogyra pustulosa*) and echinoderms (predominantly the crinoid *Millericrinus lusitanicus*; also the echinoids *Pseudocidaris mammosa* and *Paracidaris florigemma*) play an important role at some sites. Microbial crusts are common in most localities and contain a diverse flora and fauna consisting of various microbes, algae and microproblematica (e.g. *Bacinella irregularis*, *Tubiphytes morronensis*), encrusting foraminifera (e.g. *Placopsilina*, *Bullopore*, *Koskino-*

bullina cf. *socialis*), bryozoans and serpulids. A diverse encrusting and boring fauna composed of serpulids, bryozoans, thecideidid brachiopods, lithophagid bivalves, and *Trypanites* occurs on the undersides of corals and, partly, coralline sponges.

Environmental interpretation: The faunal composition and diversity of this coral/coralline sponge association varies considerably along the outcrop belt, but is sufficiently homogeneous to be regarded as the time-averaged relic of a single community. The structure of the association and the sediment characteristics indicate a very shallow-water setting of probably less than 20 m in depth. Sponge and coral morphotypes point to an environment of low or moderate energy levels. Generally, the fully marine water was fairly clear and sedimentation rate was very low. Occasional storms account for episodically raised water energy (toppling of corals, winnowing) and a greater influx of fine-grained particles.

Serra Isabel (Portugal)

Setting and composition: The second association is found within the Abadia Formation, which developed towards the centre of the Lusitanian Basin (Fig. 1). It consists of a more than 800 m thick succession of marly clays, marls and siltstones with intercalations of coarser, partly graded sandstones which may be interpreted as turbidites. Faunal content is mostly poor but changes from neuston-dominance (ammonites, belemnites) to benthic communities in the upper part. This general shallowing trend, together with the abundance of turbidites and other gravitational features (mud pebble breccia, slumpings), and with the occurrence of seismic clinoforms in the subsurface allows interpretation of the Abadia Formation as a huge slope system prograding southeastwards towards the basin centre (LEINFELDER, 1987; LEINFELDER & WILSON, 1989; NOSE et al., 1992).

The association occurs about 40 m below the top of the Abadia Formation, below the hilltop Serra Isabel in the vicinity of the small town Arruda-dos-Vinhos. It occurs in a 250 cm thick unit of clayey marl with some thin, partly silty and strongly ferruginous calcareous marlstones. In contrast to the neighbouring parts of the section, this Serra Isabel unit is very rich in fossils. The benthic association has a lense-like distribution and can laterally only be traced for several tens of metres. However, predisposition for similar biogenic faunal concentrations was great in this level, because at other localities comparable associations are found at about the same stratigraphic position within the Abadia Formation (NOSE et al., 1992; WERNER et al., in prep.)

Crinoids and corals are the dominant faunal elements (*Millericrinus lusitanicus* - *Dermosmilia* cf. *sim-*

plex association). Facies and faunal distribution is, however, not homogeneous within the unit and can be differentiated into two subfacies and sub-associations. The more prominent subfacies consists of a biogenic concentration of skeletal elements of *Millericrinus lusitanicus* across a small area of about 5 m². Crinoid roots are partly preserved in life position. The crinoidal hardparts are heavily encrusted by microbial crusts, partly forming thrombolitic patches, and by foraminifera (e.g. nubeculariids, *Placopsilina*), bryozoans ("*Berenicea*", *Stomatopora*), serpulids (e.g. *Serpula deshayesea*), microproblematica (*Tubiphytes morronensis*) and thecideidid brachiopods. Besides the crinoids, a diverse echinoderm fauna (15 taxa, e.g. *Diplocidaris gigantea*, *Pseudocidaris lusitanicus*, *Plegiocidaris marginata*) and brachiopods (e.g. *Terebratulina substriata*, *Trigonellina* sp.) lived preferably in the area of the crinoid mound.

The second subfacies is dominated by corals and surrounds the crinoid-thrombolite mound. Phaceloid corals are the prevailing morphotype (e.g. *Dermoseris delgadoi*, *Dermosmilia* ssp., *Thecosmilia* sp.). Solitary corals (e.g. *Montlivaltia*, *Axosmilia*, *Epistreptophyllum*) and massive forms (e.g. *Microsolena*) are less important constituents. In this subfacies, coralline sponges (including the sclerosponge *Neuropora*) occur regularly, yet they play a very subordinate role. They encompass 5 taxa and are represented by cylinders (e.g. *Eudea cribraria*), branching (*Neuropora*) and crustose forms (*Eudea incrustans*).

Bivalves particularly comprise cementing species (e.g. *Nanogyra nana*, *Atrreta unguis*, *Plicatula ogerieni*) as well as many shallow burrowing (e.g. *Nicanella*, *Protocardia intexta*, *Mesosacella sanctaecrucis*, *Palaeonucula menkii*) and some deep burrowing taxa (*Pholadomya protei*, *Homomya hortulana*, *Pleuromya sinuosa*). Epibyssate forms (*Juranomia*, pectinids) are somewhat less common. In a few layers, clusters of the thin-shelled pectinacean *Aulacomysella abadiensis* occur. Gastropods are represented by 13 species, but only *Diatrypesis guerreri* occupies a high rank in the trophic nucleus (WERNER et al., in prep.).

The epifaunal elements of this subfacies are heavily encrusted by foraminifera (e.g. nubeculariids, *Bullopore*, *Placopsilina*), serpulids, bryozoans, and thecideidid brachiopods. In some horizons, microbial crusts cover hardparts or form small thrombolite knobs. The crusts contain additional encrusting components such as a low-diverse cyanobacterial flora (e.g. *Girvanella*, *Cayeuxia*), *Tubiphytes morronensis*, foraminifera, bryozoans, skeletal elements of dictyid sponges and, rarely, coralline sponges.

Boring organisms are not very frequent in both subfacies, though thick monaxone spicules enriched in pat-

ches within microbial crusts points to the occurrence of boring sponges. The nectic fauna is represented by cephalopods (perisphinctids, *Aspidoceras*, *Glochiceras*, belemnites) and remains of the coral reef fish *Microdon* cf. *bernardi*.

Environmental interpretation: The fine-grained character of the sediment together with the apparent lack of reworking of shallow burrowers indicate a continuously tranquil environment. The relative richness in ammonites points to an open marine, deeper habitat. The intense encrustation, the dominance of corals and crinoids, the high carbonate content of some horizons and the ferruginous impregnations point to very low, occasionally zero siliciclastic sedimentation. Most likely, the high species diversity and the co-occurrence of deep burrowing, shallow burrowing, epibyssate and cementing bivalves is due to telescoping of different communities in a single stratigraphic level during times of general low sedimentation rates. This way, a soft-bottom fauna was gradually replaced by a firm-bottom community. However, apart from iron and manganese concentrations, classical hard-ground features such as a bored substrate are not present. The Serra Isabel faunal concentration and similar occurrences at the same horizon can be interpreted as a condensed section in a sequence stratigraphic context (WERNER et al., in prep.; LEINFELDER, in prep.) The occurrence of deposit-feeding bivalves (*Mesosaccella*, *Palaeonucula*) points to a relatively high organic content of the substrate. Thin-shelled pectinaceans (e.g. *Aulacomyella*) are now commonly interpreted as potential chemosymbiotic forms, which may indicate dysaerobic pulses at the sediment-water interface during growth of the association at Serra Isabel (cf. KAUFFMAN & SAGEMAN, 1990; SEILACHER, 1990; ABERHAN, 1992). Additionally, FRENEIX & QUESNE (1985) assume an oxygen-depleted biotope for *Aulacomyella abadiensis*, due to its occurrence in bituminous horizons. Hence, the second subfacies represents a time-averaged relic of several subsequent communities, whereas the crinoidal subfacies can be interpreted as the relic of a single community.

The *Millericrinus lusitanicus* - *Dermosmilia* cf. *simplex* association thrived in an open marine habitat on a slope situated within the lower photic zone and below storm wave base. The co-occurrence of ammonites and a moderately diverse coral fauna indicates a minimum depth of 50 m and a maximum depth of about 60 to 70 m.

Faulenhau (southwestern Germany)

Setting and composition: The Faulenhau locality is situated in the Swabian Alb (30 km northeast of Ulm, near the village Westerheim, Fig. 1). The occurrence of the ammonite *Aulacostephanus eudoxus* at the fossil locality

and a find of *Sutneria subeumela* several metres above indicates a position in the upper part of the *eudoxus* zone (late Middle Kimmeridgian). No good outcrop exists and quantitative collections were made over several years on a bare, horizontal field, where fossils were concentrated within a fixed area of 10 × 10 m. The collected fauna is certainly derived from a marly level, since well preserved, isolated faunal elements cannot be obtained from limestone facies in the Swabian Alb. Moreover, no limestone rubble exists on the ploughed field. Thin marl horizons rarely occur in the *eudoxus* zone which, in the Swabian Alb, is predominantly characterised by calcareous sponge-crust facies (e.g. GEYER & GWINNER, 1984). At the Faulenhau site, underlying and superimposed rocks are represented by sponge-crust biohermal limestones (KRAUTTER, in press) and it is assumed that the collected fauna relates to a small, probably laterally restricted faunal meadow within a very narrow horizon.

The fauna is dominated by sponges, which comprise 75 % of the entire fauna (164 specimens) (Fig. 2). Both siliceous sponges (87% of sponge fauna) and coralline sponges (13 %) occur together (Fig. 3; Tabl. 1). Siliceous sponges commonly exhibit calcareous preservation and comprise both hexactinellids (Dictyida 31 % of sponge fauna, Lychniskida 10 %) and lithistids (42 %). Coralline sponges are exclusively represented by Calcareia (Tabl. 1, Fig. 3) and are mostly silicified. The dominant growth forms are cup shapes (37 %, e.g. *Hyalotragos*, *Cnemidiastrum*, *Cypellia*) and cylinders (28 %, e.g. *Radiscispongia*, *Cylindrophyma*, *Craticularia*). Less common are plates (10%, e.g. *Platychonia*, *Stauroderma*) and knobby to ball-shaped specimens (11%). Most taxa exhibit only a single morphotype (e.g. *Radiscispongia*, *Cylindrophyma*), whereas some clearly show variable growth forms (e.g. *Cnemidiastrum*, *Tremadictyon*). Cups and plates reach up to 20 cm in size. Cylinders grow up to 15 cm, whereas knobs and balls are smaller than 10 cm.

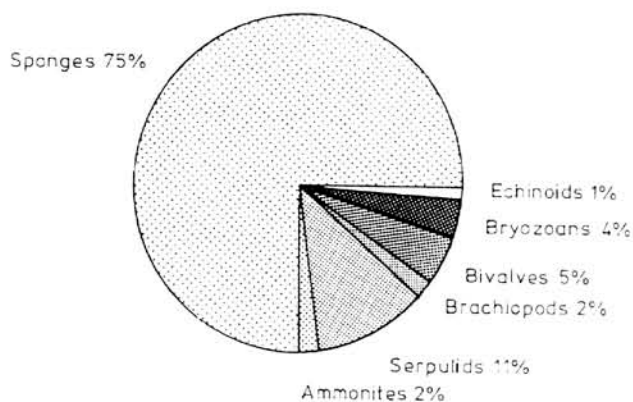


Figure 2. Faunal composition of the reefal association at Faulenhau, Swabian Alb, based on quantitative collections. Note that sponges dominate by far.

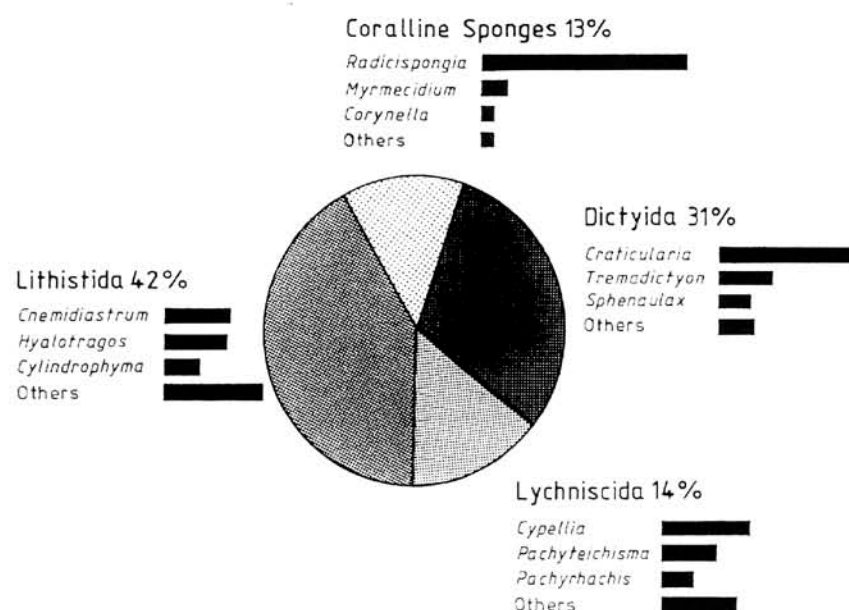


Figure 3. Sponge composition of the reefal association at Faulenhau, Swabian Alb. The association exhibits a slight dominance of hexactinellids (Dictyida, Lychniskida) over lithistids, and contains an unusually high percentage of coralline sponges (Calcarea). The relative abundance of dominant taxa is given for each sponge group.

Table 1. Faunal list of the *Craticularia parallela* - *Radicispongia radiformis* association at Faulenhau, Swabian Alb.

Echinoids

cidaroid echinids

Brachiopods

rhynchonellid and terebratulid forms

Bryozoans

Stomatopora sp.

"*Berenicea*" sp.

Ammonites

Aulacostephanus eudoxus (D'ORBIGNY)

Bivalves

Atreta sp.

gen. et sp. indet.

Serpulids

Dorsoserpula sp.

Cycloserpula sp.

Coralline Sponges

Radicispongia radiformis (GOLDFUSS)

Myrmecidium hemisphaericum (GOLDFUSS)

Corynella sp.

gen et sp. indet.

"Lithistida"

Cnemidiastrum ssp.

Cylindrophyma milleporata (GOLDFUSS)

Hyalotragos pezizoides (GOLDFUSS)

Hyalotragos cf. *patelloides*

Hyalotragos sp.

Platychonia sp.

Lecanella pateraeformis ZITTEL

Pachycothon quenstedtii KOLB

Dictyida

Craticularia parallela (GOLDFUSS)

Craticularia paradoxa (GOLDFUSS)

Craticularia sp.

Tremadictyon reticulatum (GOLDFUSS)

Tremadiction sp.

Sphenaulax costata (GOLDFUSS)

Stauroderma sp.

cf. *Casearia articulata* SCHMIDEL

Lychniskida

Pachyteichisma ssp.

Cypellia rugosa (GOLDFUSS)

Cypellia sp.

Pachyrhachis cupula (SCHRAMMEN)

Sporadopyle ssp.

Additional benthic faunal elements are terebratulid and rhynchonellid brachiopods, a few limid bivalves and some cidaroid echinids. Only a third of the sponges is encrusted by serpulids (*Dorsoserpula*, *Cycloserpula*), bryozoans ("*Berenicea*", *Stomatopora*) and poorly preserved cementing bivalves (?*Atreta*). However, the den-

sity of epibionts is extremely low; only 5 % of the encrusted sponge specimens exhibit more than 5 individuals of epibionts; most have only one or two. No microbial crusts overgrow the sponges or the other faunal elements.

Environmental interpretation: The very low percentage of encrustation indicates that growth was terminated by a sedimentation event prior to post-mortem encrustation. Hence, the faunal assemblage can be interpreted as the relic of a single community, possibly representing only one or a few populations, and the unusual co-occurrence of siliceous sponges and a high proportion of coralline sponges is obviously not due to condensation of several communities. Despite the general lack of encrusters, sedimentation rate must have been very low during the growth of this *Craticularia parallela* - *Radicispongia radiciformis* association. This assumption is supported by the predominance of sponges adapted to firm substrates. Coralline sponges generally need a firm ground for settlement (BERGQUIST, 1978; VACELET, 1988; MÜLLER, 1984). This is also true of most of the siliceous sponges, whereas the subordinate occurrence of the soft bottom dweller *Tremadictyon radicum* (cf. MÜLLER, 1991) points to less stabilized sea floor patches.

A more detailed environmental interpretation of the association is difficult, since the faunal composition does not allow a precise interpretation of water depth and other environmental parameters. The sponge fauna is highly diverse and no taxa clearly dominate. On the other hand, the accompanying fauna has a very low diversity and abundance. Since aragonitic faunal elements are preserved both in silicified and calcitic modification, diagenetic dissolution of other faunal elements, such as corals can be excluded. Consequently, the environment

offered optimum growth conditions for sponges and very poor conditions for other faunal elements. This can be explained, to some extent, by the stability of the firm substrate. The co-occurrence of large proportions of hexactinellids, lithistids, and coralline sponges is very unusual. In the Swabian and Franconian Alb, fossil assemblages rich in coralline sponges are normally associated with abundant corals, whereas siliceous sponges are absent or subordinate (e.g. the coral localities at Nattheim, Gerstetten, and Laisacker; cf. GEYER, 1953; MÜLLER, 1984; WAGNER, 1963). Among the siliceous sponges, lithistids are considered to mostly grow in shallower water than hexactinellids (e.g. REID, 1968; VACELET, 1988), so that only an overlap of coralline sponges and lithistids would be expected. In some cases, a general shallowing trend in the southwest German Upper Jurassic is recognised by the change of hexactinellid dominance in the Oxfordian to lithistid dominance in the Kimmeridgian (GEYER & GWINNER, 1986; KEUPP et al., 1990). In contrast to this trend, hexactinellids dominate in the Kimmeridgian sponge association at Faulenhau. The lack of microbial crusts cannot be interpreted as due to a position below the photic zone, since encrustation rate is generally extremely low. The high proportion of siliceous sponges, the intercalation within siliceous sponge-crust facies and the apparent lack of corals indicates that the *Craticularia parallela* - *Radicispongia radiciformis* association thrived in somewhat deeper water. However, a more detailed bathymetric interpretation cannot be obtained by focussing on the Faulenhau association alone.

GENERIC SIMILARITY AND RICHNESS

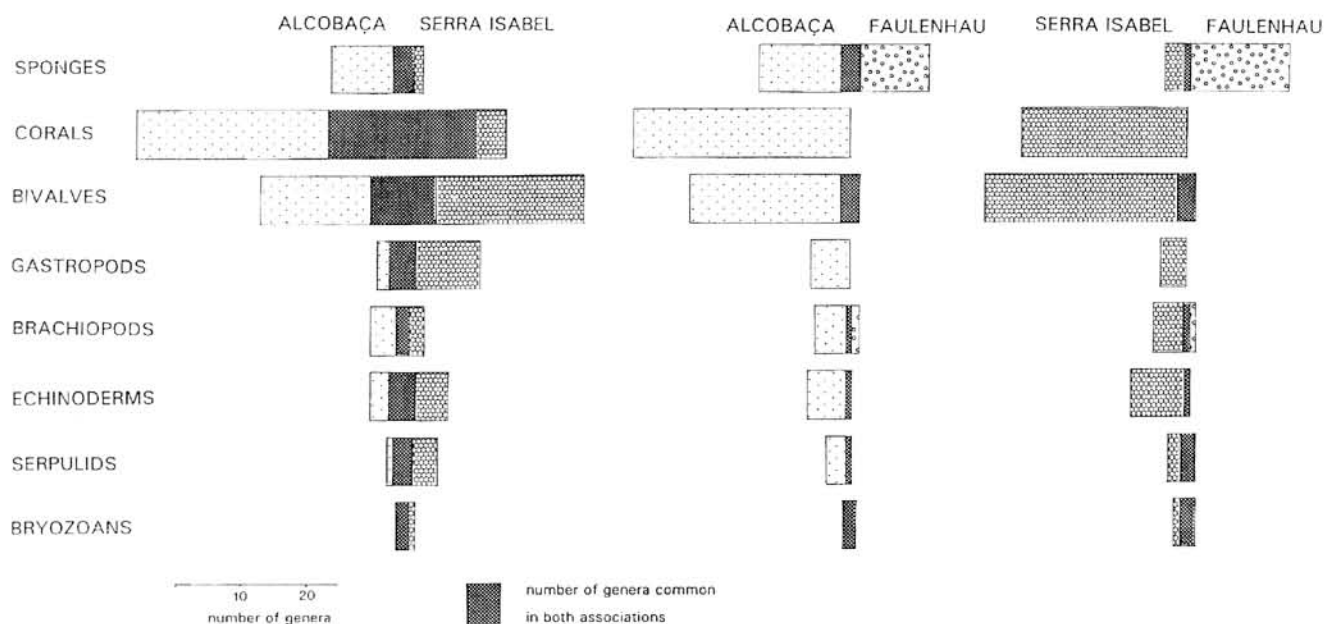


Figure 4. Generic similarity and richness of the associations at Alcobaça, Serra Isabel and Faulenhau. Note absence of corals at Faulenhau. Similarities are greatest between Alcobaça and Serra Isabel, which is mostly related to the coral fauna. Several genera are common in two or all three associations among all faunal groups.

DISTRIBUTION PATTERN OF SPONGE MORPHOTYPES

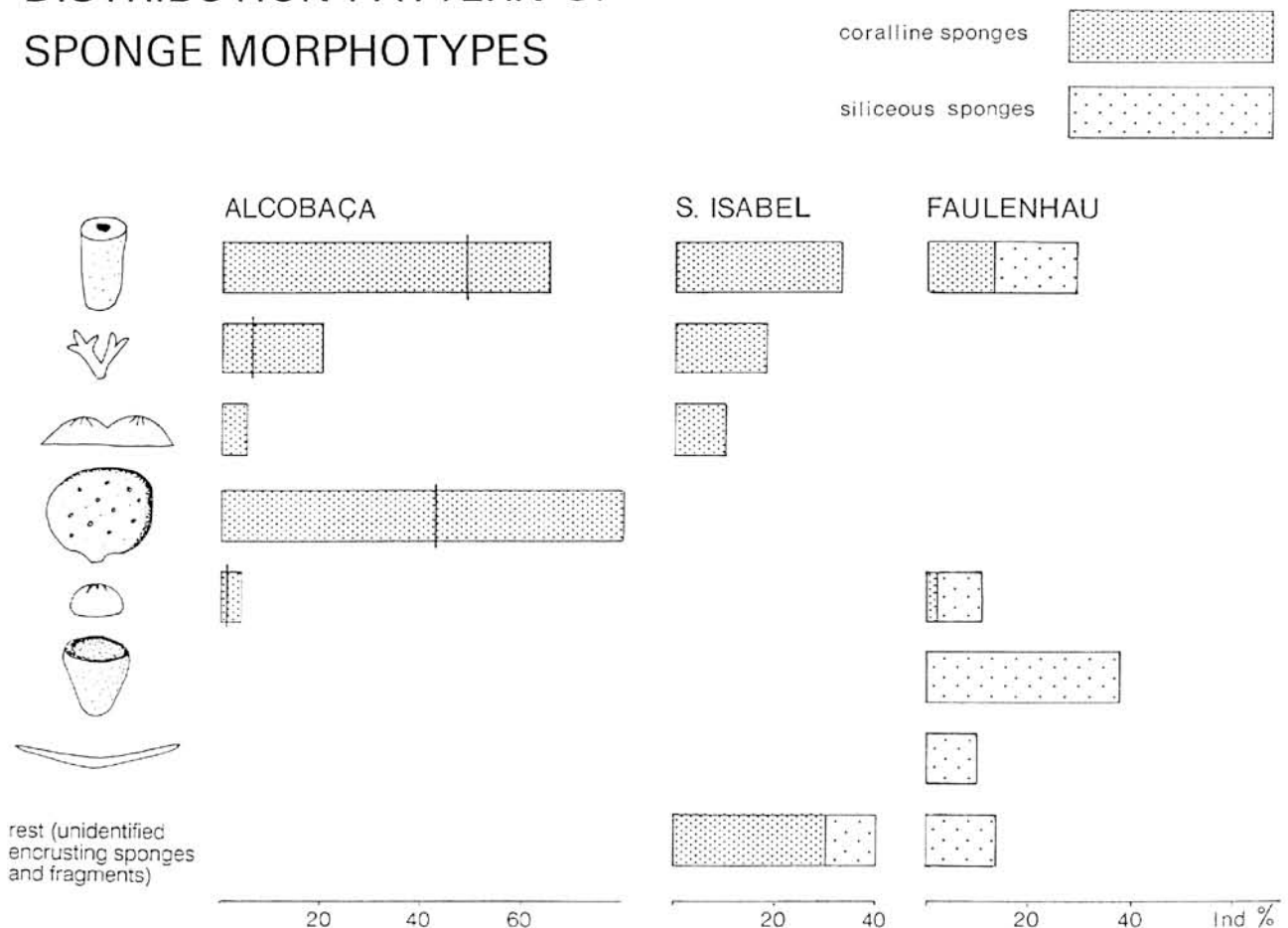


Figure 5. Distribution pattern of morphotypes of the two sponge groups "coralline sponges" and "siliceous sponges" for the three associations studied. Morphotypes comprise cylinders, branched forms, cushions, fans, knobs, cups and flat plates. (For Alcobaca, the length of the bar indicates the maximum abundance, whereas the cross line refers to the arithmetical mean value across the measurements of all localities.) Fan shapes dominate at Alcobaca, cups and plates at Faulenhau. – Cylinders dominate at Serra Isabel, but are also important at the other localities. The change from fan shapes to cylinders to cups and plates is thought to reflect changes in the filter feeding behaviour of sponges related to increasing water depth (see text).

Comparison

The three associations clearly represent very different environmental settings, which accounts for the obvious differences in their faunal composition. However, several environmental factors were equal or at least very similar in all three cases.

All three associations were found in a similar, silty to marly fine substrate characterized by low water energy and low to very low sedimentation rates. Thus the benthic fauna had very comparable conditions for its settlement so that changes in water energy and substrate characteristics can be largely ruled out as factors responsible for faunal differences. The same is true of salinity which was normal marine and stable in all examples. Due to the "middle" Kimmeridgian age, evolutionary aspects can be excluded as well. Compositional differences of the three associations were not due to chance,

since many similarities exist despite regional distances and different palaeogeographic settings. Hence, remaining controlling factors responsible for the observed differences in community composition are light, bathymetry, submarine relief, nutrients, and oxygen levels. For the two Portuguese examples a different water depth is evident already by their sedimentological character and palaeogeographic framework. Hence, the examples provide a good possibility to calibrate the gradual compositional differences between reefal associations from different water depths. Many other environmental factors, particularly illumination, nutrients, and oxygen levels are always (light) or occasionally (nutrients, oxygenation) correlated with water depth, so that the influence of these factors on faunal composition and structure will be also discussed.

Comparison of reefal associations commonly centres on comparing the different baffling, constructing,

DISTRIBUTION PATTERN OF CORAL MORPHOTYPES

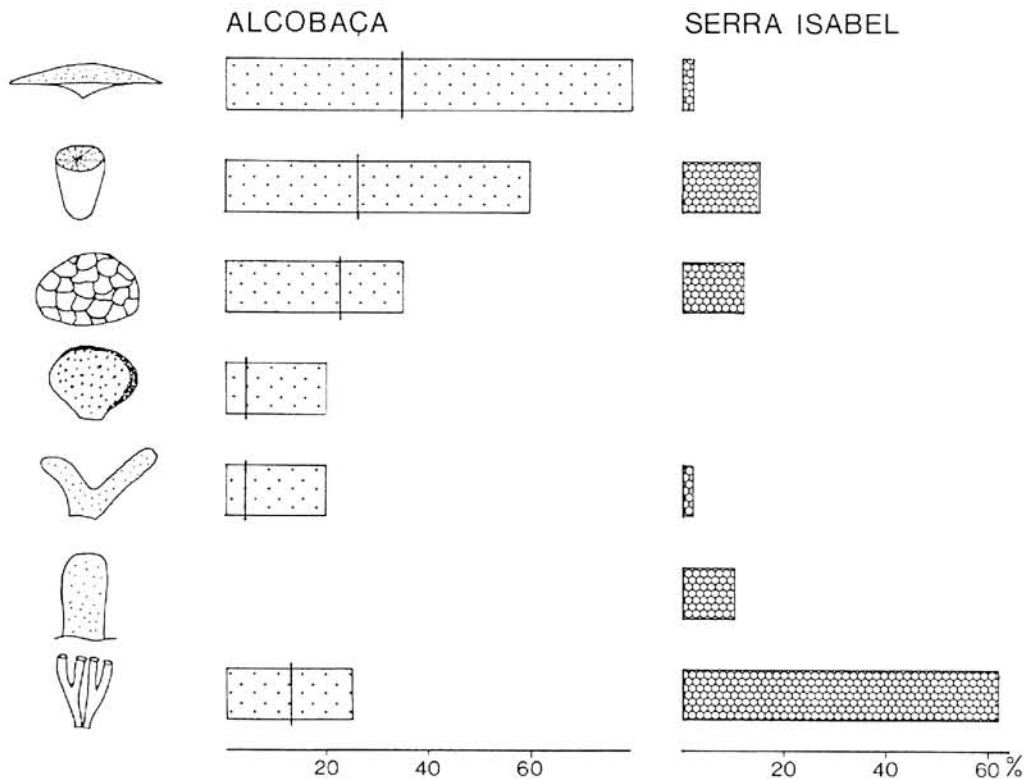


Figure 6. Distribution pattern of coral morphotypes (inverted cone shape, solitary, massive, fan, ramose, columnar, dendroid) for the Portuguese associations. (For Alcobaca, the length of the bar indicates the maximum abundance, whereas the cross line refers to the arithmetical mean value across the measurements of all localities.) Inverted cone shapes dominate in the shallow-water, low-energy association at Alcobaca, whereas dendroid shape is the predominant growth form in the deeper water environment at Alcobaca.

binding and dwelling guilds (FAGERSTROM, 1987; 1991). Members belonging to the same guild are then compared by considering their morphotypes and growth forms. According to this concept, taxa and their relative frequencies are not directly compared at lower levels (genera, species). This is in part a necessary simplification for hard reefal limestones since determination of taxa is commonly difficult if not impossible in unoriented thin-sections and abundance numbers of taxa are even more difficult to obtain. The marly reefal associations discussed here provide a good opportunity to test whether results derived from simple morphotype comparison are in accordance with results distilled from taxa-based semi-quantitative data.

Comparison of generic richness

As a first step we present a general comparison of all three associations based on generic richness (Fig. 4). The comparison of the two Portuguese localities reveals a fairly symmetrical trend, i.e. there are comparable numbers of genera occurring only in one of the two associations. The largest differences occur in corals due to

the very high number of coral taxa at Alcobaca. On the other hand, the corals also exhibit the highest percentage of genera common in both associations (23 genera). In the other faunal groups, 3 to 10 genera are common in both. The absence of corals in Faulenhau leads to an unsymmetrical pattern when compared with the Portuguese examples, but in all other groups except for the gastropods there are a couple of genera in common.

At the generic level, the similarities between the Portuguese associations are greater than with the Faulenhau example. This is, however, only due to the lack of corals at Faulenhau and the scarcity of siliceous sponges in the Portuguese examples. Within the coralline sponges, *Myrmecidium hemisphaericum* and the genus *Corynella* occur in all three associations. As for the distribution of brachiopod, serpulid and bryozoan taxa, similarities are much greater.

Sponge and coral morphotypes

A morphotype comparison of the baffling and constructing reef guild is given separately for the sponges

DISTRIBUTION PATTERN OF BIVALVE LIFE HABIT GROUPS

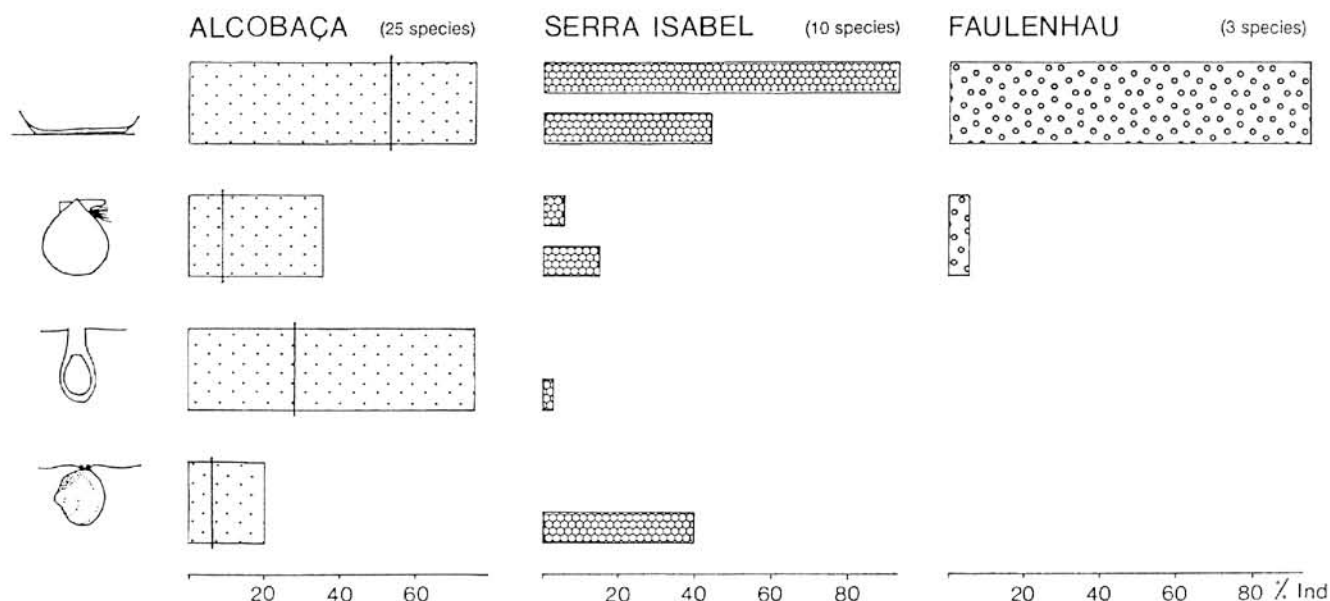


Figure 7. Distribution pattern of bivalve life habit groups (cemented, epibyssate, boring, shallow burrowing). (For Alcobaca, the length of the bar indicates the maximum abundance, whereas the cross line refers to the arithmetical mean value across the measurements of all localities.) Cemented taxa dominate in all three examples. Boring bivalves are almost exclusively restricted to the Alcobaca example, which points to deeper water settings for Serra Isabel and Faulenhau.

(Fig. 5) and for the corals (Fig. 6). The morphotypes of both siliceous and coralline sponges were classified into cylinders, branched forms, cushions, fans, knobs, cups and flat plates. In the shallow-water association from Alcobaca cylinders and fans dominate, and morphotype diversity is rather high. In the somewhat deeper setting of Serra Isabel only cylinders and branching forms of the sclerosponge *Neuropora* flourished. At Faulenhau, coralline sponges occur almost exclusively as cylinders. Among the siliceous sponges, cylinders are of moderate importance, whereas cups represent the dominant growth form.

The change of growth form dominance from fans and cylinders to cylinders to cups (Alcobaca, Serra Isabel, Faulenhau, respectively) is thought to reflect a change of environmental factors related to different water depth. There is, however, not much information about the relationships of morphotypes to life habits in sponges and in how far morphotypes of coralline sponges and siliceous sponges are comparable. Cylindrical sponges are sometimes explained as an adaption to a sluggish water current, in that cylinders act as chimneys, this way facilitating outflow of exhalant water and hence accelerating water circulation through the sponge (RIGBY, 1987) or facilitating the removal of waste water (WARBURTON, 1969). On the other hand, cylindrically growing coralline

sponges may simply try to reach higher filter feeding levels. Similarly, a fan shape might be favourable for filter feeding within flowing water whereas cup shapes and plate shapes could represent an adaption to very reduced sedimentation rates and/or reduced competition for space. Plate shape is particularly difficult to explain, since this growth form is hardly represented among modern sponges. Since many modern sponges contain symbiotic cyanobacteria (SARA, 1971; VACELET, 1971; WILKINSON, 1978; WILKINSON & EVANS, 1989), in some fossil taxa, plate shape might be an adaption to low illumination. Another explanation for plate shape would be that due to the position of the inhalant system at their undersides, platy sponges preferentially grow close to the substrate in order to be able to stir up bacteria-sized organic material which settled on the sea-floor. In the examples presented here, it is not clear which depth-related environmental factors determined the shape of the sponge morphotypes.

The distribution pattern of coral morphotypes (Fig. 6) reveals distinct differences between the Alcobaca and Serra Isabel associations. At Alcobaca, the inverted cone shape growth form of *Comophyllia* and *Meandראה* dominates, while these taxa are absent at Serra Isabel. Fan shapes occur exclusively, massive and ramose forms more frequently in the shallow-water environment of Al-

cobaça. Dendroid growth forms occur frequently in both localities, which can be explained by the low-energy characteristics not only at Serra Isabel but also in the protected shallow-water environment at Alcobaça. The dominance of dendroid growth forms in the deeper setting of Serra Isabel apparently results from a decrease in the abundance of other growth forms.

Important factors for determining the growth form of corals are light, water energy, nutrients and sedimentation rate (e.g. GEISTER, 1983; FAGERSTROM, 1987; GRAUS & MACINTYRE, 1989; HUBBARD, 1973; HUBBARD & POCKOCK, 1972). For instance, the enlargement of the upper surface area in the modern corals is commonly related to increasing water depth and thus explained as an adaption to lower illumination (KÜHLMANN, 1982; LEVINTON, 1982). This is strongly contrasted by the examples discussed here where forms with a large surface are almost exclusively restricted to the very shallow Alcobaça association. Hence, the comparison at the morphotype level does not yield clear results. However, at the generic and species level, changes in growth form can, in some taxa, be related to an increase in water depth. *Convexastrea sexradiata*, for instance, exhibits massive or fan-shaped forms at Alcobaça, but columnar forms at Serra Isabel. Similar changes can be observed in microsolenids with crustose to massive forms at Alcobaça and crustose to columnar forms at Serra Isabel.

Bivalves

In all three examples the bivalves are strongly dominated by cemented species (Fig. 7). Epibyssate taxa are of medium importance. Lithophagid boring bivalves are an important constituent in the shallow-water association at Alcobaça, but are rare or lacking at the other localities. Requirements of boring bivalves include a very low sedimentation rate. Since the other faunal elements, particularly the corals and sponges, and sedimentological features indicate very reduced sedimentation rates for all three examples, sedimentation was certainly not responsible for suppressing boring bivalves at Serra Isabel and Faulenhau. Boring bivalves have their distribution maximum in very shallow water, so that again water depth might, to some extent, be responsible for the differences in the distribution pattern (EKDALE et al., 1984).

Except for the boring bivalves, the distribution of the other bivalve morphotypes alone does not provide any significant information about the biotope. Only a comparison at the species level reflects the enormous dissimilarities, most of which can be also attributed to different water depths and related factors.

Fig. 8 presents the depth distribution of some fixo-sessile bivalves at the species level which has been cali-

DEPTH DISTRIBUTION OF SOME FIXO-SESSILE BIVALVES IN THE KIMMERIDGIAN OF PORTUGAL

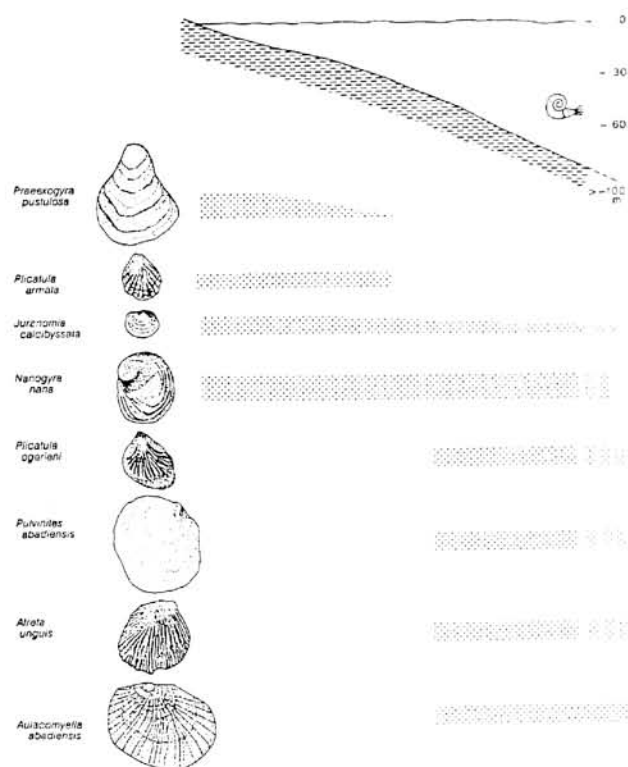


Figure 8. Depth distribution of some fixo-sessile bivalve species occurring in the associations discussed here (except for *Plicatula armata*). The bathymetry has been calibrated by previous studies on Portuguese bivalve associations of Kimmeridgian age. (FÜRSICH, 1981; FÜRSICH & WERNER, 1986, 1988, 1989; WERNER, 1986). This pattern supports the sedimentologic interpretation of a shallow-water character at Alcobaça and a deeper environment at Serra Isabel.

brated by previous studies of Portuguese Kimmeridgian bivalve faunas (e.g. FÜRSICH, 1981; FÜRSICH & WERNER, 1986, 1988, 1989; WERNER, 1986). The depth distribution is given for taxa which occur in the associations discussed here.

Among the cementing bivalves, *Praeexogyra pustulosa* and *Plicatula armata* are exclusively restricted to shallow water settings. *Nanogyra nana* is ubiquitous and commonly very abundant, hence not useful as an environmental indicator. On the other hand, *Plicatula ogeriense*, *Pulvinites abadiensis* and *Atreta unguis* are restricted to deeper offshore habitats.

Since at Faulenhau fixo-sessile bivalves are too rare and too poorly preserved to yield statistically relevant data, Faulenhau bivalves are not regarded in Fig. 8. However, ?*Atreta* sp. could be found in Faulenhau as well as in other sponge reef localities of the Swabian Alb. During the Late Jurassic, the genus *Atreta* seems to have been entirely restricted to deeper settings, which is in accordance with the occurrences at Faulenhau.

Echinoderms

The abundant occurrence of the possibly up to 1 m high crinoid *Millericrinus lusitanicus* at both Portuguese localities evidences an eurytopic character of the taxon, whose adaptional strategy was to reach a high filter level. According to A. VADET (Boulogne-sur-Mer; written comm.) the regular echinid *Paracidaris florigemma* and *Pseudocidaris mammosa* of Alcobça are considered to be typical high-energy coral reef forms, whereas *Diplocidaris gigantea* and *Pseudocidaris lusitanicus* found at Serra Isabel are representatives of tranquil water settings. *Plegiocidaris ?marginata* is considered to be ubiquitous and actually also occurs at both sites. The general characterization of the Serra Isabel setting is in accordance with the interpretation based on the echinids. Based on the overall faunal and sedimentological characteristics, the association at Alcobça did not grow in a high-energy reefal settings. In this case, this is partially in contrast to the evidence given by echinids.

Encrusting fauna

Organisms encrusting skeletal hardparts, chiefly foraminifera, bryozoans, serpulids, brachiopods, and bivalves occur in all three associations. They are abundant in the Portuguese localities, but fairly rare at Faulenhau. Encrusting bivalves were already considered above. Fig. 9 shows a comparison of small encrusting organisms from all three localities. Although the three associations clearly grew in different environments, no general differences in the distribution of morphotypes and even genera are apparent. This is particularly true of the serpulids and bryozoans, whereas among the encrusting brachiopod *Crania* appears to be restricted to shallow water.

As with other groups, different environmental conditions may become apparent in most cases only at the species level. However, the same encrusting foraminifera identified at the species level occur both in Alcobça and Serra Isabel. The absence of foraminifera at Faulenhau might be due to the general low degree of encrustation at this site, whereas the abundance of cryptic habitats was certainly highest at Alcobça.

Microbial crusts

Apart from the individual encrusters mentioned above, microbial crusts, commonly also termed cryptalgal crusts, are very common in the Portuguese examples, whereas they are almost absent at Faulenhau. The crusts form overgrowths on skeletal hardparts and sometimes develop into small thrombolitic knobs. The crusts are similar in general morphology and structure, whereby dense or laminoid peloidal micritic areas are prevailing. However, some of the accompanying floral and faunal encrusters or crust dwellers show clear differences in

SMALL ENCRUSTERS

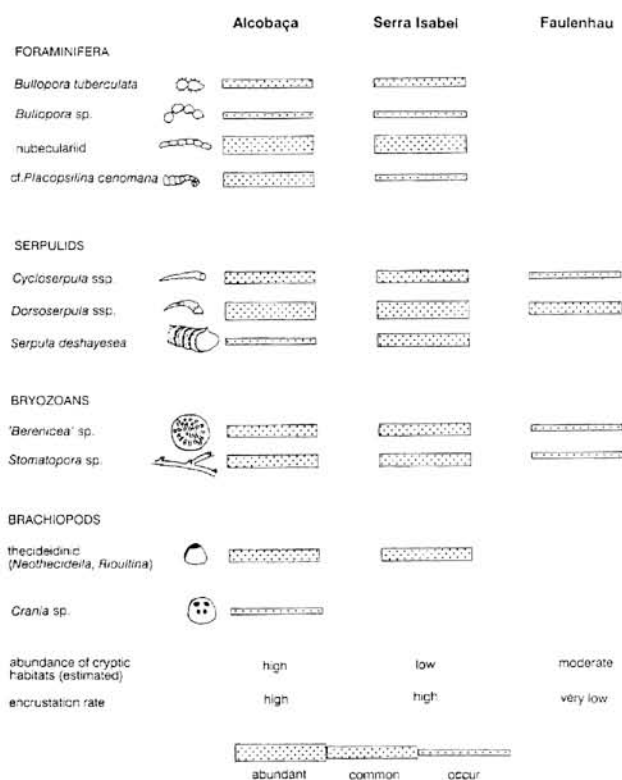


Figure 9. Encrusting fauna of the three associations studied (for cemented bivalves see Figs. 7, 8). No significant trends are obvious. The macrofauna at Faulenhau shows a very low encrustation rate. Note that even at the generic and specific level many taxa occur in two or three associations.

composition between Alcobça and Serra Isabel (Fig. 10). Porostromate algae or cyanobacteria show a markedly decrease in diversity towards the deeper water (that is Serra Isabel) as do other microproblematic forms. In the case of autotrophic forms this certainly reflects a decrease in light intensity.

Foraminifera do again not show any significant differences. The same is true of the possible microbial form *Tubiphytes* which is abundant at both Portuguese localities. This is in accordance with the partial abundance of the form in the high-energy, shallow-water calcareous Ota reef of Kimmeridgian age of Portugal (LEINFELDER, 1992) and its common occurrence in deeper water siliceous sponge facies of southern Germany (KEUPP et al., 1990) and southern Portugal (e.g. RAMALHO, 1988). Other elements of the crusts are encrusting coralline sponges, whereas intergrown hexactinellid sponges only occur at the deeper water locality Serra Isabel.

Discussion

Fig. 11 summarizes the major trends derived from the comparative analysis of the three benthic associa-

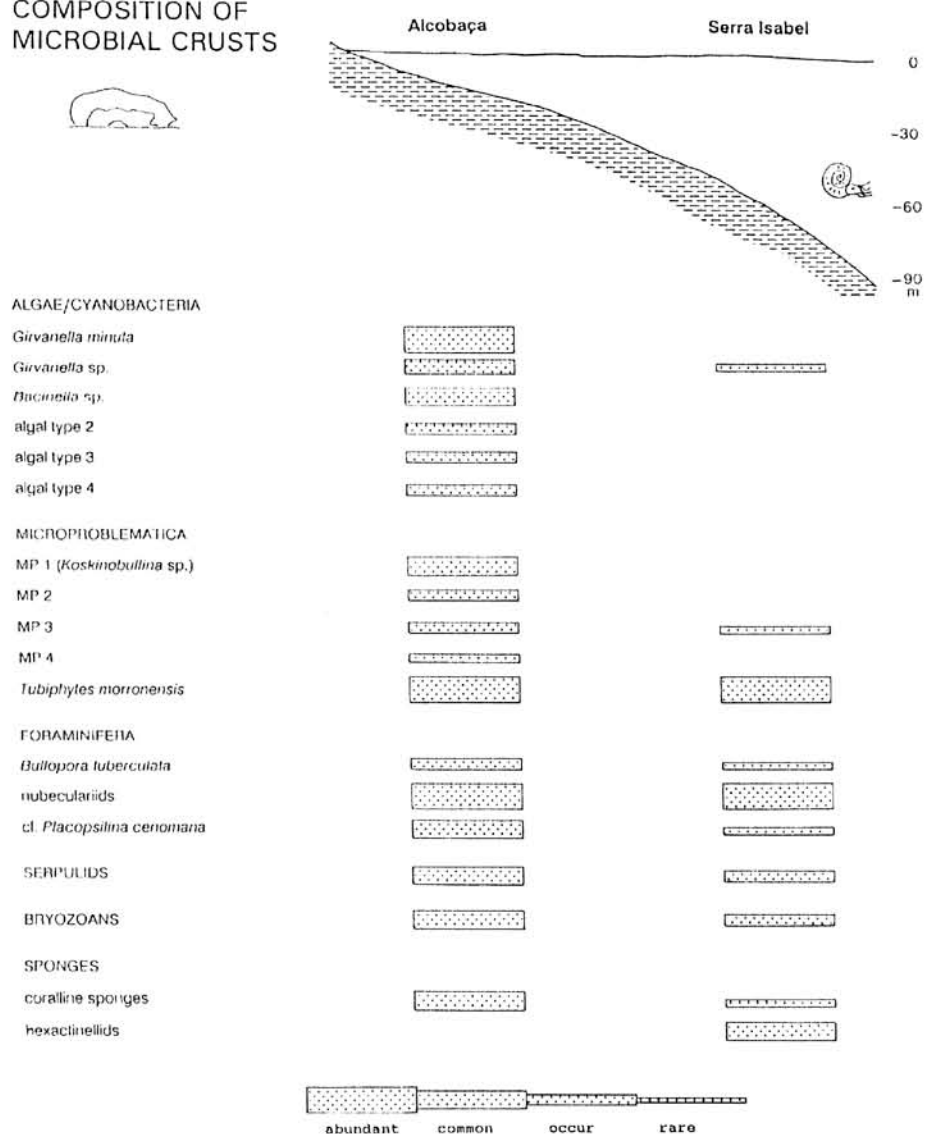
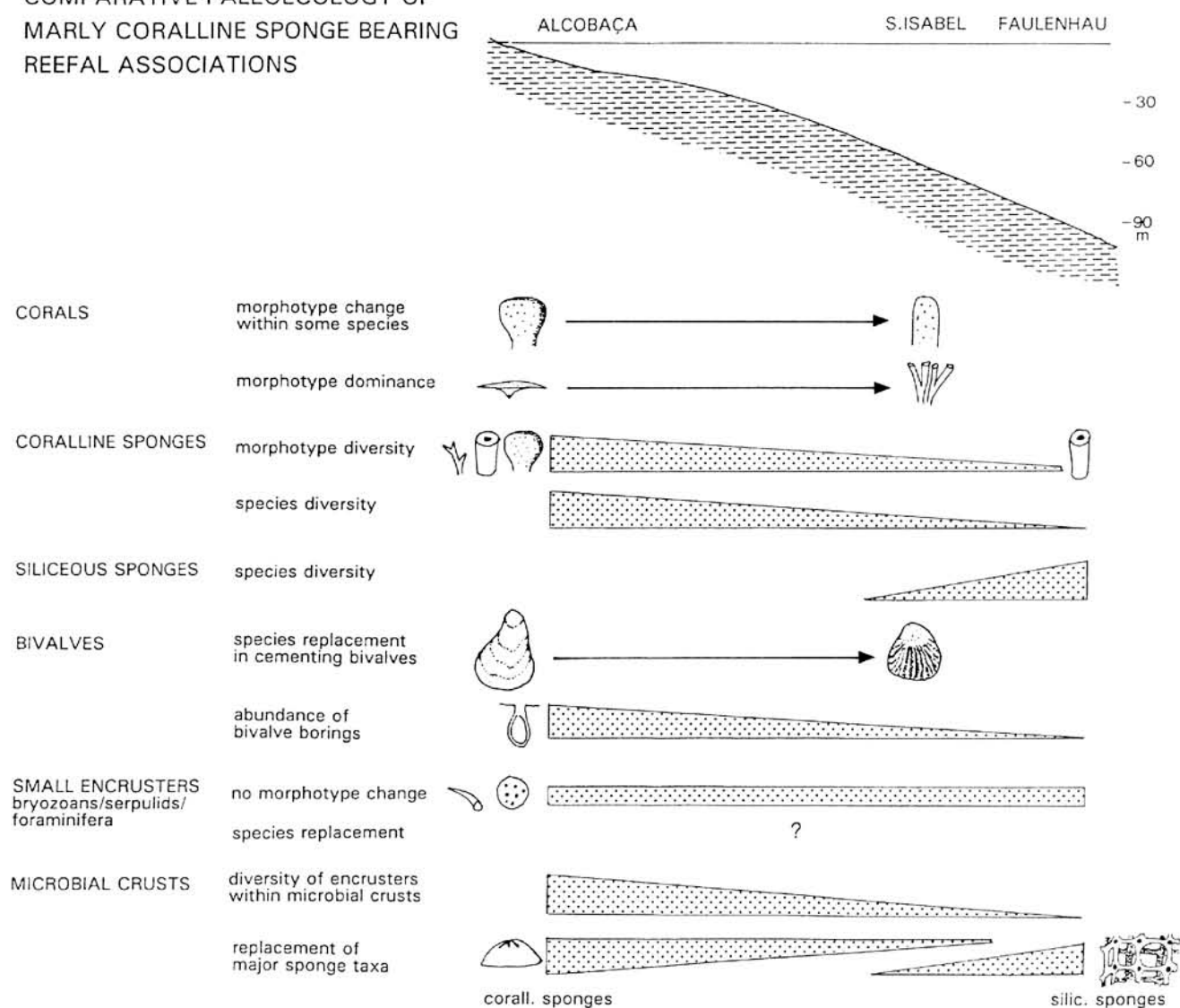
COMPOSITION OF
MICROBIAL CRUSTS

Figure 10. Encrusting organisms dwelling within microbial crusts (Portuguese examples). Algal type 2-4 and MP 1-4 refer to organisms described in FÜRSICH & WERNER (1991). Although further data are needed, the occurring algae and cyanobacteria as well as several microproblematica appear to be eurybath, whereas the occurring bryozoans, serpulids, foraminifera and *Tubiphytes* are not strongly depth-related. The distribution of encrusting sponge groups supports the trend.

tions. Since changes in factors such as substrate stability, energy level, salinity as well as evolutionary change can be ruled out, most of the differences in faunal composition can be explained by differences in water depth. The three associations can be grouped along a bathymetric gradient with Alcobaça representing the shallowest, Serra Isabel an intermediate, and Faulenhau the deepest position. For the Portuguese localities this interpretation can be independently drawn from sedimentological and sequential analysis, although more precise estimations of absolute water depths can be only derived from a palaeoecological analysis. Based on the enormous diversity of corals and the accompanying fauna, particularly fixo-sessile bivalves, water depths well below the intertidal zone but less than 20 m are likely for the Alcobaça occurrence, whereas the lower diversity and different

spectrum of corals, together with the occurrence of ammonites, siliceous sponges, presumed light-dependant members of crusts (e.g. *Girvanella*) and depth-diagnostic bivalves point to water depths of about 50 to 60 m for Serra Isabel. Using the gradients established by the comparison of the sedimentologically and palaeoecologically calibrated Portuguese occurrences, the rather unusual and sedimentologically not interpretable association at Faulenhau can be placed in water deeper than at Serra Isabel, possibly around 70 - 90 m.

Bathymetric gradients for the discussed faunal and floral groups are as follows: Among corals, some species show a bathymetric change in morphotype. The dominance of inverted cone shapes in shallow water is replaced by the dominance of dendroid growth forms to-



These faunal gradients are expected to be useful for bathymetric interpretation of other Upper Jurassic reefal associations. However, a combination of gradients of different faunal groups is a prerequisite in order to gain reliable results. Since environmental parameters are strongly related, misinterpretations are programmed

when conclusions are based on the trend of only a single faunal group. For instance, it is well known that coral diversity not only changes with water depth, but also in a given shallow setting with changing water energy (e.g. GEISTER, 1986). The increase of both siliceous and calcareous sponges at the expense of corals could be sometimes caused by a slight increase in sedimentation or nutrients or lowered oxygenation, factors which are often strongly related. This can be observed in many modern Caribbean coral reefs which undergo environmental pollution (KÜHLMANN, 1985, 1986). Similar to what is known from some modern symbiotic coral species which are adapted to great depth (e.g. *Leptoseris*, cf. KÜHLMANN, 1982), quite a few taxa of siliceous sponges are well adapted to shallow water, although the majority lives in deeper water (LEVI, 1964; REID, 1968; VACELET, 1988). Hence, it is normally not possible to discuss water depth and other environmental parameters by using very general group characteristics.

The *Craticularia parallela* - *Radicispongia radiformis* association of Faulenhau is a perfect example in this regard. The co-occurrence of hexactinellid siliceous sponges and coralline sponges is very unusual. Classically, hexactinellid sponges are considered as elements of deeper water, coralline sponges as dwellers of shallow environments. Commonly, lithistid siliceous sponges are considered as inhabiting shallower water than hexactinellid sponges (e.g. KEUPP et al., 1990), so that a possible bathymetrical overlap of lithistids and coralline sponges would be expected. It may also be dangerous to draw environmental interpretations based on the non-occurrence of some groups. The Faulenhau association is largely devoid of crusts, a fact which could be interpreted as being deposited below the photic zone. However, taking the scarcity of other encrusters into consideration, the lack of crusts seems to be more likely due to an only short-term interruption of sedimentation rate, leading to the proliferation of only one or very few populations which became buried prior to post-mortem encrustation.

Oxygen levels also considerably influence the composition of reefal associations. Reduced oxygenation seems to suppress some elements and could favour growth of siliceous sponges some of which apparently do not demand high oxygen levels due to their enormous surface and simple structure (cf. BAÇESU, 1963; REID, 1968; RHOADS & MORSE, 1971; BRACHERT, 1992). Actually, in the vicinity of the Serra Isabel location, at the same horizon which hosts the association discussed here, limestone lenses occur which contain a siliceous sponge - microbial crust association at the base and a rich coral association just a few decimetres higher in the same bed. Since considerable bathymetric changes can be clearly excluded at the scale of one bed, the determining factor appears to be a slightly to strongly dysaerobic

bottom water, possibly coinciding with a slightly elevated nutrient level at the start of growth of the limestone lens and normal oxygenation at the top of the structure (WERNER et al., in prep). Given a low sedimentation rate, microbial crusts may thrive both under high and low oxygenation, and similar dense to pelletal fabrics are apparently produced both by autotrophic and heterotrophic, aerobic and dysaerobic coccoidal cyanobacteria and bacteria (cf. GERDES & KRUMBEIN, 1987; LANG, 1989; RIEGE et al., 1991). On a dysaerobic sea floor, many elements will be oppressed and microbial crusts will have a greater tendency to form pure thrombolites. However, in the present example the occurrence of crusts and small thrombotic structures does not seem to be generally related to dysaerobic conditions. In many crusts "filaments" occur which is possibly a hint to an aerobic upper part of the crust, since "filamentous" anaerobic or dysaerobic bacteria and cyanobacteria (e.g. the facultatively anaerobic *Oscillatoria*) are almost always coccoidal (cf. COHEN et al., 1975, 1977; HÖHN, 1987). On the other hand, the occurrence of potential chemosymbiotic pectinids at Serra Isabel might point to short phases of reduced oxygenation (LEINFELDER et al., in prep.; WERNER et al., in prep.).

If keeping the complexity of reefal communities in mind, a combination of faunal gradients together with a thorough comparative quantitative to semi-quantitative analysis of the faunal composition and structure, if possible at the species level, is considered to be a powerful tool for palaeoenvironmental interpretation.

Conclusions

1. Three Kimmeridgian reefal associations, two from the Lusitanian Basin of Portugal and one from the Swabian Alb of southwestern Germany exhibiting a largely different faunal composition and structure share a considerable proportion of coralline sponges as the main unifying element. The *Comophyllia polymorpha* - *Crispispongia* cf. *expansa* association (Alcobaça, Portugal) is dominated by corals and coralline sponges, the *Millericrinus lusitanicus* - *Dermosmilia* cf. *simplex* association (Serra Isabel, Portugal) is characterized by corals and crinoids but in addition contains ammonites, coralline and siliceous sponges, whereas the *Craticularia parallela* - *Radicispongia radiformis* association (Faulenhau, Germany) exhibits an unusual faunal spectrum dominated by hexactinellid, lithistid, and coralline sponges.

2. Semi-quantitative analysis and comparison of the three associations reveal that all grew in a low-energy,

normal marine salinity, low-sedimentation regime on a stable silty to marly sea-floor. The obvious differences in faunal composition are clearly related to differences in water depth. For the Portuguese examples, differences in water depth can, less accurately, be reconstructed from the sedimentological and sequential character of the host rock. Sedimentological and sequential data for Faulenhau are not available; however from the depth ranges reconstructed for the Portuguese examples the bathymetric position of the Faulenhau association can be extrapolated. The water depth of the associations at Alcobaça, Serra Isabel, and Faulenhau is interpreted to be in the order of less than 20 m, 50-60 m and 70-90 m, respectively.

3. Comparison at the guild and morphotype level alone is no good means for discriminating genetic differences of given associations, even when using semi-quantitative data. Only at the generic, and even more so at the species level differences become distinct. At the species level, morphotype changes of corals and sponges can be very diagnostic for environmental interpretation. Besides the baffling and encrusting reef guilds, fixo-sessile bivalves and floral encrusters are of great value for determining water depths. Negative criteria must be used with caution. In the Faulenhau example, the absence of crusts is thought to be caused by the onset of sedimentation prior to a possible overgrowth of the sponges by crusts and not by a position below the photic zone.

The main faunal and floral trends from Alcobaça (shallow) to Serra Isabel (medium deep) to Faulenhau (deep) are: decrease in the diversity of corals, coralline sponges and "algae"; increase in the diversity of siliceous sponges; change in the composition of encrusting bivalves, and decrease in the activity of boring bivalves. Some species and some genera (e.g. *Atreta unguis*, *Plicatula ogieri*) can be regarded as bathymetric markers, whereas for most taxa a combined pattern is needed for environmental interpretation. Many other species are eurytopic (e.g. *Myrmecidium hemisphaericum*, *Nanogyra nana*). The data base for the establishment of bathymetric marker fossils or fossil sets has to be enlarged in the future, but it is thought that application of this concept will also be possible to hard limestone facies where quantitative or semi-quantitative data sets often cannot be elaborated.

4. Bathymetric changes are naturally interconnected with other factors. In the Portuguese examples, the decrease in illumination is apparent by a decrease in diversity of hermatypic corals and algae. A greater predisposition for phases of lowered oxygenation with increasing water depth is indicated at some thin levels at Serra Isabel (deposit-feeding bivalves, potential chemosymbiotic bivalves), but this is thought to be partly decoupled from bathymetry, being linked by nutrient increase in the

course of rapid sea level rise (LEINFELDER et al., in prep.; WERNER et al., in prep.). At Serra Isabel, decoupling of oxygen and, possibly, nutrient gradients from bathymetric gradients apparently caused decimetre-scale upward changes in faunal composition: The occurring siliceous sponges, which were apparently adapted to slightly reduced oxygenation and, possibly, elevated nutrient levels, were replaced by a fauna dominated by hermatypic corals, which are characteristic for reduced nutrient levels and high oxygenation. Applying this to a larger scale, the differences between the Faulenhau example and the Serra Isabel example could not only be attributed to a greater depth but, at least partly, also to a slightly elevated nutrient level at Faulenhau. On the other hand, the decrease in diversity of coralline sponges from Serra Isabel to Faulenhau shows that nutrient levels were only an additional factor and that the association at Faulenhau was clearly deposited in water deeper than at Serra Isabel.

5. The comparative palaeoecological study presented here clearly shows the different depth distribution of Upper Jurassic coral reef associations and siliceous sponge reef associations. It is expected that the majority of Upper Jurassic siliceous sponge - microbial crust mounds deposited along the northern shelf of the Tethys grew in water deeper than the Faulenhau example, i.e. below 70 to 90 m, although siliceous sponge facies possibly could have occurred at lower depths in regions or at times of increased nutrient levels.

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