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ORIGINAL ARTICLE

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Significance of stromatoporoids in Jurassic reefs and carbonate platforms—concepts and implications

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Abstract Although many case studies describe stromatoporoid-rich Jurassic reefs, there are only few reliable data as to their distribution pattern. This is in part due to a largely taxonomic and systematic focus on the enigmatic stromatoporoids which now are interpreted as a polyphyletic informal group of demosponges by most specialists. The common co-occurrence of Jurassic scleractinian corals and stromatoporoids might, at first hand, point to very similar environmental demands of both organismic groups, but autecological considerations as well as evaluation of stromatoporoid distribution patterns should allow for a much more refined interpretation. This study concludes that Jurassic corals and stromatoporoids show a relatively broad overlap of environmental demands but their maximum ecological tolerances appear to differ considerably. Jurassic corals were dominating in mesotrophic to mildly oligotrophic, slightly deeper settings, where they largely outcompeted stromatoporoids. On the other hand, stromatoporoid growth was particularly favoured in very shallow water, strongly abrasive, high-energy settings as well as in possibly overheated waters. Many taxa and growth forms were very tolerant towards frequent reworking and redistribution, a feature which is compatible with the sponge nature of the stromatoporoids. As such, stromatoporoid facies may be common in low-accommodation regimes, giving rise to frequent "shelf shaving" and redistribution across wide shelf areas. The mixed coral-stromatoporoid reefs from the margins of isolated Intra-Tethys platforms are interpreted to be indicative of oligotrophic normal marine waters. This is corroborated by statistical cluster analysis of stromatoporoid taxa from representative areas. In addition, Arabian stromatoporoid occurrences might have been adapted to overheated and slightly hypersaline waters. There also are a few exceptional stromatoporoid taxa which might have had environmental tolerances different from the bulk tolerances of other Jurassic stromatoporoids. Part of our interpretations are preliminary and should stimulate further research. However, the present results already help explain the observed compositional differences between Jurassic North Tethys/North Atlantic, Intra-Tethys, and South Tethys shallow-water reefs and platforms.

Keywords Reefs · Platforms · Stromatoporoids · Corals · Jurassic · Ecology · Palaeobiogeography · Trophic mode · Tethys · Atlantic

Introduction

Fossil stromatoporoids include about 110 genera (Cook 2002) and are particularly frequent in Middle Palaeozoic, chiefly Ordovician to Late Devonian reefs, representing prominent frame builders, together with tabulate corals. Different stromatoporoid assemblages as well as different dominance patterns occur in reef front, reef core, reef crest, and 'lagoonal' settings, making Palaeozoic stromatoporoids useful palaeoenvironmental tools (Kershaw 1984; Nestor 1984; Kershaw and Keeling 1994; Kershaw 1998; Kershaw and Brunton 1999; Wood 1999, 2000).

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Jurassic stromatoporoids (incl. chaetetids) have also been described in a wealth of predominantely taxonomic–systematic studies, but both their global and regional distribution patterns, and their environmental demands are far from being understood. Within Jurassic reefs, stromatoporoids may occur both with or without corals, and, strongly contrasting most Ordovician to Devonian examples, many Jurassic coral reefs appear to be fully or largely devoid of stromatoporoids. Jurassic stromatoporoids may also occur in a patchy manner within micrite-dominated, apparently low-energy ramps and sheltered lagoons. However, distribution patterns of Jurassic stromatoporoid-bearing and stromatoporoid-dominated reefs were hardly ever described in detail, and actually, this paper can only be regarded as a first step towards such an approach. The various types of Jurassic reefs, reef organisms, and reef associations have proven to be very diagnostic for reflecting distinct palaeoenvironmental settings, including structural, oceanographic, sea level, and climatic aspects (e.g., Leinfelder 1993, 1994a, b, 2001; Nose 1995; Insalaco 1996; Leinfelder et al. 1996, 2002; Schmid 1996). The partial co-occurrence of corals and stromatoporoids, as well as their partial mutual exclusion show that environmental demands of both, Jurassic corals and stromatoporoids, require further explanation. This paper presents first concepts and results to whether such distribution pattern might be governed by (a) biogeographical differences or (b) overlapping but otherwise different environmental demands of stromatoporoids *vs.* corals, or (c) both, by focusing on Upper Jurassic reefs. We believe that a better integration of stromatoporoid characteristics into Jurassic reef analysis should allow not only to further refine Jurassic reefs as basin analysis tool but also to better understand the evolution of reef ecosystems through time.

This paper has been written in honour of Erik Flügel (†2004) who greatly contributed to the knowledge of Palaeozoic and Jurassic stromatoporoids, and who has stimulated process-oriented, comparative research on reefs by initiating the German Priority Program on Reef Evolution (1990–1996), by organising and editing the volume on “Phanerozoic Reef Pattern” (Kiessling et al. 2002), and especially by his understanding and friendly way of performing research and teaching, all of which will be unforgotten by us and the palaeontological–sedimentological community.

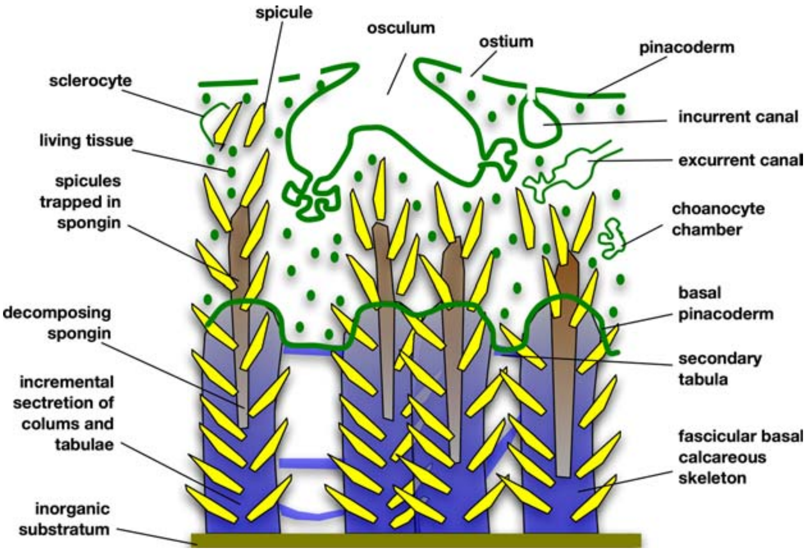
Identifying Jurassic stromatoporoid patterns—a bunch of problems

There are several reasons why Jurassic stromatoporoids have not yet been integrated into a global view of Jurassic reef characteristics and variations. Even more recent papers on stromatoporoids just state that these organisms may be frequent elements in Jurassic shallow-water reefs and normally occur together with corals (e.g., Termier et al. 1985; Wood 1987, 1999). Termier et al. (1985) and Wood (1999) have noted that from the Middle Jurassic to the Cretaceous stromatoporoids were particularly frequent along the South Tethys margin. Our own working group has described and established stromatoporoid-rich reef types at a local or regional base (e.g., Ellis et al. 1990; Nose 1995; Schmid and Jonischkeit 1995). However, because of the poor general knowledge on the controls of stromatoporoid distribution, we have not generally separated stromatoporoid-rich reefs from coral reefs in our overall assessment of Jurassic reef types but simply have positioned stromatoporoids within the coral end member reef types, stating that they may occur in very variable quantities (e.g., Leinfelder 1993; Leinfelder et al. 1994; Leinfelder 2001). Only recently, apparent differences in the distribution of stromatoporoids within Jurassic reefs have been mentioned in an attempt to evaluate reef patterns on a global scale (Leinfelder et al. 2002). In fact, based on a global database by Kiessling and Flügel (2002), we have found much larger proportions of stromatoporoids within low latitude, South and Intra-Tethys reefs than in the bulk of North Tethys and Atlantic reefs, which is in accordance with a similar qualitative statement by Wood (1999).

The poor knowledge of stromatoporoid distribution patterns is also due to the fact that taxonomic identification of stromatoporoids encounters many problems. Earlier, most Jurassic stromatoporoids were largely considered as of hydrozoan nature, but some were attributed to other enigmatic groups such as spongiostromariids, dysjectoporoids, or even seen as relics of tabulate corals, among other interpretations (see Wood 1987 for review). Jurassic stromatoporoids also appear to be frequently confused with the specialised coral group of the microsolenids whose perforated and pennulate structure may result in strong morphological similarities at least in certain thin section cross-cuttings. Even bacinellid or *Lithocodium* structures were discussed as possibly having systematic affinities with stromatoporoids (cf. Turnsek and Buser 1966; Leinfelder 1986, also for other references). Sometimes, chaetetids have been separated from the stromatoporoids proper (e.g., Fischer 1970), in other cases the term stromatoporoids is used as the higher hierarchical taxon. Moussavian (1989) considers the genus *Pseudochaetetes* synonymous with the red algal genus *Solenopora*, and sees the genus *Ptychochaetetes* as junior synonym of the genus *Eurysolenopora*, which was interpreted by Dietrich (1930) as red alga but placed by Moussavian (1989) into the chaetetids.

Fossil, including Jurassic, stromatoporoids are now generally considered as sponges with a calcifying basal skeleton, but from this interpretation several other problems arise: (1) in principle, sponge specialists such as Reitner (1992), or Wood (1987) only consider fossil stromatoporoids as sponges when megascleres, or their relics such as pseudomorphs, are preserved within the calcareous skeletons (Figs. 1, 7D). However, there are still many taxa which, to date, did not reveal any traces of the existence of silica spicules, and even Wood (1987) includes *Burgundia* (Fig. 13J) which does not show any unequivocal spicule relics into the stromatoporoids, because of its typical sponge filter system. Since in such cases attribution to the sponges is not provable, should such non-spiculate taxa be considered stromatoporoids or not? (2) Taxonomic fea-

Fig. 1 Stromatoporoid sponge organisation scheme, based on a milleporellid stromatoporoid. Blue basal calcareous skeleton, yellow sponge spicules, soft tissue is between green lines. Simplified after Wood (1987)



tures and morphologic nomenclature of Jurassic stromatoporoids are now in part completely different from characteristics used earlier when most stromatoporoids were considered hydrozoans (e.g., Lecompte 1956). This makes determination down to the species level difficult and hence poses a strong obstacle against identifying stromatoporoid distribution patterns at a higher taxonomic resolution. (3) Many older species and even genera might be synonymous. For instance, Wood (1987) has synonymised five species of the genus *Burgundia* Dehorne to the single species *Burgundia ramosa* Pfender. (4) Similar to corals, stromatoporoids often occur in sediments devoid of good biostratigraphic markers which together with taxonomic uncertainties blurs exact vertical and spatial distribution patterns of stromatoporoid taxa.

Wood (1987: Table 1) gives an in-depth report on the confusion of systematic attribution of stromatoporoids ranging from sponges (e.g., Steininger 1834; von Rosen 1869; Twitchell 1929; Hartmann and Goreau 1970; Stearn 1972, 1975; Termier and Termier 1987) to hydrozoans or other Cnidaria (e.g., Dehorne 1920; Lecompte 1956; Galloway 1957; Flügel 1958; Flügel and Hötzl 1966; Turnsek 1966; Nestor 1981; Mori 1984), to foraminifers, bryozoans, cyanobacteria, and the specialised sclerosponges (Sandberger and Sandberger 1850–1856; Kirkpatrick 1912; Kazmierczak 1976; Hartmann 1979). Sclerosponges were later attributed to represent a subgroup of the demosponges. Today, sponges with calcareous skeleton are often attributed to either (a) sclerospongid demosponges, (b) sphinctozoan sponges (the majority of which should belong to the demosponges) or (c) the order Calcarea (without silica spicules). Some specialists have reserved the sclerosponge group to extant forms and consider stromatoporoids as a distinct subgroup of the demosponges (Hartmann 1979). Another view would even include the Calcarea forms (also known as pharetronids) into the demosponges (Termier et al. 1985). We follow the view of Reitner (1992) and Wood (1987) who have focused on megasclere and (wherever preserved) microsclere arrangement as characteristics of extant and fossil stromatoporoids and have convincingly shown that stromatoporoids (including chaetetids and all modern sclerosponges) are a polyphyletic group. The stromatoporoid bauplan is a mere organisation scheme occurring within very different groups of demosponges (Cook 2002; Reitner and Wörheide 2002). In other words, different groups of demosponges, such as the Ceractinomorpha or Tetractinomorpha may all contain soft sponges, silica-spiculed sponges, and silica-spiculed sponges with a basal calcareous skeleton, the latter of which represent stromatoporoids (Fig. 1). In this view, chaetetids may be interpreted as just another variation of the organisational mode of the polyphyletic stromatoporoids which is why we include them into the stromatoporoids *sensu largo* for this study. However, by far not all Jurassic stromatoporoid taxa have revealed siliceous spicules, or their pseudomorphic relics, or at least distinct microstructures considered to be diagnostic of the sponge origin of stromatoporoids. Therefore, it remains to be proven whether all Jurassic stromatoporoids were calcifying demosponges, or, whether some or many actually, in part, belong to other groups.

Obviously, these remaining uncertainties still thwart the inclusion of Jurassic stromatoporoids into palaeoecological studies. As to the evaluation of older literature, the problem remains to the individual researcher how he or she deals with the taxonomic groups mentioned therein. If faunal lists of Jurassic reef reports mention hydrozoans, should these now be considered stromatoporoids or could there have been some true hydrozoans, red algae, or whatsoever included in these lists? Or could stromatoporoids have been confused with microsolenid corals or other organisms? And, since stromatoporoid taxa are in demand of revision, how meaningful are species or genera distribution patterns? Despite all these problems, we attempt to demonstrate in this paper that stromatoporoid occurrences, composition, and distribution deserve special attention both for the environmental interpretation of Jurassic reefs and the understanding of reef evolution.

Table 1 Identified upper Jurassic reefal stromatoporoids and chaetetids from Portugal and Spain. From Nose (1995), extended. The taxa list for the Lusitanian Basin also includes some taxa from a drillhole at S'Tiago de Cacem which is transitional between the Lusitanian Basin and the western Algarve. Note that *Ptychochaetetes* is considered as junior synonym of *Eurysolenopora* by Moussavian (1989) which according to the author is nevertheless a chaetetid taxon. (Note also refers to other tables of this paper)

Lusitanian Basin (partly after Dehorne 1922; Termier et al. 1985)	**Algarve** (partly after Rosendahl 1985)	**Celtiberian Ranges** (mostly after Fezer 1988)
Actinostromaria jeanneti	*Actinostromaria coacta*	*Actinostromaria orthogonalis*
Actinostromaria sp.	*Actinostromaria jeanneti*	*Actinostromaria* sp.
Actinostromaria stellata	*Actinostromaria tokadiense*	*Burgundia wetzeli*
Astrostylopsis circoporea	*Astroporina orientalis*	*Calciagglutispongia yabei*
Burgundia trinorchii	*Burgundia trinorchii*	*Cladocoropsis mirabilis*
Cladocoropsis mirabilis	*Cladocoropsis mirabilis*	*Dehornella choffati*
Dehornella arrabidensis	*Cylicopsis florida*	*Dehornella crustans*
Dehornella choffati	*Dehornella choffati*	*Dehornella hydractinoides*
Dehornella hydractinoides	*Dehornella crustans*	*Disparistromaria oxfordica*
?Dehornella omanensis	*Dehornella harrarensis*	*Disparistromaria tenuissima*
Milleporidium lusitanicum	*Disparistromaria tenuissima*	*Milleporidium crassum*
Milleporidium sp.	*Hudsonella lucensis*	*Milleporidium formosum*
Periomipora elegantissima	*Milleporidium formosum*	*Milleporidium kabardinense*
Sarmentofascis fasciculata	*Milleporidium lusitanicum*	*Milleporidium lusitanicum*
Sobralispongia densespiculata	*Milleporidium variocellatum*	*Milleporidium* sp.
	Parastromatopora japonica	*Milleporidium variocellatum*
	Periomipora elegantissima	*Shuqraia heybroecki*
	Sarmentofascis benesti	*Steineria* sp.
	Shuqraia arrabidensis	*Steineria undulata*
	Shuqraia heybroeki	
	Syringostromina pruvosti	
	'Stromatoporina tornquisti'	
Bauneia multitabulata	*Chaetetopsis crinita*	*Blastochaetetes flabellum*
Blastochaetetes cf. *capilliformis*	*Chaetetopsis krimholzi*	*Pseudoseptifer angustitubulosus*
Neuropora lusitanica	*Neuropora* sp.	*Pseudoseptifer chablaisensis*
Neuropora sp.	*Ptychochaetetes* cf. *ehrenbergi*	*Pseudoseptifer geyeri*
Pseudoseptifer angustitubulosus	*Ptychochaetetes* cf. *peroni*	*Pseudoseptifer* sp.
Ptychochaetetes globosus	*Ptychochaetetes globosus*	*Ptychochaetetes peroni*
Ptychochaetetes peroni		*Ptychochaetetes ponticus*
		P. (Axiparietes) orbignyi
		Ptychochaetetes sp.

Methods

This study is based on a variety of methods. We use both quantitative and qualitative approaches to highlight distribution patterns and to identify ecological demands of Jurassic stromatoporoids. Distribution of stromatoporoid occurrences within Jurassic reefs is based on the evaluation of the quantitative PaleoReefs database of Kiessling and Flügel (2002), as extended and used by Leinfelder et al. (2002), which is paralleled by reconnaissance study and literature evaluation for selected regions from the North Tethys epicontinental seas, North Atlantic rift, Apulian and Dinaric platform, Turkey and Arabian platforms, which all assess both reefal and level-bottom stromatoporoid occurrences.

The above database has been extended for Upper Jurassic reef sites by including coral taxa, down to the species level, from available literature and own data. Coral taxa have been evaluated by Goldberg (2004) and Goldberg and Leinfelder (unpublished) and provided some results which are important for this study. Taxa distribution for Upper Jurassic, and in two case examples probably including some Callovian stromatoporoids both on the genus and species level was compiled for nine representative regions and cross-compared by statistical cluster analysis using the software Palaeontological Statistics (PAST), vers. 1.29 (Hammer et al. 2004) in order to identify possible regional distribution patterns. We have used both R and Q mode analysis and run several different algorithms for both presence–absence data of species and genera, and abundance data of species per genus. We cross-checked a great variety of methods to conclude that for presence–absence data the Unweighted Paired Group Average Method (UPGMA) with the Dice algorithm and the UPGMA with the Raup and Crick index were most appropriate. The Dice algorithm (also known as Sorensen) considers both matches and mismatches but puts greater weight on joint occurrences than on mismatches. The Raup and Crick index uses the 'Monte Carlo' randomisation procedure by comparing

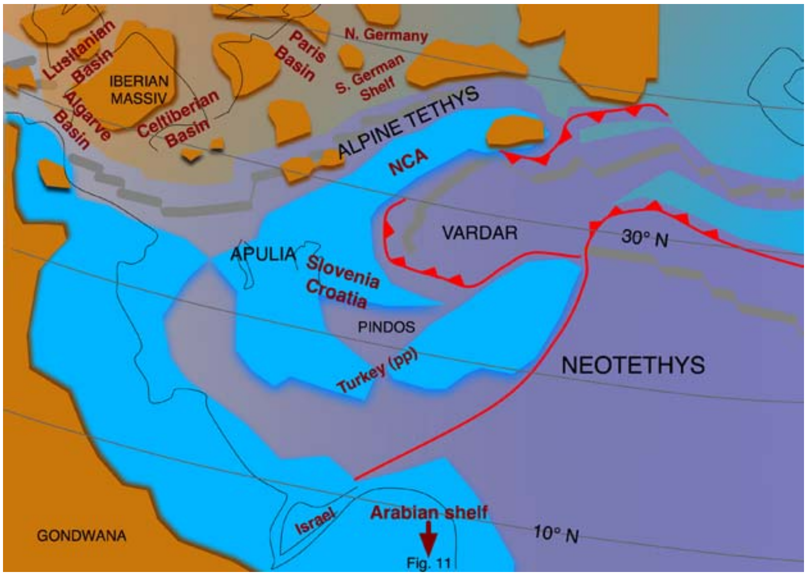


Fig. 2 Simplified palaeogeographic sketch for the Upper Jurassic of the European to Arabian area. Study regions with stromatoporoids are marked with dark red labelling. Change of shelf sea colouration indicates increase in siliciclastic influx. Note frequent basement islands on the northern Tethys and North Atlantic shelf seas. Shelf configuration and palaeolatitudes after Stampfli et al. (2002), land distribution after Ziegler (1988), and various sources. Note that Intra-Tethys shelf outlines do not correspond with shallow-water carbonate platform outlines. Rather, this shelf area was strongly differentiated into shallow isolated carbonate platforms such as the Dinarid Platform (Slovenia, Croatia), the platforms of the Northern Calcareous Alps (NCA) or other isolated Apulian platforms and basinal shelf areas in between (see Dercourt et al. 2000; Velic et al. 2002). Note that the configuration of the Pindos oceanic area (here based on Stampfli et al. 2002) is also matter of debate. See also Fig. 11 for southward extension to the Arabian shelf

the number of positive entries between two samples (in our case used for Q-mode analysis, i.e., taxa occurring at least in two regions) with the distribution of co-occurrences of 200 random replicates. This method hence focuses even stronger on positive co-occurrences than the Dice algorithm (Hammer et al. 2004). We also cross-compared occurrence pattern of genera weighted by their species number. Such abundance data demand a distance-reflecting method and algorithm. Therefore, for such data we have applied both the Ward's-method which uses an Euclidean algorithm and the UPGMA-method with the Morisita algorithm (cf. Backhaus et al. 2003; Hammer et al. 2004).

Evaluation of ecological behaviour of stromatoporoids is based on the patterns identified by the above methods and the additional discussion of morphological criteria, faunal assemblages, sedimentary characteristics, and palaeogeographic framework.

Distribution of Jurassic stromatoporoids: a regional and global approach

In quite some Middle to Upper Jurassic coral reefs stromatoporoids, chaetetids and related organisms may be found sporadically, at times even in larger proportions. However, it is rare that stromatoporoids actually dominate European or North American Jurassic reefs. There are a couple of exceptions which we have found particularly in Portugal and Spain. On the other hand, stromatoporoids (incl. chaetetids) are frequent in Jurassic reefs from South Tethys epicontinental seas as well as isolated Intra-Tethys platforms. In addition to reefal settings, there are quite some reports on moderate to rich occurrences from stromatoporoids in lagoonal, muddy to peloidal settings from both North and South Tethys seas (Fig. 2, see also Fig. 11). Most Upper Jurassic coral reefs with and without stromatoporoids concentrate along the Northern Hemisphere at around 20–40° palaeonorth (Fig. 3).

A "quantitative" global overview on stromatoporoid occurrences

Using the PaleoReefs Database

The PalaeoReefs Database (Kiessling and Flügel 2002) is a computerised database which included about 325 major Jurassic reef sites (each of which may contain many individual reefs; Leinfelder et al. 2002) when being published. This database may be used for a first quantitative view on stromatoporoid distribution within Jurassic reefs. According to this database, only about 7% of all Jurassic reef sites contain reefs rich in stromatoporoids (when querying the database for reefs with considerable amounts of stromatoporoids, hydrozoans, or spongiostromariids, assuming synonymity for these categories). This value increases to about 10% when referring to Upper Jurassic reefs alone (Fig. 4). Nearly all of these are of low latitudinal, mostly South Tethys origin. They include reefs from Austria, northern and southern Italy and Sicily, Montenegro and Serbia, as well as from the Middle East. Interestingly, stromatoporoid-rich reef sites strongly concentrate around

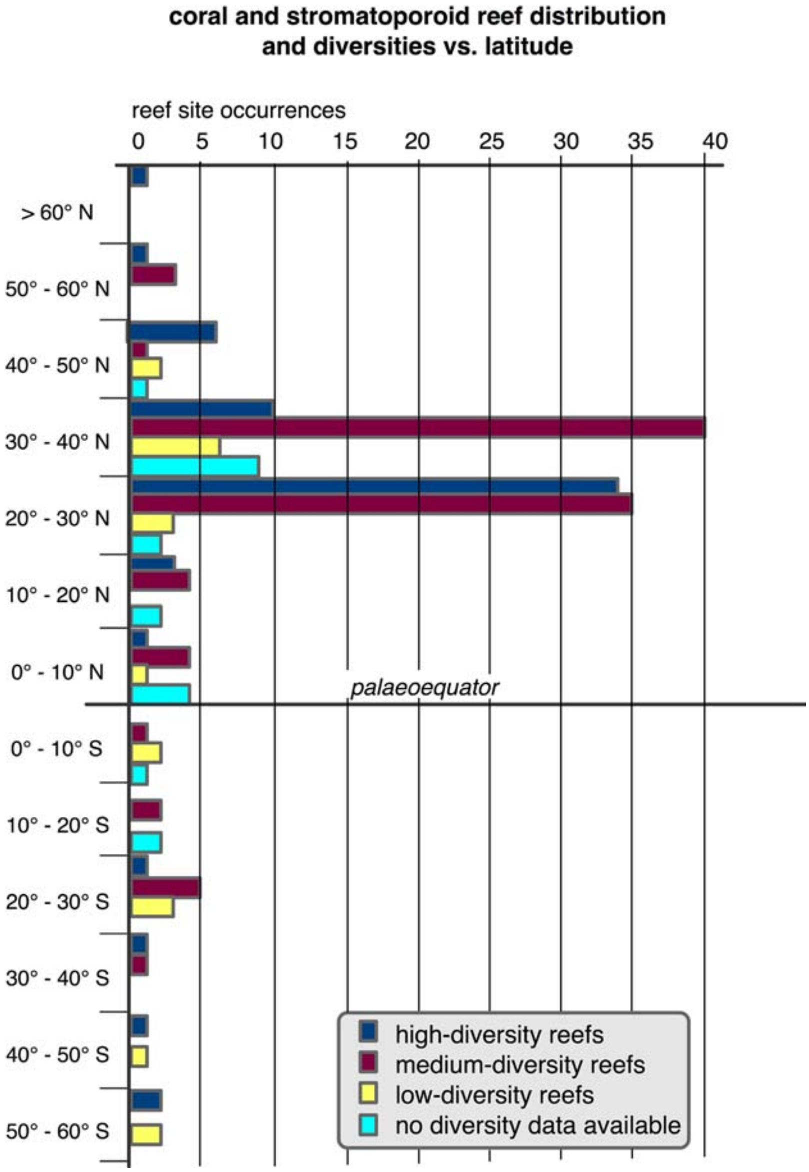


Fig. 3 Upper Jurassic coral and stromatoporoid reefs are not only most abundant but also contain many medium to high-diversity reefs 20–40°N (palaeolatitude). These include both the North Tethys and Lusitanian Basin reefs and, in part, Intra-Tethys reefs. Despite the availability of a huge Arabian carbonate platform system (see Figs. 2, 11), reefs are astonishingly rare around the palaeoequator. Based on the PaleoReefs Database, modified from Leinfelder et al. (2002)

25°N (palaeolatitude), although this might be partially (though certainly not fully) biased by Jurassic outcrop conditions and sampling. A couple of reef sites rich in stromatoporoids also have been reported from the high palaeolatitude areas of Japan (e.g., Yabe and Sugiyama 1930, 1935) and Patagonia (Ramos 1978). Another roughly 10% of all Upper Jurassic reef sites are labelled as coral reefs with characteristic, moderate to considerable, amounts of stromatoporoids, chaetetids or probably equivalent organisms such as "hydrozoans" and "spongiomorphids". Both these categories, i.e., coral-stromatoporoid or stromatoporoid-dominated reefs, sum up to 28% of all Upper Jurassic reefs (Fig. 4).

Again, most of these reefs characterised by variable amounts of stromatoporoids, are situated on the southern side of the Tethys (Fig. 5), although differences are not as strong any more as when only focusing on stromatoporoid-dominated reef facies. As above, data might be biased by state of knowledge and analysis. Also, some corals (especially microsoleniid corals) might have been mistaken as stromatoporoids in to date poorly analysed reefs. In addition, the above figures might have Middle East reefs somewhat underrepresented owing to a restricted data access in areas of hydrocarbon exploration.

Interestingly, there are no Jurassic reefs recorded in the PaleoReefs Database which contain both siliceous sponges and stromatoporoids (or any other kind of coralline demosponges) at the same time. However, such reefs did exist in the North Atlantic realm. This is mostly due to the fact that the coralline demosponge *Neuropora* may occasionally occur in such reefs. *Neuropora* is now interpreted as a chaetetid sponge (Reitner 1992) and is known to have a much wider bathymetric distribution than other "sclerosponges" (cf. Werner et al. 1994; Krautter and Hartmann 1999). As a whole, the PaleoReefs Database suggests that Jurassic stromatoporoids, if occurring, are clearly related

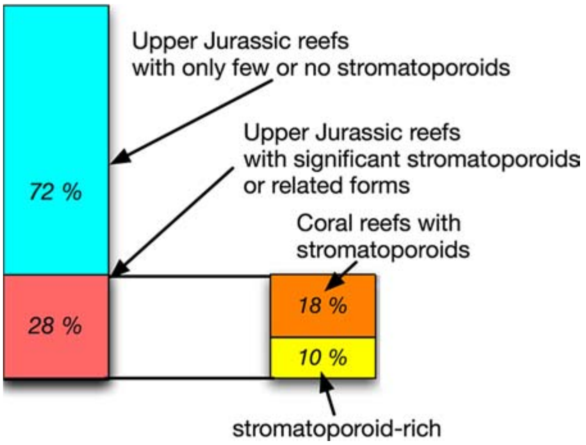


Fig. 4 Occurrences of Upper Jurassic reefs characterised by noticeable to rich proportions of stromatoporoids and chaetetids (and organisms considered as hydrozoans and spongiomorphids which are very likely to be synonymous) which are categories used by the PaleoReefs Database (Kiessling and Flügel 2002). Evaluation is based on the extension of this database as used in Leinfelder et al. (2002) and extended by Goldberg and Leinfelder (unpubl. results). Database as used for this study comprises 227 Upper Jurassic reef site entries. About 30% of the reef sites report stromatoporoids, 10% of all Upper Jurassic reef sites are rich in stromatoporoids. See text for details

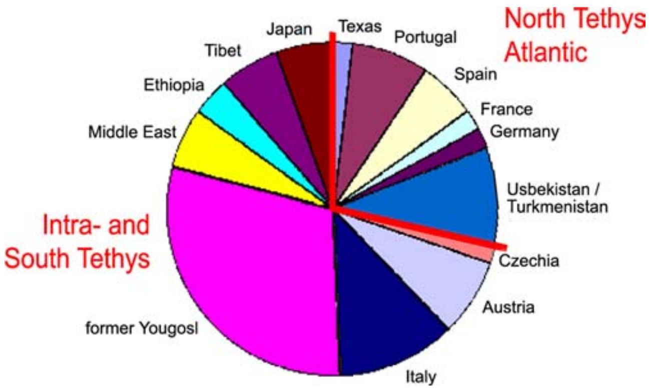


Fig. 5 Abundance and distribution of Upper Jurassic reefs characterised by significant stromatoporoids. Such reefs comprise only about 30% of all Upper Jurassic reefs. Based on the PaleoReefs Database (see caption for Fig. 4). South Tethys reefs dominate over the rest of the locations. Probably reef site occurrences of former Yougoslavia are slightly overestimated in relation to the Middle East and possibly other areas owing to bias in available publications. Note that this is a global compilation as based on the PaleoReefs Database, from which only selected representative key areas will be highlighted in the subsequent part of this study

to coral reef facies, either representing additional faunal elements or, in less frequent cases, constituting noticeable to dominating proportions of the reef building guild. Occasionally, corals can be entirely substituted by stromatoporoids, chaetetids, or related organisms, especially in level-bottom settings. However, level-bottom stromatoporoid associations from lagoons are often considered to be non-reefal and hence have by definition not been included in the PaleoReefs Database. Such associations also provide important information on regional distribution patterns, and, therefore, are considered in the subsequent part of the study.

Stromatoporoid distribution: a regional qualitative overview based on selected key areas

Northern Tethys shelves and North Atlantic margin

Portugal: Stromatoporoids (incl. chaetetids) may be frequent, but hardly dominating elements in both reefal and inner ramp/lagoonal facies. They occur both in the North Atlantic Lusitanian Basin and in the North Tethys Algarve Basin (Fig. 2) as well as in drillholes in between. Our previous studies on reefs and platform facies show that stromatoporoids are regular accessory elements in most coral reefs, particularly in those with no siliclastic influence (cf. Rosendahl 1985; Leinfelder 1986, 1992, 1994b; Ellis et al. 1990; Nose 1995; Schmid and Jonischkeit 1995; Schmid 1996). Figure 6 sketches the variable occurrences of stromatoporoids *sensu latu* within carbonate-dominated settings of the North Tethys shelf and the North Atlantic marginal seas. Whereas the occurrence of distinct coral reef types is strongly controlled by slope angles and sedimentation-/resedimentation processes, stromatoporoids and chaetetids appear to be more randomly admixed, at least in shallow-water settings. Interestingly, pharetronid and inozoan calcifying sponges can be much more frequent than stromatoporoids, at places even forming high-diversity calcisponge meadows within marls. Calcisponges may be associated with small microbial buildups, corals, bivalves, and, rarely stromatoporoids (Werner et al. 1994; Nose 1995).

Stromatoporoids within reefs from the Lusitanian Basin: Lusitanian Basin stromatoporoids (Table 1) include various species of *Actinostromaria, Burgundia*, *Dehornella*, and *Milleporidium*; chaetetids include *Ptychochaetetes, Blastochaetetes*, and *Chaetetes* (*Pseudoseptifer*). Stromatoporoids (*s. str.*) occur particularly as thin overgrowths of corals (especially *Dehornella crustans*) but are somewhat more common within debris-rich, bioclastic to oolitic facies, where *Burgundia trinorchii* may be fairly common and even may form small patch reefs with colonies up to 20 cm thick (Nose 1995). We would like to note that muddy boundstones at the base of the Amaral Formation with a poorly preserved fauna were earlier described as ?*Actinostromaria* association (Nose 1995). Reexamination revealed that both supposed stromatoporoids as well as the supposed *Microsolena* corals (Nose 1995) have to be attributed to patch reefs of the microsolenid coral *Dendrarea* (Nose unpubl. results). Another reef type with stromatoporoids are high-diversity, microbial crust-rich coral boundstones composed largely of massive coral colonies and microbial crusts. Nose (1995) interpreted such coral-stromatoporoid-chaetetid-microbial reefs as being positioned on ramps just below the fair-weather wave base, but undergoing episodical storm perturbances, as documented by intercalated debris beds and lenses. Reefs may attain several metres to tens of metres in height. The Kimmeridgian Ota Reef, most

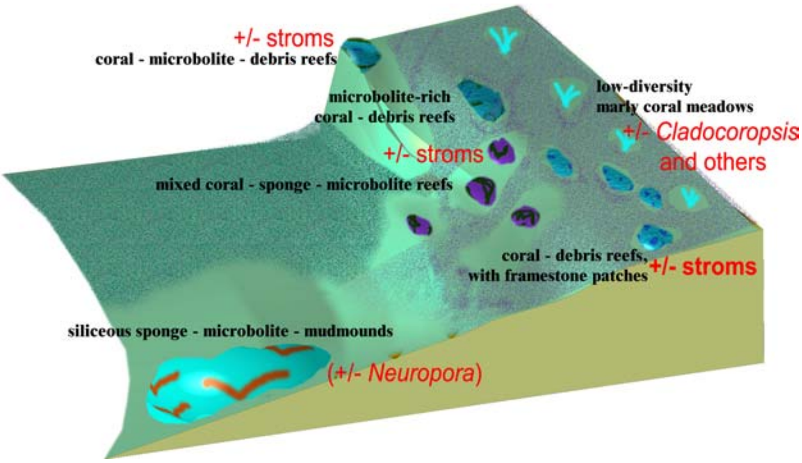


Fig. 6 Simplified sketch of carbonate platform facies from various regions north of the Tethys Ocean with variable occurrences of stromatoporoids and chaetetids (indicated as '±stroms'). From Leinfelder (2001, modified)

of which is of coral-debris-microbial crust character also includes accessory to regularly occurring *Dehornella, Actinostromaria, Bauneia*, and *Ptychochaetetes*. Again, this was a reef with highly abrasive character (Leinfelder 1992, 1994b). Chaetetids and some stromatoporoids also are frequent in platform bordering bioclastic sand bar-patch reef associations of the Upper Oxfordian Montejunto platform and may occur in other reefs, though only as accessory elements (Ellis et al. 1990; Leinfelder 1994b). However, there are many coral reefs with no signs of stromatoporoids at all, particularly in slightly clayey settings.

Stromatoporoids within Algarve reefs: Coral reefs are also widespread in the Eastern Algarve Basin. Stromatoporoid taxa are similar to the Lusitanian Basin but comprise additional forms (e.g., *Hudsonella, Astroporina, Shuqraia, Cylicopsis, Cladocoropsis*, and *Chaetetopsis*; see Table 1). The genus *Astroporina* was synonymised with *Dehornella* from Wood (1987). In the Algarve, stromatoporoids and chaetetids might be not only accessory but also occur as intercalations of pure stromatoporoid/chaetetid meadows with massive, knobby, platy, and even branching morphologies. At the base of such reefs, transitions to siliceous sponge-coral facies occurs which is evidence of rapid shallowing within such reefs. Possibly the stromatoporoid-chaetetid-intercalations reflect the shallowest part of such successions, although they are normally not positioned at the top of the reefs.

An isolated ramp-type carbonate platform surrounded by deeper water settings developed on a rising salt pillow during the Oxfordian-Kimmeridgian of the eastern Algarve. This São Romão Limestone is particularly rich in stromatoporoids. Schmid and Jonischkeit (1995) have provided a detailed analysis of this platform. The succession reflects a rapidly prograding ramp which can be subdivided into four stages. Coral-stromatoporoid patch reefs and biostromes developed throughout stage B to C to the seaward side of oolitic and bioclastic shoals. These reefs are of the coral-debris type *sensu* Leinfelder (1993), and generally do not show much microbial crusts. Their shallow-water rudstone character suggests that they have undergone strong abrasion which possibly was favourable for the development of the stromatoporoids *Milleporidium, Burgundia, Dehornella* (Fig. 7C), and *Actinostromaria*, although *Dehornella* and *Actinostromaria* are also known from muddy ramp settings. *Burgundia* may form nearly monospecific small patch reefs. *Hudsonella, Parastromatopora*, and *Ptychochaetetes* occur sporadically within these reefs. A peculiar feature is the richness of *Cladocoropsis* meadows in inner ramp settings (see below).

Portuguese stromatoporoids in lagoonal facies: Dehorne (1917, 1920) mentioned many stromatoporoid occurrences from Upper Jurassic lagoonal facies of the Lusitanian Basin and the Algarve. Fauna is dominated by branching forms, which today are mostly attributable to *Dehornella* (e.g., *D. hydractinoides*). Stromatoporoids may be relatively frequent within certain horizons of a mixed salinity, mud-dominated carbonate succession, co-occurring with brachiopods, rhynchonellids, gastropods, bivalves, and rare corals. The systematic description of calcifying sponges from the Upper Jurassic of Portugal by Termier et al. (1985) also assigns most of their material to micritic, shallow-water, low-energy environments, being associated with lituolid foraminiferans, dasycladacean algae, and cayeuxiid cyanobacteria. Fauna listed by these authors include *Peromipora elegantissima, Astrostylopsis circoporea, Sarmentofascis fasciculata, Shuqraia arrabidensis, Syringostromina pruvosti*, and *Bauneia multitabulata*. Judging by own examinations (Felber et al. 1982; Leinfelder 1983), most of the widespread inner to mid-ramp, lagoonal-type, micritic successions of both the Lusitanian Basin and the Algarve Basin are either very poor in organisms or are dominated by bivalve and gastropod associations. However, horizons with stromatoporoids occur sporadically and then can reveal a variety of mostly very small specimens and taxa. Only lagoonal-type inner ramps with higher proportion of high-energy settings, such as within the São Romão limestone exhibit richer stromatoporoid fauna, such as *Cladocoropsis* meadows and patch reef type stromatoporoid clusters (Schmid and Jonischkeit 1995). Well-sheltered lagoons of rimmed carbonate platforms, such as the Ota lagoon, are, however, mostly devoid of stromatoporoids (Leinfelder 1994b).

Portuguese stromatoporoids from non-reefal environments appear to mostly include taxa known from

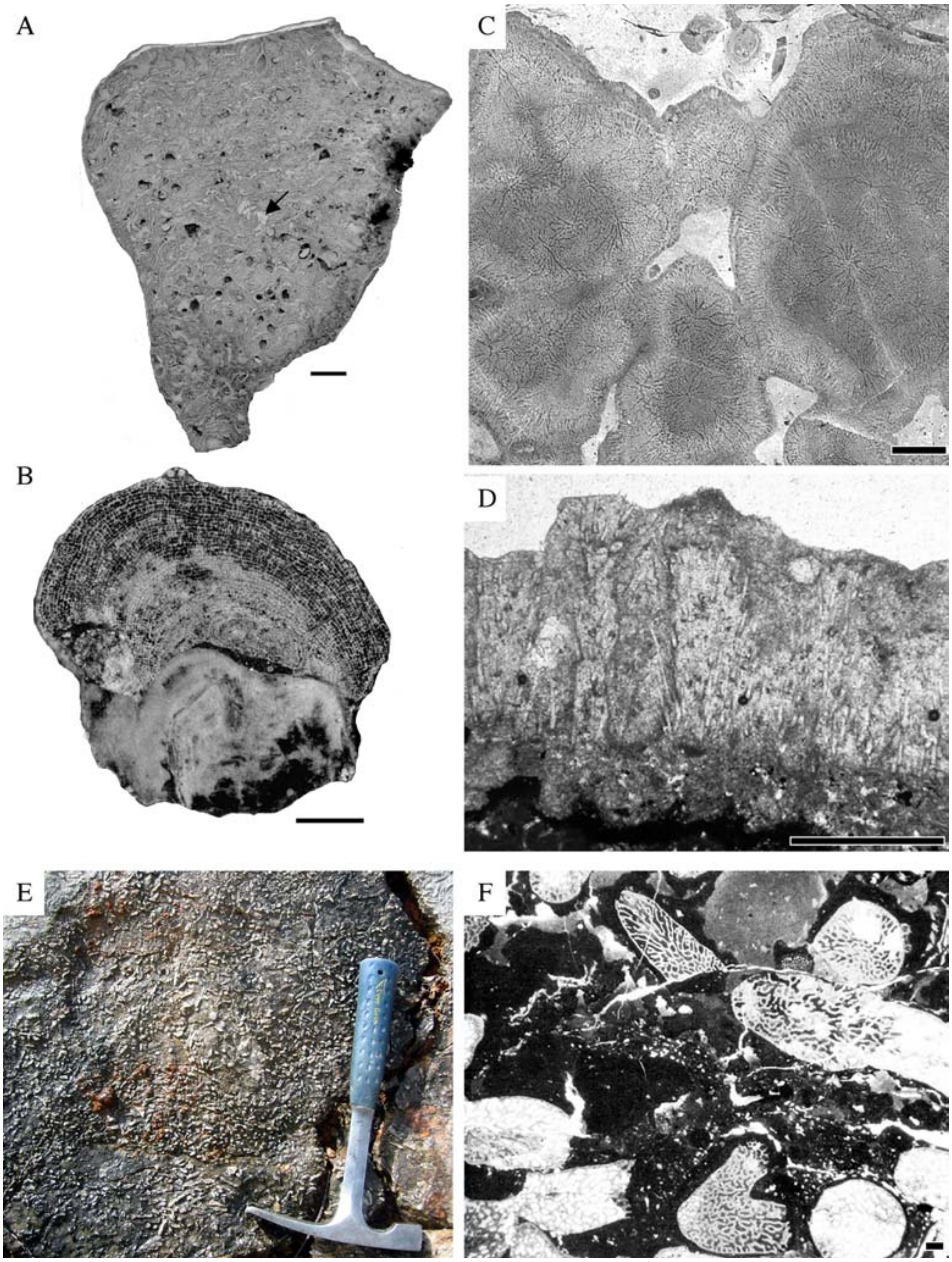


Fig. 7 Upper Jurassic stromatoporoids and stromatoporoid facies from Portugal and Spain. **A** Heavily bored coenosteum of *Burgundia trinorchii* Dehorne (longitudinal section). The polished slab reveals a laminate structure of the highly morphovariable calcareous skeleton of this stromatoporoid genus (type "lamellaire-meandriforme" *sensu* Schnorf-Steiner 1955). Note intergrowth with various microencrusters (light grey veneers within skeleton) and the ancestral coralline red alga *Marinella lugeoni* Pfender (arrow), Amaral Formation (Upper Kimmeridgian), Lusitanian Basin, Portugal; scale bar 1 cm. **B** *Calciagglutispongia yabei* Reitner (longitudinal section). Polished slab of a hemispherical stromatoporoid specimen developed on a microsolenid scleractinian coral; Sot de Chera Formation (Lower Kimmeridgian), Terriente, Celtiberian range, Eastern Spain; scale bar 1 cm. **C** Branching colony of *Dehornella crustans* Hudson (transverse section) with astrorhizae. Polished slab; São Romão Limestone (Kimmeridgian) near Ponte da Velha Sara, eastern Algarve; scale bar 1 mm. **D** *Sobralispongia densespiculata* Schmid and Werner (in press). This taxon shows a dense sponge spiculation and the fascicular structure of the secondary basal calcareous skeleton. Transverse thin section. Transition from Abadia to Amaral Formation near town Sobral, Upper Kimmeridgian, Lusitanian Basin, Portugal; scale bar 1 mm. **E** In-place biostrome of the branching stromatoporoid *Cladocoropsis mirabilis* Felix. This is a unique preservation since *Cladocoropsis* is easily reworked elsewhere. São Romão Limestone near Amendoeira, Upper Oxfordian, eastern Algarve, Portugal. Length of hammer is 28 cm. **F** *Cladocoropsis* biostrome similar to above, showing stabilisation by dense microbial crusts which prevented complete reworking of the biostrome. Thin-section; São Romão Limestone (Kimmeridgian) near São Romão, eastern Algarve; scale bar 1 mm

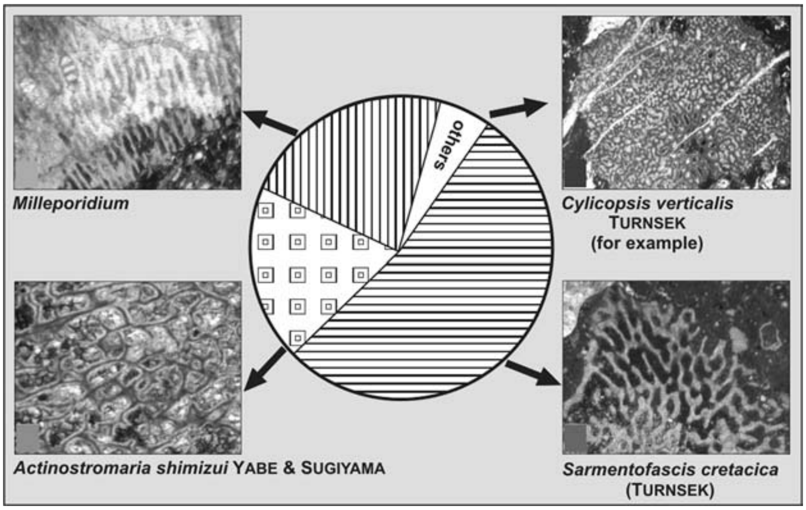


Fig. 8 Quantitative distribution of prominent stromatoporoids in platform-derived allochthonous debris from the Upper Jurassic Barmstein Limestone, based on data from more than 200 thin-sections. See Gawlick et al. (in press) for more details

reefal settings, making interpretation difficult. There is, however, one important exception. Open lagoons can be characterised by meadow-type biostromes of the branching stromatoporoid *Cladocoropsis mirabilis* which is largely unknown from reef settings. Besides the S. Romão Limestone, similar facies occurs in the transitional platform-slope zone of the Montejunto Limestone (Leinfelder 1994b). The dependence of *Cladocoropsis* occurrences on lagoonal-type facies has been highlighted by previous studies such as Flügel (1974) and Turnsek et al. (1981). Whereas higher diversity stromatoporoid horizons within ramp or lagoonal micrites might reflect a complete cessation in background sedimentation or even winnowing of muds down to hardened surfaces, *Cladocoropsis* meadows were possibly able to cope with short sedimentation and resedimentation intervals, judging from its branching behaviour. Usually *Cladocoropsis* meadows are not preserved *in situ* but are fragmented by storms. Exceptionally, an *in situ* meadow is, however, preserved at several locations of the São Romão platform (Figs. 7E, F).

Celtiberian Basin of eastern Spain: Observations and hence general conclusion for stromatoporoid distribution patterns in the Upper Jurassic of Spain are mostly coherent with the Portuguese examples (Nose 1995) and, therefore, will not be repeated here. However, there are some additional observations worth mentioning.

Chaetetids are more frequent in the shallow-water facies of the Montes Universales than they are in Portugal. Occasionally they form entire patch reefs (Fezer 1988; Nose 1995), which is not the case in Portugal. But even within the coral reefs chaetetids may be more frequent, whereas stromatoporoids have about the same abundances as in Portugal. Taxa are listed in Table 1.

Chaetetid-rich reef types in the Celtiberian Range (e.g., Frías de Albarracín) are of the coral-debris-type, that is, they do not include microbial crusts. Contrasting the Portuguese examples, these may contain a high proportion of detrital sand-sized quartz and it is under these circumstances that chaetetids actually occur in considerable numbers. Chaetetids and stromatoporoids (*s. str.*) are massive, with individual colonies up to 15 cm, which may cluster to patch reef aggregates. The reef bodies exhibit biostromal character, grading laterally into siliciclastic, intraclastic, oolitic, bioclastic grainstones and siliciclastic sandstones. Obviously, water energies were considerable during the growth of these reefs and it must be assumed that abrasion caused by detrital quartz and carbonate grains was high. This appears to have strongly favoured growth of chaetetids, stromatoporoids, and especially the dominating *Ptychochaetetes globosus*. Another Celtiberian example of a siliciclastic stromatoporoid environment stems from the Terriente region in the Celtiberian Range. Here, a marly to sandy stromatoporoid-bearing coral biostrome, initiated on a distinct, thin coral thrombolite level, developed in a slightly deeper, quiet, but storm influenced setting. Stromatoporoid fauna is dominated by "*Actinostromaria tokadiense*" revealing typical spherical/hemispherical to mushroom-shaped morphology. The lower parts of the coenostea are often developed as stalks (Geyer 1965; Flügel and Hötzl 1966; Nose 1995). Abundant allochthonous ooids as well as intercalations of sandstones and graded ooid–oncoid grainstones point to an instable muddy substrate affected by punctuated storm events which washed in the ooids (cf. Fezer 1988; Nose 1995). Spherical, ball-shaped morphs of "*A. tokadiense*" have been interpreted as rolling stromatoporoids comparable to extant roll corals (Nose 1995).

For our regional comparison of stromatoporoid taxa we follow Reitner (1992) who has found considerable differences in the structure of the secondary skeleton between the Spanish material of *A. tokadiense* and the original material described from the Torinosu limestone of Japan by Yabe and Sugiyama (1935), and, therefore, established the new taxon *Calciagglutispongia yabei* for the Spanish occurrences (Fig. 7B).

Stromatoporoid distribution for Spain is not unequivocal: There are other coral reef types without siliciclastics, with a lot of carbonate mud involved, hence from obviously more tranquil environments, which locally may be also rich in chaetetids (with other forms, such as *Ptychochaetetes pon-*

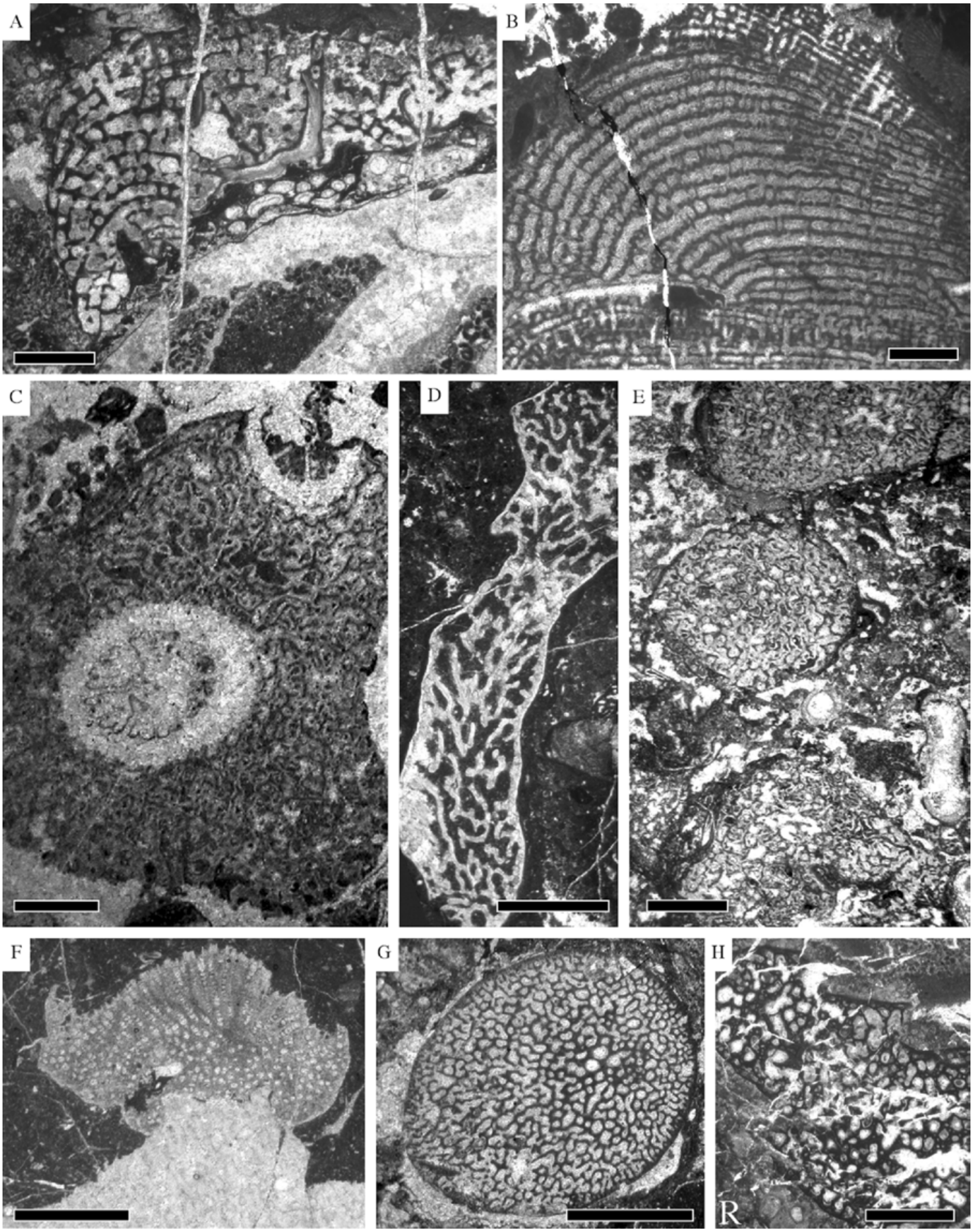


Fig. 9 Upper Jurassic Stromatoporoids from Intra-Tethys carbonate platforms (all thin-sections). **A** *Calciagglutispongia yabei* Reitner, overgrowing serpulids, Plassen Formation, Kimmeridgian, Gerhardstein near Lofer, Austria; scale bar 2 mm. This is the first finding of *C. yabei* outside the type locality at Terriente, Spain. **B** *Ellipsactinia caprense* Canavari, Kimmeridgian?—Tithonian?, Jainzen near Bad Ischl, Austrian Salzkammergut; scale bar 2 mm. **C** *Actinostromaria* sp., overgrowing branching coral, Plassen Formation, high-energy coral-stromatoporoid debris facies, Upper Kimmeridgian, Krahstein near Bad Aussee, Salzkammergut, Austria; scale bar 1 mm. **D** *Cladocoropsis mirabilis* Felix. Kimmeridgian?, Jainzen near Bad Ischl, Salzkammergut, Austria; scale bar 2 mm. **E** *Actinostromina grossa* (Germovsek). Kimmeridgian-Tithonian, Brnje, Croatia; scale bar 2 mm. **F** *Neuropora lusitanica* Termier, Termier and Ramalho overgrowing *Milleporidium* sp., Plassen Formation, Kimmeridgian, Trisselwand near Lake Altaussee, Salzkammergut, Austria; scale bar 2 mm. **G** *Cylicopsis verticalis* Turnsek, Tithonian, Sandling near Bad Aussee, Salzkammergut, Austria. Specimen resedimented within slope facies, from mass-flow deposits; scale bar 2 mm. **H** *Tubuliella fluegeli* Turnsek. Note the problematicum *Radiomura cautica* Senowbari-Daryan and Schäfer (left bottom, R). From Upper Jurassic mass flow deposits, Kurbnesh, Central Albania; scale bar 3 mm

ticus, *P. peroni*, *Pseudoseptifer angustitubulosus*). These reefs may be even termed coral-chaetetid mud mounds. In additon, the most impressive reefs of Spain, which are coral-microbial reefs forming bodies up to 10 metres or more, may also contain noticeable, though still accessory amounts of chaetetids and stromatoporoids (*Milleporidium formosum*, *Dehornella* cf. *choffati*, *Chaetetes chablaisensis*). These examples suggest that only at the species level is the distribution pattern of stromatoporoids and chaetetids characteristic of ecological differences.

France: Several recent studies have presented detailed comparative organismic and sedimentological studies on Oxfordian reef facies in the Paris Basin (Chevalier et al. 2001; Laternser 2001; Olivier 2003; Olivier et al. 2004). Despite this thorough approach, no important stromatoporoid-chaetetid facies could be identified. Especially stromatoporoids are astonishingly rare, but chaetetids occur sporadically as accessory element, normally overgrowing dead coral colonies (e.g., *Ptychochaetetes* sp., *Dehornella crustans*). Occasionally isolated colonies are developed which may grow up to 10 cm, at one locality up to 25 cm (Laternser 2001), which is thought to be exceptional. The only stromatoporoid reef-type structure known is a late Upper Jurassic monospecific *Burgundia trinorchii* biostrome from Vers (Dept. Saône-et-Loire, southeastern Paris Basin) which was described by Dehorne (1920). The biostrome has a lateral extension of 20 m, is about 1 m thick, and is composed of massive to nodular *Burgundia* stromatoporoids which may be up to 50 cm in diameter. Stromatoporoids mostly grow on top of each other but one specimen overgrows a coral and another one encrusts oolitic sediment which represents the underlying bed. Nerineids represent the accompanying fauna, bivalves, gastropods, and brachiopods occur in the calcareous sands beneath. Bodeur et al. (1985) identified *Cylicopsis verticalis, Chaetetopsis* sp., and the neuroporid *Sqamipora verticillata* from Kimmeridgian to Tithonian reefal to lagoonal sediments of Languedoc. Bernier (1984) mentions the Upper Kimmeridgian "Calcaires à stromatoporoidés de Matafelon" from the French Jura ranges between Lyon and Matafelon (N Dept. Ain), containing hemispherical to branching stromatoporoids. *Cladocoropsis* occurs as well. According to Meyer (2000), stromatoporoids were omnipresent during the Kimmeridgian, typically appearing in back reef and lagoonal carbonate sediments, but occasionally also within reefs. Except for *Cladocoropsis*, both Bernier (1984) and Meyer (2000) do not describe taxa which makes evaluation of the French stromatoporoid occurrences difficult to date.

Especially the rarity of stromatoporoids in the well-developed coral reefs and lagoons of the Oxfordian carbonate platforms is puzzling given the great variety of coral reef types and micritic to sparitic circumreefal sediments. *Cladocoropsis* is, however, relatively widespread from the Bathonian throughout the Upper Jurassic, occurring in Lorraine, Boulogne, French Jura Ranges, as well as the French and Spanish Pyrenees, where it is frequently associated with oolites and other calcareous sands, *Thaumatoporella* and foraminiferans (Peybernés 1976; Bernier 1984; Bernard 1988 in Lathuilière et al. 2003; Meyer 2000).

Germany: The Upper Jurassic of southern Germany is characterised by a largely shallowing upwards succession from basinal marls and bedded ammonitic limestones into which siliceous sponge-microbial mud mounds become increasingly intercalated upwards, to shallower facies which first develops on top of large sponge mudmounds giving rise to mixed coral-siliceous sponge facies, then pure coral facies (Gwinner 1976; Meyer and Schmidt-Kaler 1990; Leinfelder 1993; Laternser 2001; Schmid et al. in press). Again, stromatoporoids and chaetetids normally only occur very sporadically, but may be slightly more frequent at places. This is the case for parts of the Kimmeridgian Arnegg reef (Laternser 2001), chiefly in its transitional basal coral-siliceous sponge facies. The occurrence and relatively high abundance of encrusting chaetetids up to 27 cm in diameter and 4 cm in height is puzzling. Poor preservation did not yet allow for taxonomic determination. This finding is somewhat contradictory to the established view of chaetetids as indicators of very shallow environments, since dominance of platy corals as well as the composition of the reef builders, and position between pure siliceous sponge and pure coral facies indicates a setting in depths of several tens of metres. However, a similar new finding from slightly deeper waters has been made recently for Portugal as well (unpublished results). The probably northernmost occurrence of a chaetetid (*Ptychochaetetes polyporus*) outside of the Tethyan realm is described from the Oxfordian/Lower Kimmeridgian of northern Germany (Deister mountains; Helm and Schülke 2000; Helm et al. 2001; Reuter et al. 2001). This chaetetid species is very frequent within diverse shallow-water coral microbialite biostromes ("florigemma bed", "Obere Korallenbank") and overgrows corals or encrusts reef debris (Helm et al. 2001).

Some chaetetids are also known from debris-rich coral facies of southern Germany. Flügel (1979) reports *Ptychochaetetes grimmeri* from the Kelheim and Saal area of the Franconian Jura Range, where it occurs in reef-derived debris within lithographic limestones and in debris-type coral reefs. By comparing with other areas, in particular with a back-reef *Ptychochaetetes*-zone of the Swiss St. Ursanne coral reef (cf. Pümpin 1965), Flügel concludes that the genus is a characteristic element of small high-energy coral reefs. Meyer (1977) mentions encrusting *Burgundia* cf. *trinorchii* and rare *Milleporidium* sp. from debris-rich, micritic late Upper Jurassic coral reefs of the Regensburg and Kelheim area. These stromatoporoids co-occur together with the coral *Microsolena*, stromatolites, *Lithocodium*, and *Thaumatoporella*. Klug (2004) identified the chaetetid *Calcistella* which frequently overgrows corals within the debris-type coral reefs of Saal. *Neuropora* is a ubiquitous element in various facies of the Saal coral reefs and lagoons. Some other earlier reports of stromatoporoids from the Franconian Alb have turned out to be misidentifications of microsolenid corals.

Southern Tethys and Intra-Tethys shelves

As mentioned above, South and Intra-Tethys reefal and platform environments (Fig. 2) are obviously much richer in stromatoporoids (incl. chaetetids) than North Tethys and North Atlantic environments. Some regional examples should illustrate this observation.

Northern Calcareous Alps (Austria): Earlier reports and descriptions of stromatoporoids (formerly designated as hydrozoans and tabulozoans) were hardly ever correlated with microfacies aspects, making environmental interpretation very difficult. Many of the papers on stromatoporoids of the Alps actually are from that time. In addition, too many species seem to be established, or are at least suggested (e.g., undescribed new species A–E for *Actinostromaria* in Fenninger and Hötzl 1965).

True reef framestones are relatively rare, but occur at Rötelstein, Trisselwand, Plassen etc., all located in the Austrian Salzkammergut (Steiger and Wurm 1980; Schlagintweit et al. 2003; Gawlick et al. 2004a). Up to 1000 m of platform facies (cumulative thicknesses) may occur (Fig. 10). A total of 68 species of stromatoporoids (including a few chaetetids) have been reported from the reefs and lagoonal settings (Table 2; Figs. 9A–D, F, G) but corals only amount to relatively few species of even fewer genera altogether (five genera, if excluding Kühn (1935), who has described more genera which are, however, not accepted by many researchers). Autochthonous and allochthonous

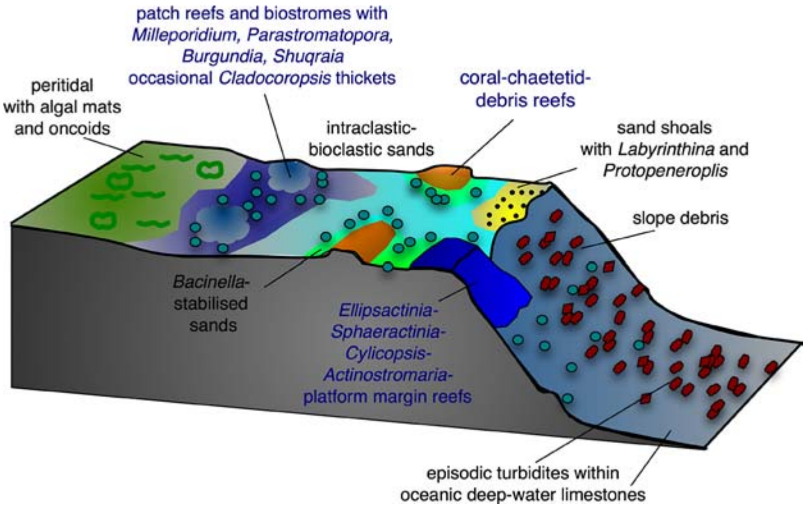


Fig. 10 Sketch of facies and stromatoporoid distribution of the Plassen-type intra-ocean carbonate platforms of Austria. Compiled after Fenninger and Holzer (1972), Steiger and Wurm (1980), Rasser and Sanders (2003), Schlagintweit et al. (2003, in press)

Table 2 Faunal list of Upper Jurassic stromatoporoids/chaetetids from the Austrian Calcareous Alps, compiled from various sources. List is largely based on Darga and Schlagintweit (1991), Dya (1992), Fenninger (1969, 1972), Fenninger and Holzer (1972), Fenninger and Hötzl (1965), Flügel (1964), Gawlick et al. (in press), Steiger (1981), Steiger and Wurm (1980), and own observations. Note that at least some published occurrences of *Actinostromaria tokadiense* rather represent *Calciagglutispongia yabei* (Schlagintweit unpubl. results), but "true" *A. tokadiense* might occur as well

Actinostromaria coacta ?
Actinostromaria jeanetti
Actinostromaria limitaris
Actinostromaria lugeoni ?
Actinostromaria shimizui
Actinostromaria tokadiense
Actinostromaria verticalis
Actinostromarianina dehornae
Actinostromina grossa
Actinostromina oppidana
Astrostylopsis circoporea?
Astrostylopsis radiata
Astrostylopsis tubulata
Bauneia cf. *multitabulata*
Burgundia alpina
Burgundia steinerae
Calciagglutispongia yabei
Cladocoropsis lata
Cladocoropsis mirabilis
Cylicopsis floridana
Cylicopsis verticalis
Dehornella aff. *harrarensis*
Dehornella sp.
Ellipsactinia caprense
Ellipsactinia polypora
Ellipsactinia ramosa
Ellipsactinia ellipsoidea
Milleporella reticulata
Milleporella schlageri
Milleporidium curvatum
Milleporidium fasciculatum
Milleporidium irregularis
Milleporidium karbadinense
Milleporidium kitamiensis
Milleporidium remesi
Milleporidium styliferum
Milleporidium tressenium
Paramilleporella gracilis
Parastromatopora cf. *crassifibra*
Parastromatopora crassifibra
Parastromatopora jurensis
Parastromatopora kiiensis ?
Parastromatopora menorianaumanni
Parastromatopora pilata
Shuqraia zuffardi
Sarmentofascis cretacica
Sphaeractinia sp.
Spongiomorpha asiatica
Steineria romanica
Steineria undulata
Syringostromina pruvosti
Tosastroma kiiensis

Chaetetes spengleri
Chaetetopsis krimholzi
Chaetetopsis sp.
Neuropora sp.
Pseudoseptifer spengleri
Ptychochaetetes globosus

occurrences are also from Vienna to the Lake Achen, north of Innsbruck. Upper Tithonian to Berriasian mass-flow deposits with reefal debris (including stromatoporoids) occur intercalated in the basinal deep-water pelagic Oberalm Formation, owing their existence to synsedimentary tectonism at the frontal part of ramp anticlines that formed during Upper Jurassic thrusting (Frisch and Gawlick 2003). Stromatoporoids were reported by Steiger (1981), Fenninger (1972), and Gawlick et al. (in press) from the turbiditic Barmstein Limestones. Within the Barmstein Limestones, *Sarmentofascis cretacica*, *Actinostromaria shimizui*, and *Milleporidium* div. spec. amount to about 90% of all resedimented stromatopore bioclasts (Gawlick et al. in press; see Fig. 10). The stromatoporoid-bearing external platform facies of the Northern Calcareous Alps also comprises several other sponge taxa such as pharetronid sponges (e.g., *Thalamopora*) and additional stromatoporoids (e.g., *Murania*) which currently are under study (e.g., Schlagintweit 2004).

Steiger and Wurm (1980) have provided a first detailed facies analysis of the reefs which demonstrated a high amount of debris formation but also the dominance of encrusting reef builders, chiefly the stromatoporoids. First reinspections give clues that the majority of reefs might be similar to the coral-microbial-debris type as defined in Portugal, with corals largely being substituted by stromatoporoids (cf. Gawlick et al. 2004a). *Ellipsactinia* (Fig. 9B) appears to be the most prominent reef builder in many areas in certain stratigraphic levels (Fig. 10). *Ellipsactinia* occurs on the upper slope facies close to the platform margin, but apparently below the fair-weather wave base (see also Morsilli and Bosellini 1997).

Slovenia and Croatia: Slovenian and Croatian reefs have been studied (Table 3) under various aspects and both faunal/floral analysis as well as microfacies studies have been performed. A restriction is, that except for the coral monograph of Turnsek (1997), more recent analyses are not available.

The 200 m thick platform facies is indicated as Oxfordian to Kimmeridgian in age. Fauna is dominated by coral taxa and stromatoporoids, but chaetetids also occur with several species. We have considered 35 stromatoporoid species (including a few chatetids) for Slovenia and 49 for Slovenia/Croatia altogether. These figures are somewhat lower than the species numbers given by Turnsek (1966) and Turnsek et al. (1981), because these authors included some taxa from adjacent areas, and because we mostly excluded 'sp.'-identifications whereas coral species amount to 65 species on the Dinaric Platform (Turnsek 1997). The platfom developed on top of micritic, crinoidal, and oolitic limestones of Middle Jurassic age or directly on top of Lower Jurassic deposits. Overlying sediments are *Clypeina sulcata* micritic limestones. The Upper Jurassic reef complex of central Slovenia has been interpreted as a barrier reef complex by Turnsek et al. (1981). From N/NE to S/SW they subdivide it into a 2–5 km broad zone with fore reef and slope sediments, the central reef (11–15 km wide), and a 50–100 km broad back reef area. These zones exhibit strongly different sedimentary and faunal character.

The carbonate platform grew on an intra-ocean microplate (Dinaric-Apulian microplate) within the central to southern Tethys (cf. Ziegler 1988; Sengör 1998; Stampfli et al. 1998, 2002; Dercourt et al. 2000) and was surrounded by deeper marine areas of this microplate (Slovenian 'Trough' to the NW, Bosnian 'Trough' to the NE,

Table 3 Stromatoporoid faunal lists for Slovenia and Croatia. Faunal lists based on Milan (1969), Nikler (1978), Turnsek (1966, 1969a, b), Turnsek et al. (1981)

Slovenia		Croatia	
Parastromatoporoid-Zone	**Actinostr.-zone, cont'**	*Actinostromaria* sp.	*Milleporella fasciculata*
Dehornella omanensis	*Astrostylopsis circoporea*	*Actinostromarianina dehornae*	*Sphaeractinia cylindrica*
Disparistromaria oxfordica	*Astrostylopsis grabensis*	*Actinostromarianina lecomptei*	*Sphaeractinia diceratina*
Hudsonella lucensis	*Astrostylopsis schnorfae*	*Actinostromina grossa*	*Sphaeractinia dichotoma*
Hudsonella media	*Astrostylopsis trnovica*	*Actinostromina oppidana*	*Sphaeractinia dinarica*
Hudsonella otlicensis	*Astrostylopsis tubulata*	*Adriatella poljaki*	*Sphaeractinia steinmanni*
Parastromatopora japonica	*Coenostella thomasi*	*Astrostylopsis circoporea*	*Tubuliella fluegeli*
Parastromatopora compacta	*Cylicopsis carniolica*	*Astrostylopsis grabensis*	*Tubuliella illyrica*
Reticullina rectangularis	*Cylicopsis floridana*	*Astrostylopsis slovenica*	
	Cylicopsis lata	*Astrostylopsis tubulata*	
Bauneia multitabulata	*Desmopora listrigonorum*	*Cladocoropsis velebitica*	
Chaetetopsis crinata	*Ellipsactinia caprense*	*Coenostella thomasi*	
Chaetetopsis krimholzi	*Ellipsactinia ellipsoides*	*Ellipsactinia velebitica*	
Pseudochaetetes champagnensis	*Ellipsactinia polypora*	*Ellipsactinia caprense*	
Ptychochaetetes globosus	*Sphaeractinia dichotoma*	*Ellipsactinia ellipsoidea*	
	Sphaeractinia diceratina	*Ellipsactinia* ex aff. *portisi*	
Actinostromariid-Zone	*Sphaeractinia steinmanni*	*Ellipsactinia macropora*	
Actinostromina grossa	*Tubuliella fluegeli*	*Ellipsactinia micropora*	
Actinostromina germovsheki	*Tubuliella illyrica*	*Ellipsactinia polypora*	
Actinostromina oppidana	*Tubuliella rotunda*	*Ellipsactinia tyrrhenica*	

Krasta-Cukali 'Trough' to the SE and W; Velic et al. 2002), all of which probably bordered the Pindos oceanic area (cf. Stampfli et al. 2002; see Fig. 2). In central Slovenia the reefal belt stretches across 140 km and obviously continues across the Dinarids down to Albania to the East, and to Italy to the West (Turnsek 1966; Milan 1969). Some characteristic stromatoporoid taxa from this reef belt such as *Tubuliella fluegeli* have recently been reported also from mass-flow deposits in Albania (Gawlick et al. 2004b; see Fig. 9H). The northeastern margin of this Dinaric-Adriatic platform was characterised by a more or less continuous belt of stromatoporoid-coral, barrier type reefs (Turnsek et al. 1981; Dragicevic and Velic 1994; Turnsek 1997; Velic et al. 2002). At least locally, steep platform margin slopes are obvious by development of breccia beds and boulder-sized allochthonous blocks. The central reef area is characterised by stromatoporoid-coral-chaetetid associations, which can be separated into an actinostromariid and a parastromatoporoid zone (see already Turnsek 1966, 1969a, b). In the actinostromariid zone stromatoporoids dominate by far in abundance and volume, whereas corals are more diversified at the species level. Chaetetids occur as subordinate elements, other organisms such as foraminiferans or bryozoans are relatively rare. The high amount of debris as well as sparitic cements document higher energy settings at the platform margin. However, the adjacent parastromatoporoid zone is dominated by corals, both in terms of abundance and species number. Chaetetids and microbial crusts are also more frequent than in the actinostromariid zone. Other sedimentary characteristics are similar in both zones, however, vadose cements and vadose silts are indicative of episodical emersion of the parastromatoporoid zone (cf. Milan 1969; Turnsek 1966, 1969a, b; Nikler 1978; Turnsek et al. 1981; Turnsek 1997). The southwestern edge of the Dinarid platform was dominated by carbonate sand bars with occasional patch reefs (Tisljar and Velic 1987).

Towards S/SW the lagoonal, dark micritic, deposits exhibit frequent intercalations of *Cladocoropsis mirabilis* facies. *Cladocoropsis* prevails but is associated with frequent dasycladaceans and foraminiferans. Turnsek et al. (1981) attribute the *Cladocoropsis* facies to their back reef zone. Occasionally, these lagoonal sediments were covered by oolitic deposits and small patch reefs with faunal characteristics similar to the parastromatoporoid zone may form.

Turkey: Stromatoporoid facies is known from lagoonal *Cladocoropsis* limestones of Kuruburun, western Anatolia (cf. Fig. 2 for palaeolocation), of Upper Oxfordian to Kimmeridgian age, exhibiting a minimum thickness of 30 m. Three stromatoporoid species (*Cladocoropsis mirabilis, Shuqraia heybroeki, Milleporidium* cf. *kitaminensis*) and rare, undeterminable corals have been reported (Flügel 1974).

Middle East: The above-discussed central and southern Tethys intra-ocean platform examples differed considerably from the North Tethys-Atlantic examples by their abundance in stromatoporoids (with or without chaetetids). However, except for the lagoonal *Cladocoropsis* facies (which is also known from the North Tethys-North Atlantic), they all were closely associated with corals. A third category of reefs occurs in the Middle East where reefs or reefal meadows may be exclusively, or to a large proportion, composed of stromatoporoids.

Table 4 Stromatoporoids from Maktesh Gadol (or Maktesh Hagadol), and Maktesh Hethira, Israel (from Wood 1987, 1999). Note that age determination is not unequivocal (Lower Kimmeridgian, Wood 1987, supposed Callovian, Wood 1999)

Actostroma damesini	*Promillepora pervinquieri*
Dehornella crustans	*Shuqraia zuffardi*
Parastromatopora libani	*Steineria somaliensis*

Israel: Wood (1999: 109–110) presents an interesting case study of Jurassic patch reefs exclusively composed of stromatoporoids at Makhtesh Gadol (or Hagadol), southern Israel. The fauna was also described by Wood (1987). She attributed this site to the Lower Kimmeridgian. The reexamination of Wood (1999), however, assignes a supposed Callovian age. Besides monospecific clusters of branching forms of *Shuqraia, Promillepora*, and *Parastromatopora* domal forms also occur (*Actostroma*). The organisms colonised fine-grained, low-energy, apparently soft bottoms and formed low-diversity lensoid patches or thickets, some of which may cover wide areas. Wood highlights the fact that there is no obvious ecological succession or wave-resistant framework. Besides these patch reefs, isolated large domal *Dehornella* and *Promillepora* heads occur within oolitic shoals, showing repeated growth reorientation owing to wave or current disturbance. According to their size of up to 35 cm in diameter and the occurrence of up to 50 latilaminae, Wood (1999) assumes longevity for many individuals which together with growth reorientation suggests that these organisms were well adapted to occasional to frequent wave disturbances. Table 4 lists the faunal determination from Wood (1987, 1999; cf. Fig. 2 for palaeolocation).

Saudi Arabia and adjacent areas: During the Jurassic, the Arabian peninsula was largely part of a gigantic carbonate platform system being up to 1000 km wide (Fig. 11). The Jurassic of Saudi Arabia is mostly characterised by epeiric ramp type pure carbonate systems which are composed of oolitic, bioclastic, peloidal, algal mat sediments representing shoal, lagoonal, peritidal, and sabkha deposits, as well as occasional reef development. The Arabian platform system included several shallow intra-platform basins in variable number, extension, and configuration depending on the chosen time slice (Al-Husseini 1997; Ziegler 2001). Evaporites developed frequently, and increasingly towards the top of the Jurassic succession, evidencing episodes of hypersalinity and arid climates (Fig. 11).

Stromatoporoids are typical of the succession from the Tuwaiq Mountain Formation (Mid/Upper Callovian to Lower Oxfordian), through the Hanifa Formation (Oxfordian to Lower Kimmeridgian) to the Jubaila Formation (including the Arab D-Reservoir; Kimmeridgian pp., ages after Hughes 2004). These sediments are at outcrop around Ryadh and include the largest hydrocarbon reservoirs of the world in the subsurface (e.g., Ghawhar field) further

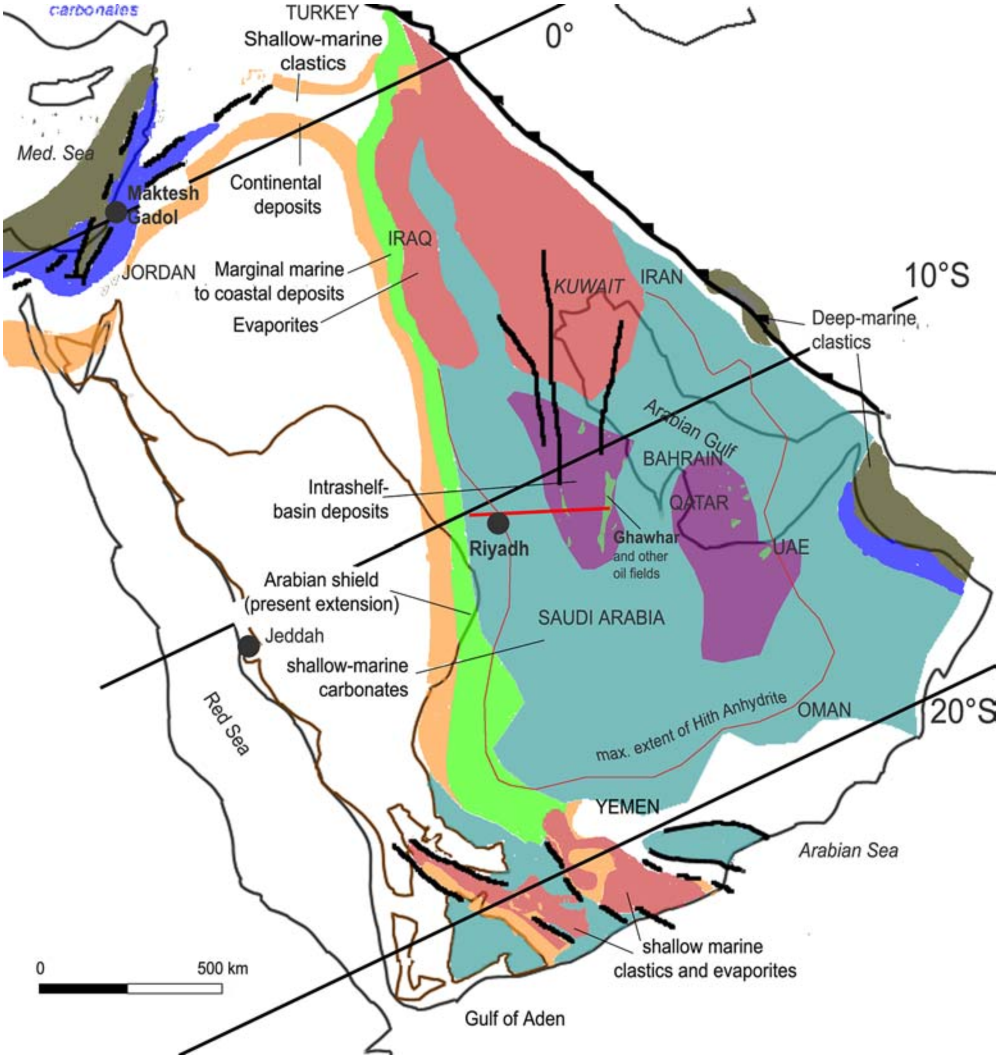


Fig. 11 Palaeogeographic map with depositional environments for the Arabian Platform for the early Late Jurassic (comprising depositional time of the Tuwaiq Mountain and Hanifa Formation. Redrawn and simplified after Ziegler 2001). The vast carbonate platform was more than 1000 km broad and probably still extended further east. For comparison: modern Great Bahama Bank is about 100 km broad (E–W). Red line spans the distance between the lithological sections shown in Fig. 12. Palaeolatitudes after Al-Husseini (1997). Note that exact position of palaeoequator is matter of debate, it might be situated about 5° (Stampfli et al. 2002) or 10° (Golonka 2002) further south than in this version (see also Fig. 2)

east (Al-Husseini 1997). Highly porous stromatoporoidal debris sheets occur in distinct levels both in the subsurface as well as at outcrop (Fig. 12) and are a major target for petroleum exploration (cf. Meyer et al. 2000). At outcrop, a spectacular coral bed occurs in the lowermost part of the Jubaila Formation. The bed stretches across an extensive area and is completely composed of in-place low-domal coral heads (Fig. 13B). A brief inspection suggests that the bed represents an in-place coral meadow which might represent a low-diversity single population. A similar bed though of supposed Callovian age has been described by El-Asa'ad (1989). No stromatoporoids or microbial crusts have been detected. Embedding sediments and position within a shallowing upward succession suggests that the coral fauna grew in slightly deeper settings, obviously during an extraordinary event favouring exhaustive but very short-termed coral growth. The coral fauna of the Middle and Upper Jurassic of Saudi Arabia was described by El-Asa'ad (1989, 1991) and includes many taxa unique to the Arabian peninsula.

Within the upper Tuwaiq Mountain Formation narrowing upwards, reefal build-ups occur in distinct levels. Their heights range from a couple of metres to several tens of metres (Fig. 13A). They are very rich in stromatoporoids but corals may occur as well, typically forming a reef cap of low-domal, broad massive coral colonies (Hughes 2004; Fig. 13C). Other bedded levels of the Tuwaiq Mountain Formation are also rich in stromatoporoids, containing horizons of mostly reworked massive to thickly branching stromatoporoids with *Burgundia* (Fig. 13J) and *Shuqraia* being common elements. Many stromatoporoid heads show signs of abrasion (Figs. 13D, E). Medium-sized coral fragments of both massive and branching corals also occur scattered but stromatoporoids dominate. Several horizons

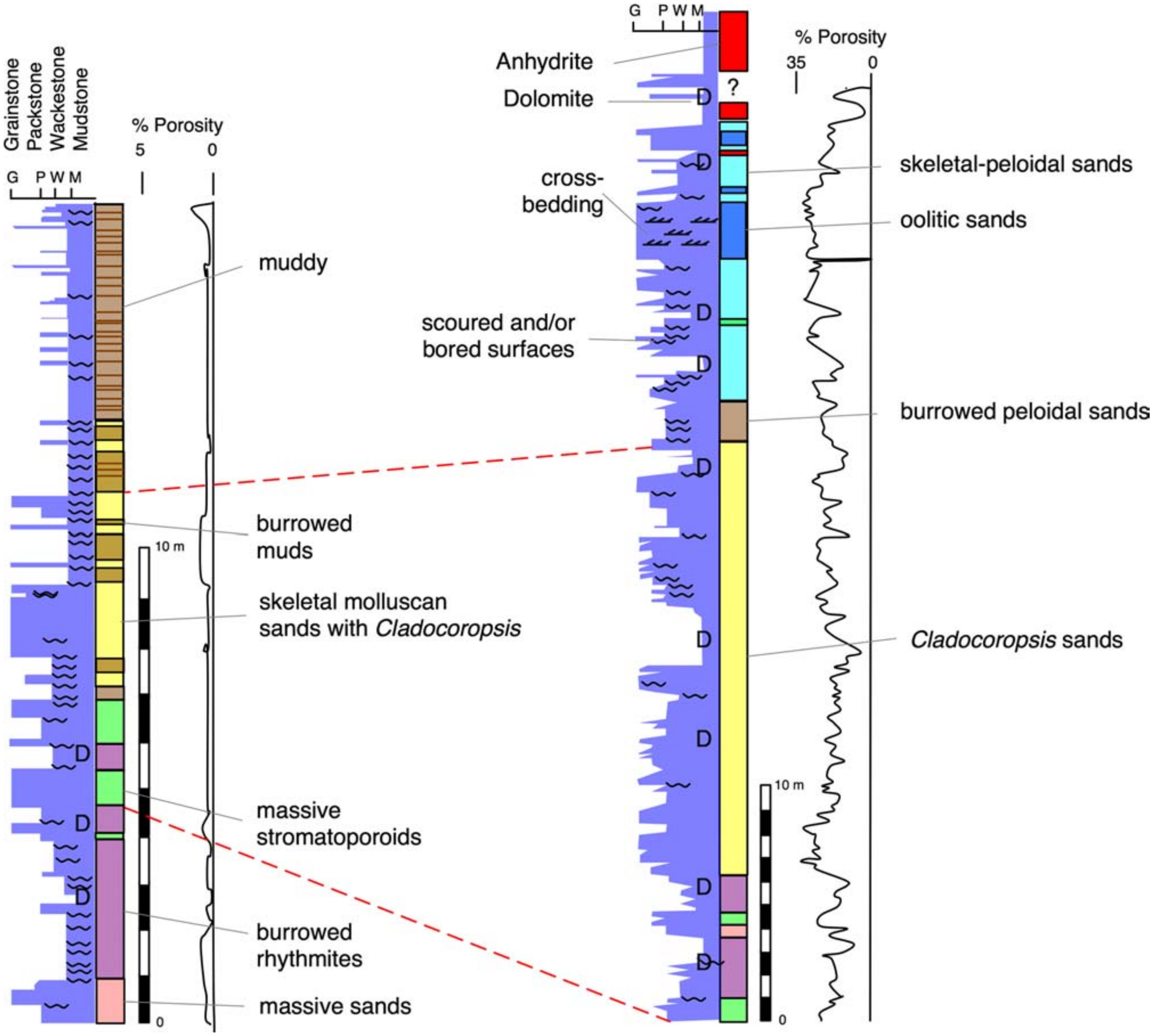


Fig. 12 Outcrop section in the Ryadh area (left, W) and subsurface section of Ghawhar field (E), including the Jubaila and Arab formation, Saudi Arabia. Anhydrites on top are base of Arab D-Hith evaporites. Highest porosities are in skeletal sands with *Cladocoropsis* and pure *Cladocoropsis* sands. Red dashed lines is a tentative lithological correlation. Sections are about 300 km apart. The Ryadh section is characterized by repetitive small-scale cycles bounded by irregular surfaces. Low cycle thickness, erosive scours, and channels, and largely lacking cross-bedding even in sands is indicative of frequent erosive and re-sedimentation events in a regime of very reduced accommodation potential. Much proximal material is transported towards east into still shallow but stronger subsiding areas. Note change of scale between sections. See Fig. 11 for locations and text for details. Simplified after Meyer et al. (1996)

show irregular lower surfaces being evidence of occasional large-scale scour events.

The superimposed Hanifa Formation is characterised by a variety of subenvironments with a generally shallowing upwards trend. Carbonate sands with stromatoporoids typically occur (*op. cit.*). Corals may occur forming small patches which tend to occur in two argillaceous intervals (El-Asa'ad 1991). The overlying Jubaila Formation with its basal coral meadow (Fig. 13B) is particularly typified of small-scale stacked cycles with frequent mottled firmground to hardground development in the lower, more muddy part, increasingly erosional cycle boundaries including large stromatoporoid and coral-filled channels in the middle part (Fig. 13F), and a dominance of coarse *Cladocoropsis* sands in the upper shallowest part (Figs. 13G–I; Hughes 1996, 2004; Meyer et al. 1996). Erosive boundaries, scoured channels, the abraded and redistributed character of stromatoporoids and corals as well as the lack of in situ reef or in-place *Cladocoropsis*-meadow facies is evidence of a high-energy, storm-abraded platform with insufficient accommodation space during the development of the uppermost Jubaila Formation which is equivalent to the Arab D reservoir in the subsurface (Hughes 2004). *Cladocoropsis* sand sheets and channels are typically associated with abundant debris of dasycladacean algae, the algal problematicum

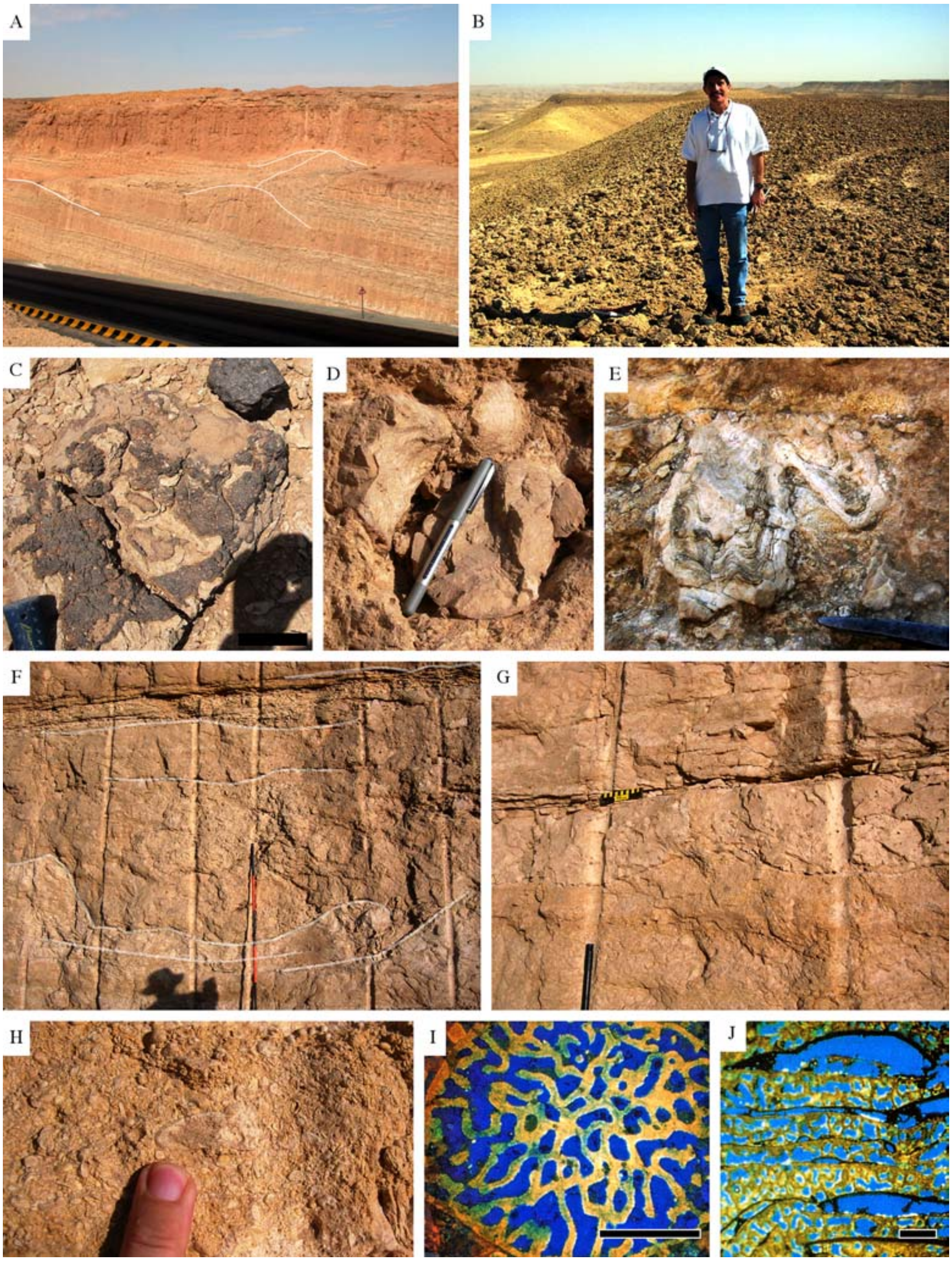


Fig. 13 Middle and Upper Jurassic stromatoporoid facies from Saudi Arabia. **A** Stromatoporoid reefs from the upper Tuwaiq Mountain Formation. Reefs are about 5 m high. Note upwards-waning morphology of reefs which are capped by a veneer of corals. Roadcut of the Mekka highway to the Tuwaiq Mountains, W Ryadh. **B** Single population coral meadow, composed of low-domal to platy coral colonies. Interpreted to represent a unique event in slightly deeper water, possibly during rapid transgression, base of Jubaila Formation, W Ryadh. **C** Platy to flat domal coral colonies frequently cap stromatoporoid reefs in the Upper Tuwaiq Mountain Formation, which is interpreted as a pre-drowning or cooling event. W Ryadh, width of hammer handle is 4 cm. **D** Sphaerical multiphase stromatoporoid colony (cf. *Burgundia* sp.) with growth reorientation, typical of an abrasive environment, upper Tuwaiq Mountain Formation, near Ryadh. Width of colony is 20 cm. **E** Another massive stromatoporoid colony, in upside-down position. Note erosional truncation beneath erosive bedding surface interpreted to represent an abrasion platform, location and formation as Fig. 13D. **F** Multistorey channel fill within middle Jubaila Formation, near Ryadh. Channel is mostly filled with reworked stromatoporoid boulders and some reworked corals. Scale bar is subdivided in 10 inch (25 cm) units. **G** *Cladocoropsis* rudstones at top of Jubaila Formation. Note irregular scoured surface above rudstones and small-scaled muddy cycles. Wadi Dirab roadcut west of Ryadh. Horizontal scale is 15 cm long. **H** Detail of *Cladocoropsis* rudstones at outcrop. Finger points to an exceptionally large *Cladocoropsis* fragment. Wadi Dirab roadcut west of Ryadh. **I** Thin-section of *Cladocoropsis mirabilis* Felix from the subsurface region at Ghawhar field. Note enormous intraparticle porosity (as indicated by blue stained stone glue), from Hughes (1996). Scale bar 1 mm. **J** Thin section of *Burgundia* sp., from the subsurface region at Ghawhar field. Again, intraparticle porosity is enormous. From Hughes (1996); scale bar ca. 1 mm

Thaumatoporella, as well as a moderately low diversity association of benthic foraminiferans including miliolids.

Toland (1994) has collected and determined stromatoporoids from Saudi Arabia and adjacent areas. Taxa are presented in Table 5.

Taxa distribution of Upper Jurassic stromatoporoids

Statistical analysis

We have chosen nine case regions from supposed Callovian to Late Kimmeridgian/Early? Tithonian occurrences which allow for statistical cross-comparison of reported stromatoporoid genera and species. Selection of regions was based on the following criteria (1) considerable amounts of stromatoporoids known; (2) reliable taxa identifications available; (3) coverage of North Tethys, North Atlantic, Intra-Tethys, and South Tethys shelves; (4) case regions within a defined area (Middle East to western boundary of Europe). Our set of nine regions (cf. Fig. 14) is considered to be representative as to the present state of knowledge. Taxa have been plotted on spreadsheet matrices, and chart diagrams as well as cluster dendrograms have been produced. Taxa identifications were mostly compiled from existing literature, with considerable additions of the present working group.

From all nine regions, the Austrian and Slovenian/Croatian carbonate platforms show both highest generic and species numbers (Fig. 14) and hence show highest *beta*/*eta*-diversities of all areas. Despite the widespread occurrence of stromatoporoids on the Arabian peninsula, *beta*/*eta*-diversities are relatively low there. The most widespread genera are (site occurrences in brackets) *Cladocoropsis* (8), *Dehornella* (7), *Shuqraia* (6), *Actinostromaria*, *Milleporidium*, *Parastromatopora*, *Ptychochaetetes* (all 5), *Astrostylopsis, Burgundia, Chaetetopsis, Steineria* (all 4; see Fig. 15). From the areas investigated, *Syringostromina, Tosastroma, Tubuliella, Siphostroma, Ellipsactinia*, *and Sphaeractinia* are restricted to intra-ocean carbonate platforms.

Interestingly, the typical genus *Ellipsactinia* which occurs widespread in reefal limestones of the Dinaric and Apulian platform, and which is also known from the adjacent Intra-Tethys areas, such as the Parnassos zone of Greece (Carras 1995), is not apparent from Arabia. On the Apulian platform there are also other places with ellipsactiniids such as the Gargano area of Italy (Morsilli and Bosellini 1997).

From the 42 genera considered, 11 genera occur in only one testing region. Some of the taxa will probably have to be revised (e.g., *Spongiomorpha*) but others might be of palaeobiogeographic value. These comprise (occurrence region in brackets) *Adriatella* (Croatia), *Axiparietes* (Spain), *Paramillepora, Siphostroma* (Austria), *Desmopora, Reticullina* (Slovenia). *Astroporina* which also appears only in one testing region (Algarve), is known to also occur in Somalia, Lebanon, and Oman (Hudson 1960), *Tosastroma* (Austria) is also known from the Torinosu Limestone of Japan (Yabe and Sugiyama 1935).

Figure 15 also shows that a few genera may include many different species. The highest species richness of *Actinostromaria*, *Milleporidium*, and *Parastromatopora* from Austria, or of *Ellipsactinia* and *Sphaeractinia* from Croatia is clearly visible in the graph.

From the 139 species, as defined for this statistical analysis, 83 occur in only one of the nine regions. This set of species includes both strongly endemic taxa as well as possible misidentifications of individual taxa which might have to be synonymised with other species in a future taxonomic revision. To date, the relevance of these taxa for palaeobiogeographic analysis is, therefore, not unequivocal and will not be further discussed here. However, Fig. 16 does show interesting patterns. The three most widespread species are (number of regions in brackets): *Cladocoropsis mirabilis* (8), *Ptychochaetetes globosus* (5), and *Astrostylopsis circoporea* (4). *Actinostromaria* (Fig. 9C), occurring in different species is also widespread.

Typical Intra-Tethys-platform species include: *Actinostromina grossa*, *A. oppidana*, *Astrostylopsis tubulata*, *A. grabensis*, *Ellipsactinia caprense*, *E. ellipsoidea*, *E. polypora*, *Sphaeractinia dichotoma*, *S. diceratina*, *S. steinmanni*, *Actinostromarianina dehornae*, *Coenostella thomasi*, *Tubuliella illyrica*, and *T. fluegeli*. All *Tubuliella* species only occur in the narrow area around Slovenia and Croatia, including a new finding from Albania (Gawlick et al. 2004b).

Typical South Tethys margin shelf species include: *Actostroma damensini*, *Parastromatopora libani*, *Promillepora pervinquieri*, and *Steineria somaliensis*.

Quite some species, such as *Dehornella hydractinoides, D. choffati, Disparistromaria tenuissima*, or *Milleporidium variocellatum* are also restricted to the Iberian case studies (see Fig. 16). However, some of these species are known from other areas not yet included in this study, so that at this stage of the knowledge, distribution pattern of individual taxa do not yet allow discrimination of biogeographical extension for individual taxa, but nevertheless gives trends and suggestions for further target areas. However, statistical cluster analysis does allow the comparison of similarities of entire faunas between the chosen case study areas (Figs. 17, 18).

Cluster analysis based on species patterns has grouped identifications of a given species together with potential ‘cf.’, ‘aff.’, or ‘?queried’ identifications of the same species as one. Such a species occurs in the matrix as *genus_X* (cf.) *species_1*, if such conferred, attributed, or queried *species_1* have been mentioned at least from one locality. Identifications of unidentified but separated species, such as ‘sp. A’, ‘sp. B’, ‘sp. C’ have been treated as one additional species, resulting in an additional *genus_X* sp. entry in the matrix. This is thought to be a valid compromise between reducing undescribed but already suggested species to one single species (species reduction) and possibly listing the same species twice (species duplication), in cases where *genus_X* sp. might represent another, already identified,

Table 5 Upper Jurassic stromatoporoids from the Saudi Arabia and adjacent areas (mostly from Toland 1994)

Early Oxfordian Assemblage (Oman, Yemen, Somalia, Saudi Arabia, Iraq)	*Shuqraia zuffardi, Dehornella harrarensis, Dehornella crustans, Actinostromarianina praesalevensis, Parastromatopora libani, Cladocoropsis mirabilis*
Middle to Late Oxfordian (Oman, Saudi Arabia, Sinai)	As above, plus: *Promillepora pervinquieri, Actostroma damesini, Steineria somaliensis, Shuqraia hudsoni.* Commonly with corals, brachiopods
Kimmeridgian (UAE, Qatar, Bahrain, Saudi Arabia, Oman, Yemen)	As Oxfordian minus *A. praesalevensis* and *P. libani*. Plus: *Burgundia ramosa. Burgundia trinorchii, Actinostromarianina lecompti, Actinostromaria* sp., abundant *Cladocoropsis mirabilis*
Late Kimmeridgian to Tithonian? (UAE)	*Burgundia trinorchii, Burgundia ramosa, Actinostromarianina lecompti, Shuqraia zuffardi*

and listed species of *genus_X*. In cases of doubt we have excluded all 'sp.'-identifications from the matrix.

Our aim was to test whether cluster analysis reveals diagnostic similarity grouping of our nine regions (Q-mode cluster analysis) in order to detect potential biogeographic or palaeogeographic patterns, such as endemism or migrational connections. We used 139 species belonging to 42 genera for the data matrix (species based Q-mode clustering). Many of these species only occur in one of the nine selected areas, which facilitate formation of distinct clusters. As discussed earlier, we cannot rule out that several species might be invalid. Since the likelihood for this is highest for species which occur only in one region, we have also produced Q-mode clusters which do not take such species into account (non-endemic species based Q-mode clustering). This would blur actual regional differences in cases were correctly established species are excluded, but at least diminishes artefacts caused by wrong taxonomy. We have also used genera-based Q-mode clustering (both for presence–absence and species-number weighted genera), in order to minimise circular reasoning.

Overregional preferential co-occurrence of taxa can be in part taken from the diagram charts. In order to statistically test region-independent likelihood of co-occurrences of taxa we have also run R-mode analysis. Again, owing to the high amount of species which only occur in one of the regions, R-mode clusters are very distinct, but mostly reflect the strong regional differences. This effect is minimised by using R-mode cluster analysis only on the remaining species or on genera. For additional information on the used cluster statistical methods and algorithms see the 'Method' section above.

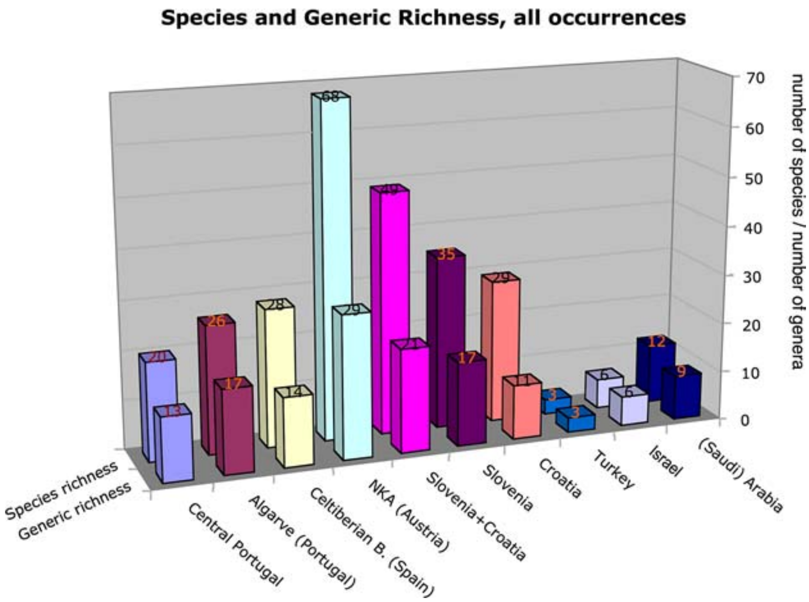


Fig. 14 Total number of stromatoporoid (including chaetetid) genera and species from Upper Jurassic (possibly including Callovian) reefs of key areas with stromatoporoid-containing reefs. Although stromatoporoid reefs are much rarer along the northern Tethys (Algarve, Celtiberian) and North Atlantic (central Portugal), their taxa numbers are relatively high. Austria has the highest generic and species diversity of stromatoporoids being followed by the second Intra-Tethys example, the Slovenian-Croatian Platform. Separate columns for Slovenia and Croatia in comparison with composite Slovenian-Croatian column show that not all taxa occur in both regions despite their vicinity (see also subsequent figures). Although stromatoporoids are frequent on the Arabian Platform this is not reflected by high taxa numbers

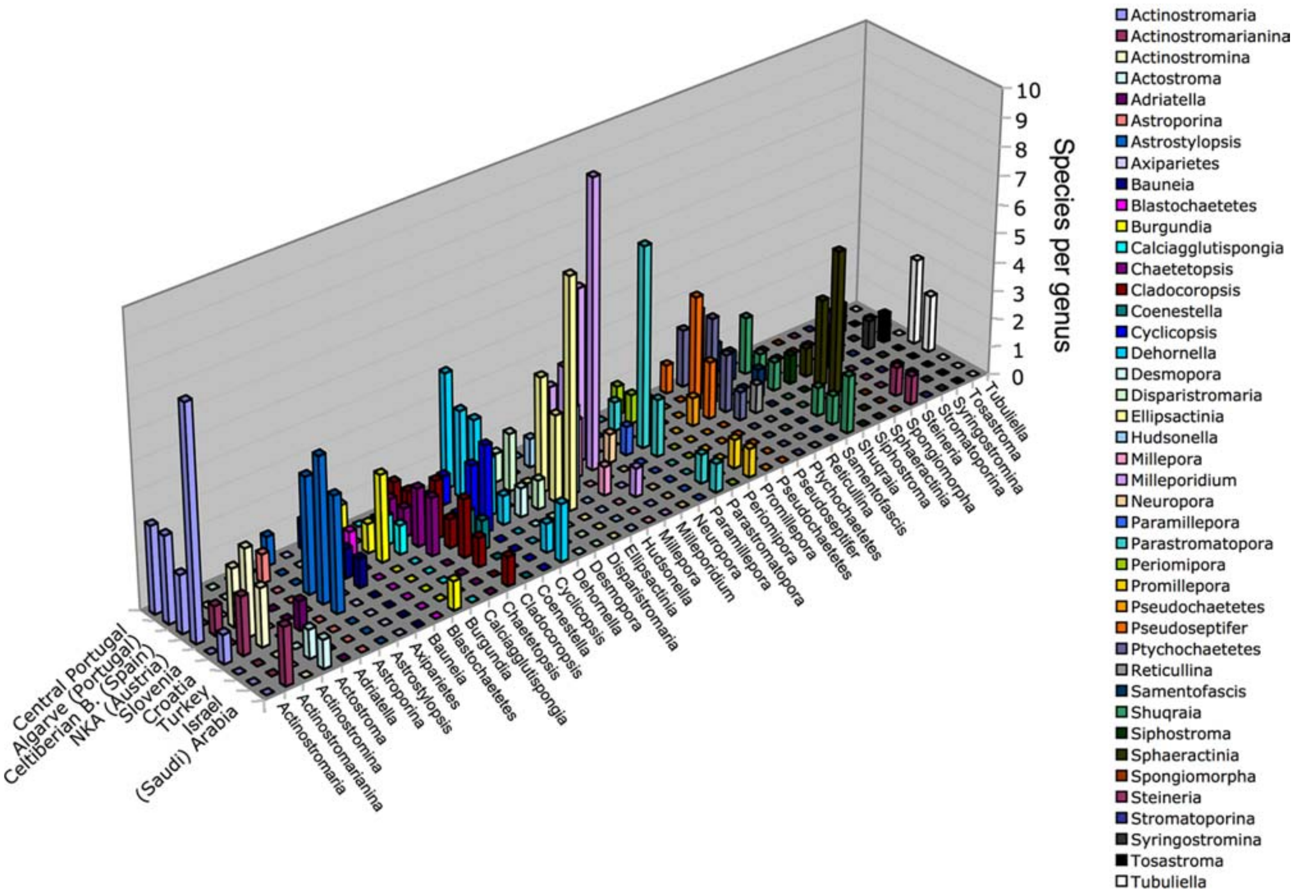


Fig. 15 Stromatoporoid species per genus and region. The three hindmost positions are Iberia, the other positions are within and at the southern margin of the Tethys. Highest species richness of *Actinostromaria*, *Milleporidium*, and *Parastromatopora* from Austria, or *Ellipsactinia* and *Sphaeractinia* from Croatia is clearly visible. *Dehornella* is another typical genus in Iberia but is spread across most other regions as well. *Cladocoropsis* occurs in all but one region. From the areas investigated, *Syringostromina, Tosastroma, Tubuliella, Siphostroma, Ellipsactinia*, and *Sphaeractinia* are restricted to intra-ocean carbonate platforms

Figures 17a–d gives the results of four different Q-mode runs, all of which result in a good cluster discrimination with interesting similarities. Despite the fact, as discussed above, that many stromatoporoid species might occur across many regions, similarity patterns are strongly highlighted. Irrespective of which method and algorithm is used, the Iberian sites, despite not showing a very high similarity (except for when using the Raup and Crick algorithm; Fig. 17c) nevertheless form a distinct cluster as do the Israelian and Arabian sites and the Slovenian-Croatian sites. The latter show higher similarities to Austria than to other clusters. Only Turkey shows variable similarities and cluster-inclusion, depending on the method. This demonstrates that for cluster comparison only regions with higher taxa numbers should be used. Depending on the algorithm and on the general method (species or genera distribution) it may appear close to the Middle East occurrences or to others. This is no surprise because the Turkish occurrence only includes a *Cladocoropsis* assemblage which is known from several other areas as well.

R-Mode cluster based on presence–absence of those species, which occur at least in two regions (Fig. 18) show that clusters may both represent distinct regions and prominent overregional co-occurrence assemblages. The fact that regional clusters for the South Tethys Middle East margin, for Intra-Tethys isolated carbonate platforms and for Iberia are so distinct, strongly suggests that provincialism of Upper Jurassic stromatoporoids was considerable, in particular since all 83 species which occur in only one of the chosen test regions have not been used for the analysis for reasons discussed above. Future integration of other areas once data will be available will have to substantiate or modify this result. Besides the endemic or regional clusters, there are a set of much more widespread clusters which also show that it was not migrational restriction which isolated the faunas. Even rarer species may show disjunct distribution. Examples are *Shuqraia zuffardi* occurring in Austria and the Middle East, *Dehornella crustans* from Portugal and the Middle East, or *Actinostromarianina lecomptei* from Portugal and Croatia. There are also overregional sets of frequently co-occurring taxa such as *Milleporidium* with *Actinostromaria,* or *Bauneia* with *Astrostylopsis*. The large cluster tentatively designated as ?pandemic in Fig. 18 also clearly shows that regional cluster formation was mostly due to adaptive strategies to regionally differing environ-

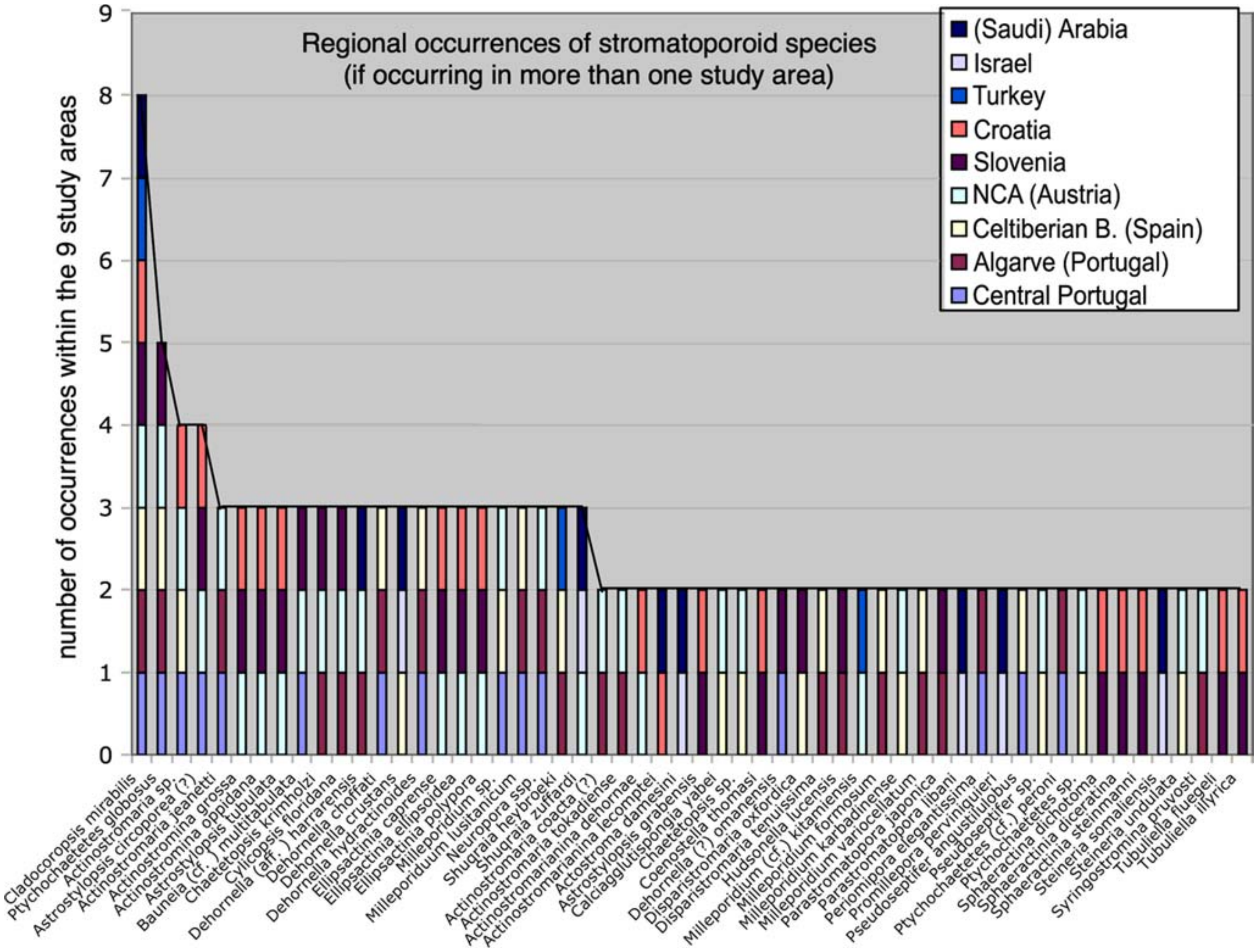


Fig. 16 Species frequencies in the test areas. Graph shows all species which occur at least in two of the test areas. Colours indicate occurrence areas. More ubiquitous and more area-restricted species can be depicted. Compare with Fig. 18. Refer to text for further discussion

mental settings rather than 'physical' isolation by currents, oceans, or land areas.

Stromatoporoid associations

This study focuses on regional patterns of stromatoporoid distributions rather than individual associations and detailed establishment of environment-diagnostic stromatoporoid associations will have to await future studies. However the present data, along with previous studies suggest that distinct environment-related stromatoporoid associations existed despite all regional biogeographical differences. The Iberian occurrences show that richer stromatoporoid associations occurred whenever many corals had more difficulties to thrive (Table 6). Thus an association dominated by various species of *Ptychochaetetes* grew in debris-rich and unstable, hence strongly abrasive settings. This is likewise true for many comparable environments from France, northern and southern Germany. However, not all chaetetids indicate such settings. A particular association including *Ptychochaetetes ponticus, P. peroni*, and *Pseudoseptifer angustitubulosus* from Spain occurred in a slightly deeper setting which was apparently adapted to background sedimentation and occasional disturbance by resedimentation events. Findings of chaetetids in similar deeper water environments (e.g., southern Germany) might indicate comparable strategies. A similar control though with possibly reduced sedimentation events is indicated by a coral-chaetetid-stromatoporoid-microbialite association which includes *Milleporidium formosum* among others. *Milleporidium*-rich associations appear also typically in shallower, but nevertheless mostly quiet settings. A typical and very widespread association is the *Milleporidium-Parastromatopora-Cladocoropsis-Burgundia-Shuqraia* association established by Fenninger and Holzer (1972) for the Plassen limestones of Austria (Table 7). This association might differentiate into various lagoonal subassociations including pure *Cladocoropsis*-meadows in shallow lagoons and inner ramp settings (see below), and to more reef type *Dehornella* and *Parastromatopora*-rich associations or *Burgundia* patch reefs, which depending on site and region might contain very different faunal elements but have in common that they are rich in reefal debris.

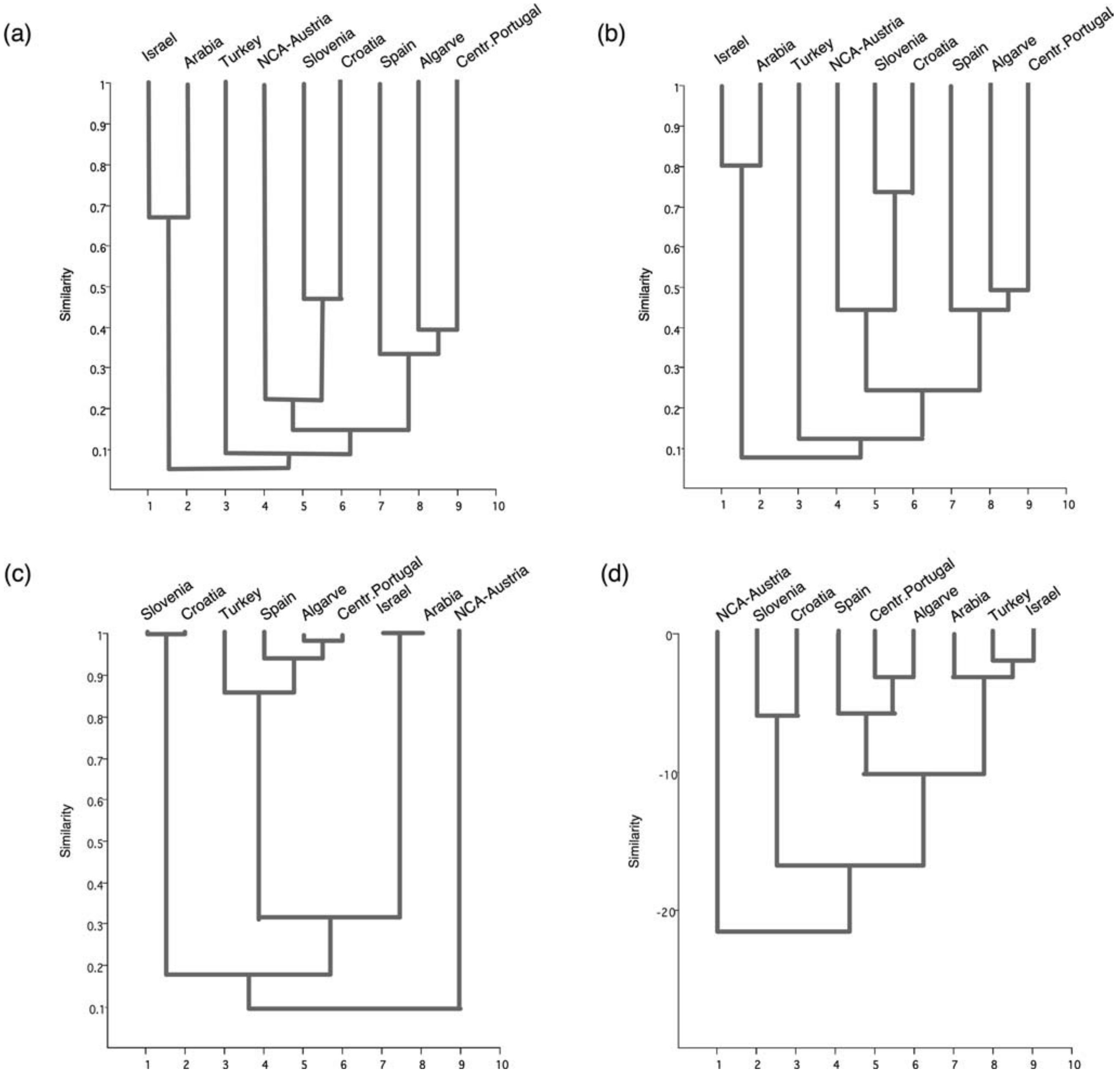


Fig. 17 Multivariate cluster analysis (Q-Mode) to highlight similarities between test regions. (**a**) Cluster based on presence–absence matrix of all species. Paired group method, Dice algorithm; (**b**) as before but only for species which occur at least in two regions; (**c**) cluster based on presence–absence matrix of all species, paired group method, Raup and Crick algorithm; (**d**) cluster based on matrix for all genera, weighted with species numbers per genus (abundance data), Ward's method. Note that irrespective of used matrix modification and similarities remain, yielding distinct clusters for Middle East, Intra-Tethys (Slovenia-Croatia and Northern Calcareous Alps), and Iberia, respectively. Turkey has too little data to appear coherent. The Raup and Crick example is shown to demonstrate how quantitative similarities are dependant on the mathematical method but qualitative results, i.e., cluster formation is irrespective of this. See text for details

Table 7 defines standard associations for the Intra-Tethys occurrences. Most typical is the *Actinostromaria-Ellipsactinia-Sphaeractinia*-reef association which is also known as Ellipsactiniid limestones, and its equivalents. As discussed above, *Ellipsactinia* is a typical platform margin/upper slope indicator and is frequently associated with sphaeractiniids and representatives of *Cylicopsis*. Our available information suggests that at least during the Upper Jurassic *Ellipsactinia* is a typical Intra-Tethys element, although so-called "ellipsactinellid" facies with *Sphaeractinia* (but obviously without *Ellipsactinia*) is known from the Lower Cretaceous Grand-Banks platform slopes (Jansa et al. 1982). Based on studies from Reitner (1992) and Reitner and Wörheide (2002) on modern *Vaceletia* which is interpreted as an aspiculate "sphinctozoan"-type sclerosponge with affinities to the ceractinomorph

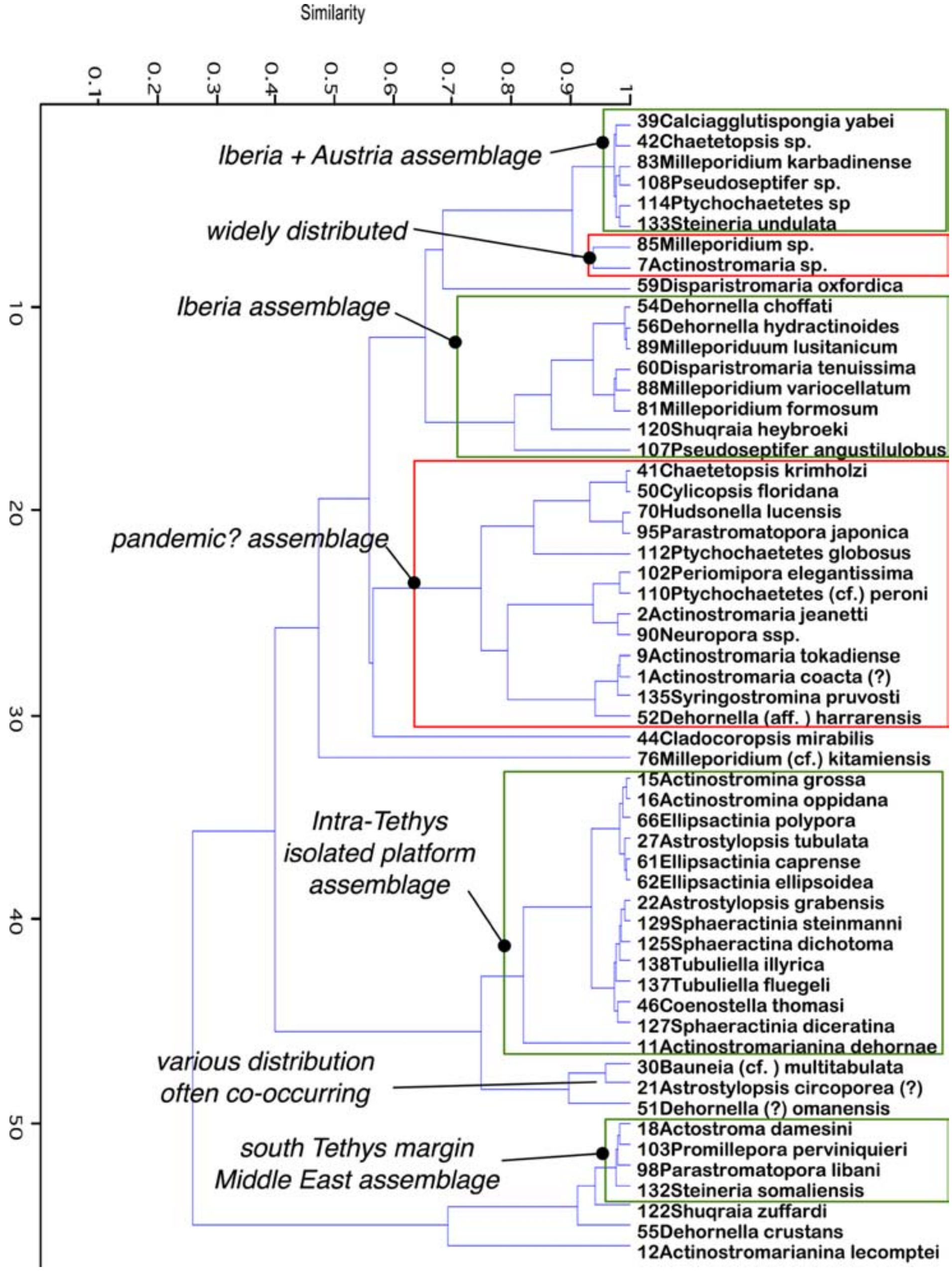


Fig. 18 R-Mode multivariate cluster analysis, using the same, but transposed, presence–absence data as in Fig. 17b (i.e., using all species which occur at least in two regions). R-mode analysis yields distinct faunal assemblage clusters of two types: distinct regional assemblages (Middle East, Intra-Tethys, Iberia) and supraregional assemblages. The present data suggest that regional clusters were important. See text for further discussion

demosponges, we suppose that *Ellipsactinia* might be a similar Jurassic counterpart and hence possibly developed environmental adaptations different from the bulk of other Jurassic stromatoporoids. All species of genus *Tubuliella* seem to be also diagnostic of this association (or set of associations). This stromatoporoid association is only part of a much broader association characterised by a dominance of scleractinian corals (cf. Turnsek 1997).

A parastromatoporoid association, characterising the back part of central reefs and back reef high-energy debris patch reefs, is well developed in Intra-Tethys platform (Parastromatoporoid zone of Turnsek et al. 1981). It shows many additional stromatoporoid elements (see Table 8) with *Disparistromaria* and *Reticullina* appearing to be additional typical taxa. Especially the chaetetid richness of this association, as well as its debris character, shows similarities with *Ptychochaetetes*-rich debris reefs and debris sheets from the North Tethys and Atlantic settings, although the taxonomic composition is different.

Not only the most widespread but probably also the most environment-characteristic stromatoporoid association is the *Cladocoropsis* meadow association. Although *Cladocoropsis* might be an infrequent element in patch reefs, it frequently dominates the association, forming extensive biostromal, mostly monospecific or paucispecific meadows which though are normally not preserved *in situ*. Evidence from the Algarve and Arabian study sites indicates that frequent reworking possibly by storms did not restrict but rather stimulate growth of this fragile branching stromatoporoid which typically occurs in reworked bioclastic sands, often with high densities. As to substrate and hydraulic characteristics, we see a good modern analogue for *Cladocoropsis* in the digitate *Porites porites* var. *furcata* coral meadows from the Caribbean which also spread rapidly once appropriate environments have been created, can even baffle sediment owing to their rapid growth rate, and are frequently fragmented by storm action. Storm fragmentation and redistribution provides additional substrates for new larvae on dead coral fragments within a muddy to sand-grained environment, and high repair and rapid growth facilitates rapid regeneration of fragmented but still living corals (Greb et al. 1996; Saric 2005).

The *Cladocoropsis* association may contain several additional stromatoporoidal elements such as *Shuqraia heybroeki* or *Milleporidium* cf. *kitaminensis* from Turkey or *Burgundia* and other *Shuqraia* species in Saudi Arabia. Additional elements such as certain *Dehornella* species occur in low-energy lagoonal settings. Locally, stromatoporoid lagoonal reefs develop from *Cladocoropsis* meadows or micritic lagoonal settings, which often are dominated by *Burgundia* or *Milleporidium*.

Palaeoecology of stromatoporoid vs. coral assemblages

Palaeobiology and general aspects of stromatoporoid palaeoecology

The interpretation of the autecology of Jurassic stromatoporoids and chaetetids is hampered by many obstacles. First of all, modern environments for these organ-

Table 6 Characteristics and possible controls on stromatoporoid/chaetetid-bearing reefs from Spain

Reef type	(1) Sand-rich coral-chaetetid-rud/boundstones	(2) Marly to silty coral stromatoporoid meadow	(3) Coral chaetetid-bioclast-float-boundstones	(4) Coral-thrombolites with chaetetids and stromatoporoids
Environment	Siliciclastic high-energy, shallow, abrasive settings	Below fair-weather wave base, mostly tranquil, affected by storm events, unstable substrate	Pure carbonate, mostly tranquil, slightly deeper setting with fine-grained sedimentation and resedimentation events	Below fair-weather wave base, with storm events, no sedimentation
Stromatoporoids and chaetetid species	*Ptychochaetetes globosus* (at places forming monospecific patch reefs)	*Calciagglutispongia yabei* (= ex *'A. tokadiense')*, *Milleporidium variocellatum,* *Milleporidium* sp., *Spongiomorpha globosa*	*Ptychochaetetes ponticus, P. peroni, Pseudoseptifer angustitubulosus*	*Milleporidium formosum*, *Dehornella* cf. *choffati*, *Chaetetes chablaisensis*
Controls favouring stromatoporoids and chaetetids	High abrasion and coarse silics are well tolerated by this species, giving it advantage over many corals	Unstable substrate and temporary reworking well tolerated especially by *C. yabei*, high regeneration potential giving it advantage over many corals	Growth strategies of these forms seem to enable adaptation to fine-grained sedimentation and resedimentation events, therefore reduced competition by corals	Stromatoporoids and chaetetids as accessory reef dwellers. Widespread hard surfaces, including undersides of overhangs, and long-term development give stromatoporoids and chaetetids a better chance

Table 7 Stromatoporoid associations in the Northern Calcareous Alps (after Fenninger and Holzer 1972; Dya 1992) in comparison with the Upper Jurassic reef barrier reef model of Slovenia (after Turnsek et al. 1981)

Fenninger and Holzer 1972 Different localities of the Plassen Formation	Dya 1992 Plassen Formation of Mt. Untersberg	Turnsek et al. 1981 Barrier-reef of Slovenia
Actinostromaria-Ellipsactinia-Sphaeractinia association ("*Ellipsactinia* limestones")	Obviously missing at Mt. Untersberg	Actinostromariid Zone (= Central Reef, frontal part)
Actinostromaria-chaetetid association	*Actinostromaria-Chaetetopsis-Ptychochaetetes* association	Parastromatoporid Zone (= Central reef, backward part)
Milleporidium-Parastromatopora-Cladocoropsis-Burgundia-Shuqraia association	*Burgundia-Cladocoropsis* association	*Cladocoropsis* Zone (= back-reef area, lagoon)

Table 8 Preliminary evaluation of facies dependent taxa distribution in the Slovenian, Croatian, Austrian, and Turkish examples. Based on Turnsek et al. (1981) and own observations. A= Actinostromariid Zone, P = Parastromatoporoid Zone

	Reef front (Actinostromariid-Zone)	Central reef (Parastromatoporoid Zone)	Back Reef/Lagoon (*Cladocoropsis* Zone)
Actinostromina grossa	x		
Actinostromina germovsheki	x		
Actinostromina oppidana	x		
Astrostylopsis circoporea	x		
Astrostylopsis grabensis	x		
Astrostylopsis schnorfae	x		
Astrostylopsis trnovica	x		
Astrostylopsis tubulata	x		
Calciagglutispongia yabei	x		
Coenostella thomasi	x		
Cylicopsis carniolica	x		
Cylicopsis florida	x		
Cylicopsis lata	x		
Cylicopsis verticalis		x	
Desmopora listrigonorum	x		
Ellipsactinia caprense	x		
Ellipsactinia ellipsoides	x		
Ellipsactinia polypora	x		
Sphaeractinia dichotoma	x		
Sphaeractinia diceratina	x		
Sphaeractinia steinmanni	x		
Tubuliella fluegeli	x		
Tubuliella illyrica	x		
Tubuliella rotunda	x		
Dehornella omanensis		x	
Disparistromaria oxfordica		x	
Hudsonella lucensis		x	
Hudsonella media		x	
Hudsonella otlicensis		x	
Parastromatopora japonica		x	
Parastromatopora compacta		x	
Reticullina rectangularis		x	
Cladocoropsis mirabilis			x
Cladocoropsis nanosi			x
Parastromatopora japonica			x
Shuqraia heybroeki			x
Milleporidium cf. *M. remesi*			x
Blastochaetetes capilliformis			x
Bauneia multitabulata		x	
Chaetetopsis crinita		x	
Chaetetopsis krimholzi		x	
Pseudochaetetes? champagnensis[a]		x	

[a] Seen as synonymous to genus *Solenopora* by Moussavian (1989)

isms are largely coelobitic (cave-dwelling; Reitner and Wörheide 2002) and obviously differ vastly from Mesozoic representatives.

Second, interpretation as a sponge might not be correct for all Jurassic stromatoporoids and chaetetids. For instance, Kazmierczak (1976) suggested a cyanobacterian nature for Palaeozoic stromatoporoids and Mesozoic ellipsactinians are still designated as hydrozoans by many recent authors, whereas others clearly consider them a member of the Porifera with stromatoporan type of organisation (e.g., Flügel 2004). Fourcade et al. (1975) suppose an affinity of *Ellipsactinia* with the genus *Verticillites*, but these authors see also affinities with the disjectoporids and an origin from Permian stromatoporoids. So, while some (or probably most) stromatoporoids should have typical ecological characteristics of sponges, others might have different general requirements, such as food characteristics or tissue repair abilities.

Third, even if the majority of Jurassic taxa considered here to be stromatoporoids actually belonged to the sponges, the polyphyletic character of stromatoporoid-sponge constructional bauplan (Cook 2002; Reitner and Wörheide 2002) makes a wide range of different environmental necessities likely, since within sponges a very wide variety of demands and abilities exist (e.g., Sara and Vacelet 1973; Krautter 1995, 1997). As to food requirements most general assumptions made for demosponges should hold true of stromatoporoids, so they may have possibly filtered on very minute particles, down to bacterial size and might probably have hosted many bacterial symbionts in their tissues. On the other hand, a few extant calcifying sponges are known to contain photosymbionts, such as cyanobacteria (Wilkinson 1978; Wilkinson and Trott 1985). The variable calcification pattern of the basal calcareous skeleton, often being characterised by stacked sets of latilaminae with apparently faster and slower upwards growth rates might be well interpreted as being caused by photosymbiontic activity, in analogy to the annual growth bands of extant zooxanthellate corals. If latilaminae were seasonal, then stromatoporoids had fairly rapid growth rates attaining rates of several millimetres to rarely centimetres per year. This is compatible with their occurrence together with scleractinian corals with comparable growth rates and with the growth of branching stromatoporoids in high-energy environments with high fragmentation rates. It however contrasts the extremely slow growth rates of modern stromatoporoid-like coralline demosponges which is at a rate of 0.05–0.4 mm per year (Benavidas and Druffel 1986; Wörheide 1998). Assuming the existence of photosymbionts within Jurassic stromatoporoids would also be fully compatible with stromatoporoid occurrence patterns, for it would easily explain the overall very shallow bathymetric distribution of stromatoporoids as well as their predominant occurrence in pure limestones of intraocean or arid position. However, this pattern does not directly prove the existence of photosymbiosis (see below).

Palaeoecological significance of stromatoporoid morphologies

Following the fundamental work of Kershaw and Riding (1978) and Kershaw (1998) based on Palaeozoic stromatoporoids, morphology of stromatoporoid colonies can be attributed to distinct morphotypes (Fig. 19). Actually, the same or similar designations as for corals can be used, since similar forms occur with the exception of tall bushy structures which are restricted to corals. As in corals, there are quite some morphovariable taxa, although different morphologies are sometimes, and probably erroneously, taken as criteria to establish different species (see *Burgundia* example, Wood 1987). Similar to corals, growth forms can be an expression of various factors, such as hydraulic energy, illumination (provided photosymbiosis was developed), and sedimentation rate. Again analogously to corals, nonenveloping growth bands (latilaminae) can cause ragged lateral outlines which are easily interpreted as representing sedimentation and non-sedimentation intervals. Some taxa, such as *Burgundia* frequently show microencrusters in their galleries. This is evidence of partial mortality of the sponge during interruptions of growth. The sponge must have then reorganised itself, secreting a new sheet of laminae on the basal skeleton (Wood 1987).

There also are a couple of gross assumptions published on the ecology of Palaeozoic and Mesozoic chaetetids, but they are not sufficient for more detailed approaches and especially do not suffice to explain all differences of occurrence patterns relative to corals. However, a couple of general observations appear useful in this regard: Chaetetids have their peak development in the Upper Jurassic and appear to be particularly interesting as a general palaeoecology indicator. According to West and Kershaw (1991), chaetetids might settle on all substrates, except for muddy soft bottoms, but have their highest diversities on hard grounds. They appear to be restricted to normal marine salinities but the genus *Chaetetes* (including the Jurassic representative *Pseudoseptifer*) might exhibit some euryhaline behaviour. Conolly et al. (1989) assume zooxanthellate photosymbiosis for Palaeozoic chaetetids restricting them to shallow-water settings. Chaetetid morphologies have also been used for interpretation of bathymetry as related to hydraulic energy. Winston (1965) attributes hemispherical forms of *Chaetetes* to coastal areas and columnar-erect morphologies to more distal settings. Flügel (1979) has used both the debris character of the host sediments as well as the globose growth form of *Ptychochaetetes* (synonymous with *Eurysolenopora*) to suggest a high-energy character for this growth form of the genus. According to Mathewson (1978), platy and foliose morphologies are related to high water energy and strong currents, whereas columnar growth should represent an adaptation towards deeper water or shallow-water calm settings. However, these general assumptions are in partial contrast with the results of our own working group (see section on Spanish and German occurrences above). West and Clark (1984) focus on changes of overall morphologies by sedimentation rate. Intermittent sedimentation may cause growth perturbances or changes from columnar to lamellar growth. Since most chaetetids have been found in pure carbonate settings, their dependence on this is emphasised by many authors, but there are reports of chaetetids in sediments rich in detrital quartz of sand size from Spanish localities (see refs. in Nose 1995).

Very rarely, stromatoporoids, including chaetetids, might occur in clayey sediments (Dehorne 1922; Flügel and Hötzl 1966). As a whole, interpretations based on morphology of stromatoporoids (including chaetetids) alone are equivocal, as Wood (1987) sums up her literature review, stating that: “...There have been many documented cases of the gross morphological plasticity of ‘stromatoporoids’ to environmental conditions, ... (e.g., Kissling and Lineback 1967; Kershaw 1981)” and that “There are two theories: one, that branching forms are found in shallow, high-energy conditions, and massive and encrusting forms in deeper, low-energy conditions; and the other theory states the opposite."

Similar to corals and other sponges, growth form appears to be species-specific in some taxa (Fig. 19). Other taxa obviously have higher phenotypic plasticity. However, this is also not necessarily environment-diagnostic, since variability is more flexible, such as that, e.g., variations in mamelons, may occur in specimens in a single stromatoporoid-population which is also true for modern representatives (Vacelet, pers. comm. in Wood 1987).

Concluding, morphological, non-taxa-based analysis of stromatoporoids is only of limited value, especially when attempting to differentiate between controls favouring stromatoporoid *versus* coral growth and *vice versa*. Phenotypic skeletal reactions appear to be largely similar in both scleractinian corals and stromatoporoids. In other words, morphological analysis of stromatoporoids might help in assessing water energy, sedimentation rate, or even water depth but it fails to answer the question why there are (1) coral associations without or with subordinate proportions of stromatoporoids, (2) mixed coral-stromatoporoid associations with considerable amounts of stromatoporoids, and (3) associations highly dominated or exclusively composed of stromatoporoids.

So what? The significance of stromatoporoid vs. coral dominance—is there any?

This section attempts to briefly evaluate all stromatoporoid characteristics discussed above, including growth morphologies, hosting sedimentary systems, regional and global taxa distribution, and palaeogeographic significance in order to deduce a concept of the ecological bandwiths and significance of stromatoporoid occurrences. This is a first evaluation, based on limited case studies and selected regions thought to be characteristic of stromatoporoid development and ecology, which attempts to stimulate further, refined research in this respect.

Bathymetric range (Fig. 20a): Both corals and stromatoporoids show a broad overlap of water depth distribution. Especially in shallow-water coral reefs stromatoporoids may or may not be frequent elements. Water depths of Upper Jurassic coral reefs are well calibrated from northern palaeohemisphere examples (Nose 1995; Insalaco 1996; Leinfelder et al. 1996; Insalaco et al. 1997; Leinfelder 2001) and it is obvious that the deeper water associations such as the widespread microsolenid biostromes are largely devoid of stromatoporoids. Although bathymetric calibration is not so well established for southern palaeohemisphere reefs, the same holds true there. In non-reefal

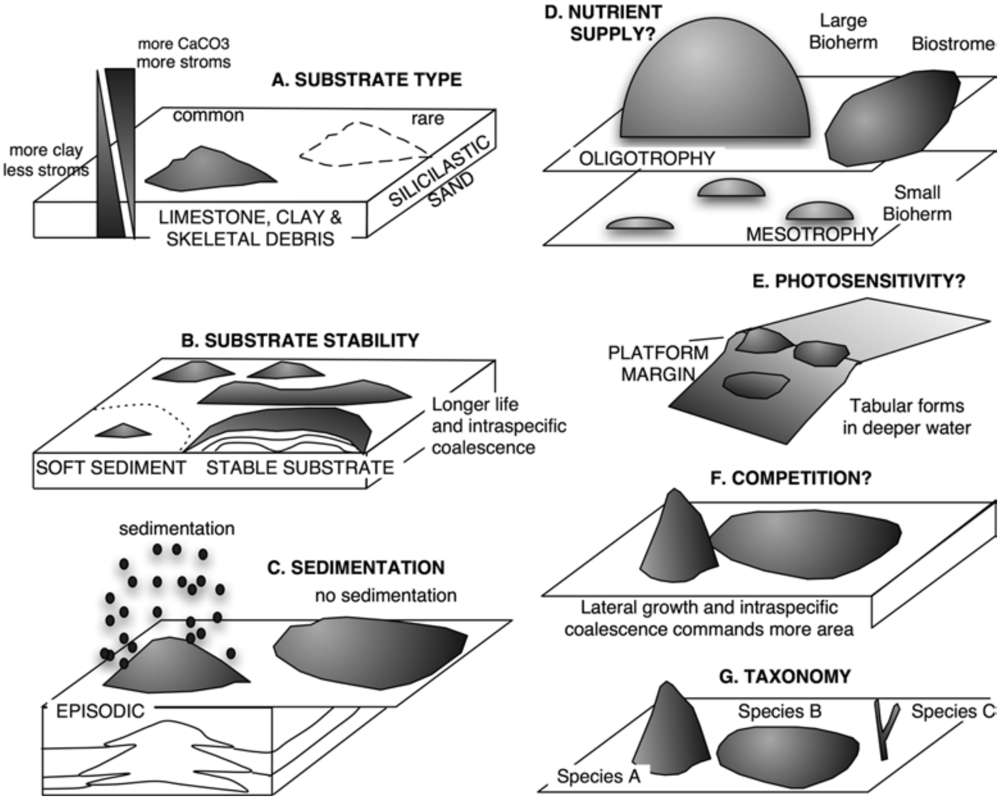
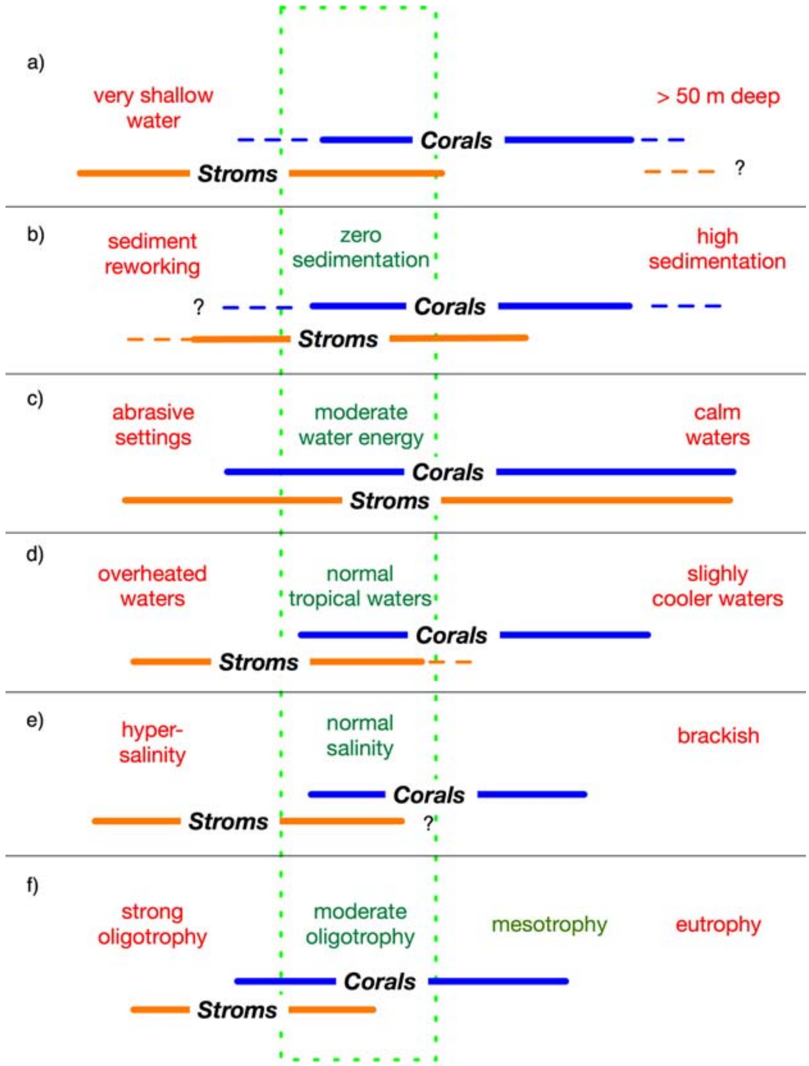


Fig. 19 Reactions of stromatoporoid growth to physicochemical and biological ecofactors. Largely based on Palaeozoic examples, from Kershaw (1998), redrawn and slightly modified. Variations in stromatoporoid shapes, sizes, and frequencies are interpreted to be controlled by substrate characteristics, substrate stability, background sedimentation rate, and, possibly, by nutrient supply, light availability, intraspecific competition, and genetic determination. Note that interpretation of stromatoporoid and chaetetid morphologies is a valuable approach for assessing a set of environmental factors. However, quite similar factors and resulting biological reactions occur in Jurassic scleractinian corals (e.g., Nose and Leinfelder 1997; Nose 1999; Leinfelder 2001). Interpretation of growth characteristics alone therefore is not sufficient for understanding the variable proportions of stromatoporoid *vs.* coral growth in Jurassic reefs and carbonate platforms

Fig. 20 Tentative sketch of environmental ranges of Upper Jurassic stromatoporoids (incl. chaetetids) and reef corals, as based on this study. Solid lines: normal distribution (note that distribution of individual taxa is much narrower), dashed lines: exceptional taxa. Co-occurrence is within dotted field. Within this field corals strongly dominate to the right, whereas stromatoporoids (stroms) become increasingly important towards its left margin



muddy settings without corals, stromatoporoids are always associated with other shallow-water diagnostic organisms such as dasyclad algae, miliolid, or lituolid foraminiferans. There very few examples from Iberia and southern Germany where isolated, larger chaetetids occur in deeper coral reef facies. Future data acquisition will have to reveal whether there are true deeper water taxa or which taxa are eurybathic. Except for *Neuropora,* which is considered as a coralline sponge by Kazmierczak and Hillmer (1974), or a chaetetid stromatoporoid by Reitner (1992), no autochthonous stromatoporoids occur in still deeper settings such as the siliceous sponge reef facies. The almost exclusive restriction of Jurassic stromatoporoids to well-lit shallow-water settings might be an indication of the possible existence of photosymbionts (see below).

On the shallow end of the bathymetric spectrum, stromatoporoids tend to become somewhat more frequent in very shallow coral reef facies such as coral-debris reefs or coral-microbialite-debris-reefs (*sensu* Leinfelder 1992, 2001). In non-reefal platform settings, chaetetids are particularly frequent also in cross-bedded sand bars or extensive sand sheets but this might be more an effect of their ability to cope up with resedimentation and abrasion (see below).

Substrate characteristics, sedimentation and resedimentation, abrasion (Figs. 20b, c): Most co-occurrences of corals and stromatoporoids along the shelf seas to the north of the Tethys and the Atlantic margin basins are 'uncritical' in respect of co-occurrence of corals and stromatoporoids. Stromatoporoids may occur as infrequent elements together with corals provided carbonate dominance exists. Stromatoporoids are obviously very rare to lacking in terrigeneously-influenced settings. A partial exception are carbonates rich in detrital quartz, but clayey sediments are almost exclusively devoid of stromatoporoids. Clayey settings *per se* do neither exclude corals, nor other shallow-water sponges. Many coral reefs from the Northern Hemisphere developed within clay-influenced settings (see below for further discussion) and other 'calcareous' sponges such as inozoans and Calcarea may be particularly abundant in clayey sediments (e.g., Fürsich and Werner 1991; Werner et al. 1994), partially exhibiting morphological adaptations such as secondary closure of inhalant pores (Krautter 1994).

Stromatoporoids occur frequently in lagoonal-type fine-grained carbonates and may occur as additional, rare element in well-preserved coral-microbial reefs below fair-weather wave base. However, the majority of stromatoporoids (including chaetetids) is from high-energy reef types as well as from grain-dominated lagoonal sediments of high-energy character (cf. Fig. 6).

Upper Jurassic corals show a wide array of adaptations to background sedimentation rate such as dominance of phaceloid or ramose corals or change from hemispherical to pseudoramose, sediment-sticking growth under high sedimentation (e.g., Leinfelder 1986, 1994b; Nose 1995, 1999). As discussed earlier, stromatoporoids might develop non-enveloping growth bands and ragged stacking of latilaminae as an adaptation to sedimentation events. The dominant occurrence in high energy environments suggests that such features are likely to be an adaptation towards frequent resedimentation rather than elevated extrinsic sediment influx. Compatible with this is the frequent occurrence of irregular, nodular to subspherical stromatoporoids in unstabilised, partly cross-bedded carbonate sands which may include high proportions of detrital quartz, and widespread abrasive and healing features, including settlement and mutual overgrowth of microencrusters and stromatoporoids, all of which is a particulate characteristic of stromatoporoids *s. str.* and, especially, chaetetids, the latter of which are largely, but not fully, restricted to such settings. This behaviour is easily explained with the sponge character of the stromatoporoids. Sponges have a very high regeneration potential and the observed features suggest that Jurassic stromatoporoids could easily recolonise a partially abraded basal skeleton. It might be assumed that similar to coralline red algae, stromatoporoids, or at least the chaetetid subgroup might even have been in demand of abrasion, either physically or biologically, in order to prevent overgrowth by soft cyanobacterial turfs or other microbial films (cf. Steneck 1985; Leinfelder and Werner 1993).

Especially the Algarve and the Arabian example show that *Cladocoropsis* was particularly well adapted to frequent erosive events. Similar to several modern acroporoid or poritid corals, fragmentation and redistribution might be part of the vegetative reproduction strategy of *Cladocoropsis*. Distribution pattern and successional characteristics of the *Cladocoropsis* carbonate sands from outcrop and subsurface data suggest that growth occurred as laterally extensive meadows which owing to overcompensation by sediment production had a very limited accommodation potential. Tropical storms caused frequent reworking of the *Cladocoropsis* meadows as well as abrasion and scouring of the inner ramp, and sediment were transported to, and resedimented in, more distal areas with a larger accommodation potential (see Fig. 12). This process prevented the establishment of longer lasting stromatoporoid reefs or thick *Cladocoropsis* biostromes but rather resulted in the stacking of very thin cycles of *Cladocoropsis* sands bounded by irregular, abrasive surfaces on inner shelf environments. In comparison with similar processes and sediment abrasion-redistribution patterns from cool-water carbonate platforms, we suggest the term "shaved tropical ramps" (in partial analogy with "shaved cool-water shelves" *sensu* James et al. 1994; see also Leinfelder et al. 2005).

In comparison with scleractinian corals, we conclude that Jurassic stromatoporoids were less well adapted to generally or even intermittent background sedimentation, and that horizons of stromatoporoids within micritic lagoonal sediments are related to interruptions in background sedimentation, e.g., during flooding events. On the other hand, resedimentation and abrasion stress both in reefal and non-reefal environments were no problem for most chaetetids and many other stromatoporoid taxa.

Salinity range (Fig. 20e): Most stromatoporoid occurrences clearly grew in normal marine settings as evidenced by moderate to high diversities of normal marine organisms, including many coral taxa, marine algae and foraminiferans, and echinoderms. A few Upper Jurassic coral taxa may occur in waters with a slight freshwater influence, the coral *Amphiastrea piriformis* even forms reefs in brachyhaline settings (Leinfelder and Werner 2004). No stromatoporoids have ever been found is such hypohaline settings, although in the Austrian Alps some apparently transported stromatoporoidal debris has been found within possibly slightly hypohaline deposits as indicated by the alga *Zergabriella embergeri* (Schlagintweit, unpubl. results). On the other hand, there are good indicators that Jurassic stromatoporoids might have tolerated, or in some cases even have favoured slightly hypersaline settings. One argument is their frequent occurrence in wide muddy lagoonal shallow-water settings, where corals are missing but dasycladacean algae and miliolids might be partially dominant. An example in Portugal shows dessication cracks, coniatolitic supratidal crusts, and gypsum pseudomorphs in a succession which also contains stromatoporoid-bearing facies (see Leinfelder 1983). Dasyclad dominance and richness of miliolid foraminiferans is also true for the widespread *Cladocoropsis* sands of Saudi Arabia (Hughes 1996, 2004). The relative scarceness of echinodermal fragments and the proximity of the Upper Jurassic formations with evaporites (Fig. 11) are additional criteria and also support the idea that at least some of the stromatoporoid taxa might have tolerated slightly higher salinities although they are absent from high salinity sabkha facies (see Toland 1994). No corals occur in such settings, indicating that corals could not extend into the hypersalinity regime. We are aware of the fact that juxtaposition and superposition by evaporites alone is no sufficient criteria for hypersalinity. Offshore Abu Dhabi, a rich assemblage of charophyte oogonia occurs in a thin layer of bituminous mudstone intercalated in the evaporites of the Arab B formation of late Kimmeridgian or Tithonian age (Al-Silwadi et al. 1996). This unique level is used as a key lithological marker, and, therefore, is not representative for the entire Arab succession. In any case, there are no stromatoporoids associated with this level. Nevertheless, evaporites are widely and contemporaneously distributed within the Arabian carbonate platform (Fig. 11), whereas equatorial humidity markers such as peat and bauxite formation were positioned much further towards west into

Gondwana mainland (Scotese 2000; Sellwood et al. 2000), or laterites further to the north (Scotese 2000). These hard data were successfully simulated by general circulation modelling, using the UGAMP GCM-programme (Sellwood et al. 2000). The Kimmeridgian UGAMP-simulation predicts high June–August draught over Saudi Arabia and monsoonal December–February rainfall mostly in more interior parts of Gondwana (Sellwood et al. 2000; Fig. 5).

Water temperature range (Fig. 20d): As to elevated water temperatures, this factor might be partially related to salinity (see above). Jurassic microsolenid coral associations, which are typically devoid of stromatoporoids, could grow in slightly deeper settings, possibly in the range of 40 m. Similar to modern tropical settings, water temperature might not rapidly cool down in such settings, but at least a few microsolenid and other probably azooxanthellate taxa even grew in oceanic deep-water settings where cooler temperatures must be assumed (Gill et al. 2004). Occurrences of Upper Jurassic coral reefs in high palaeolatitudes such as in the Neuquén Basin, or Patagonian Basin of Argentina, or in England show all signs of warm-water settings, including calcareous oolites and dasyclads (Ramos 1978; Legarreta 1991; Insalaco 1999), and hence reflect strongly equilibrated water temperatures across the palaeogeographic globe as a result of the high sea level (Leinfelder 1993, 1994a; Leinfelder et al. 2002). The dominance of coral reefs at the North Tethys margin, with palaeolatitude dominance between 30 and 45° North might give clues to overheated seas further south. On the other hand, corals, together with stromatoporoids are widespread at 20–30° palaeonorth even in shallowest, debris-rich settings (Northern Calcareous Alps (NCA) and Dinaric platforms), indicating that both groups were either adapted to elevated temperatures or that overheating did not take place in such intraoceanic settings. The chaetetids from North German Deister area appear to be the northernmost ones of shelf seas to the North of the Tethys (Helm et al. 2001). Chaetetids also still occur, and are locally abundant in the Holy Cross Mountains of Poland (Kolodzieij 2003) which were situated about 40°N palaeolatitude (see Golonka 2002). Bertling and Insalaco (1998) have noted the lack of chaetetids and stromatoporoids in the northern Paris Basin, a fact for which they consider palaeobiogeographic controls. According to these authors, stromatoporoids and chaetetids are typical Tethyan elements and should be restricted to more southerly tropical climates and "thus could not survive in the less predictable environments of the northern Paris Basin" (*op. cit.*). Although this interpretation could also explain the scarcity of stromatoporoids in the North German Basin, such a palaeoclimate zone approach does not explain why stromatoporoids are also relatively rare in the Iberian reefs whereas they are extremely frequent in the Dinaric and NCA platforms as well as in even more northward lying intraocean platforms such as the Czechian or Japanese occurrences, and still occur in the Patagonian Basin positioned at a palaeolatitude of about 70°S (see Leinfelder et al. 2002). Our data suggest that temperature did belong to the important control mechanisms supporting or oppressing occurrence of Jurassic stromatoporoids but this control obviously did not function along latitudinal gradients but rather acted on a more regional and even local scale.

A good example is the huge, up to 1000 km broad carbonate platform of Arabia (Fig. 11). Its position around the Jurassic equator, richness in evaporitic deposits, and predominance of very shallow environments often with distinct dominance of benthic agglutinating or miliolid foraminiferans and dasyclads suggests considerably overheated waters. This gives clues to the better adaptation of stromatoporoids to overheated settings relative to corals. In comparison with the northern palaeohemisphere, corals are relatively infrequent in Arabia, and, if occurring, appear to have grown in somewhat deeper settings, such as the coral facies capping stromatoporoid reefs, or the extensive single population coral bed of Saudi Arabia in the basal part of the Jubaila Formation. Sedimentological characteristics of this bed suggest that these corals grew in slightly deeper waters (unpubl. results). Interpretation of the short-term character of this single-population meadow is not unequivocal and might indicate a short-term cooling event, a short-term reduction of hypersalinity, or a short-term plankton bloom. Saudi Arabian stromatoporoid reefs around Ryadh are frequently capped by a veneer of corals which together with the distinct convex-upward shape of these reefs suggests termination of reef growth by transgressive pulses, with a last-stage 'pseudodrowning' episode by normal-temperature coral facies.

Numeric palaeoclimate modelling by Moore et al. (1992a, b), Price et al. (1995), and Sellwood et al. (2000) points to strongly overheated waters around the palaeoequator which would support the above interpretation. However, at least the Moore-modelling also indicates winter temperatures around 0–10°C for the Neuquén Basin which actually is incompatible with the warm-water coral reef development there. This indicates that the models are not yet fully compatible with hard data from the Upper Jurassic and, therefore, must be used with caution for interpretation of Jurassic palaeoclimates (Leinfelder 1994a). However, at least the UGAMP model used by Sellwood et al. (2000) is in good accordance with palaeoclimatic field indicators. This model gives annual mean temperatures for Arabia in the range of well above 28°C which is significantly higher than for the rest of the central Tethys. Hence, putting all arguments together, it appears justified to assume slightly to considerably overheated waters for the Arabian and Israel occurrences which helps explain the occurrence of pure stromatoporoid assemblages. We, therefore, conclude a higher tolerance of stromatoporoids to overheated waters relative to corals.

Trophic range (Fig. 20f): Above we have highlighted the fact that many Jurassic coral associations thrived within terrigeneously influenced settings along the North Tethys margin and the young Atlantic as well as adjacent shelf seas. Terrigeneous influence is normally paralleled by an increase in nutrients leading to an enhancement of plankton productivity (Hallock 2001; Mutti and Hallock 2003). Nose and Leinfelder (1997) and Leinfelder (2001) have given arguments for the trophic demands of Upper Jurassic reef corals from such settings, including (a) frequent occurrence of coral associations within clayey sediments, (b) a partial diversity increase of coral associations within settings slightly contaminated by clays, (c) frequent occurrence of high-integrated coral morphologies, such as meandroid, thamnasterioid, or plocoid calical types, (d) distinct water depth zonation of coral associations, (e) occurrence of modern-type double-set growth bands which are supposed to be annual, (f) slower average annual growth rates and much lower low-to-high density band ratios of Jurassic corals relative to modern corals, and (g) isotopic evidence of possible vital effects on carbon isotope fractionation (Nose et al. unpubl. data). The authors concluded that Upper Jurassic reef corals thriving within, or close to, siliciclastic settings already possessed photosymbionts, but the photosymbiotic relation was yet much less efficient. Consequently, these corals were still strongly dependant upon the availability of considerable amounts of planktonic food in order to grow. They thus had mixotrophic behaviour and were adapted to mesotrophic settings. Modern zooxanthellate corals only need very subordinate amounts of plankton in order to yield necessary nutrients and to dispose waste matter. They are, however, not dependant on the use of carbohydrates from plankton and therefore are adapted to oligotrophic settings (see Hallock 2001).

We tentatively extend the interpretation of the mixotrophy of Upper Jurassic corals from clayey settings to carbonate-dominated coral reef settings along the North Tethys, young Atlantic, and adjacent epicontinental seas. Reasons for this are threefold. First, this area was an archipelago of numerous larger islands (see Fig. 2), shedding siliciclastic into adjacent basins which themselves were therefore a mixture of siliciclastics and carbonates. Shallow-water cabonate platforms in these settings were relatively narrow and hinterlands were never far, suggesting a considerable land-derived influx of nutrients (Fig. 21a). Second, coral growth even within carbonate platforms is often best developed wherever clayey deposits are intercalated. To present but a few examples, this holds true of the widespread microsolenid facies at the base of many European carbonate platforms and for other well known reefs of Portuguese, Spanish, French, and German settings. Third, multivariate cluster analysis of coral taxa from all available data of Upper Jurassic reefs worldwide shows that the majority of coral taxa has a wide distribution both in clayey and carbonate rich setting, but that there are noticeable regional differences (Goldberg 2004; Goldberg and Leinfelder unpubl. results). As an example, most of the South Arabian coral species listed by El-Asa'ad (1989, 1991) are not known or very rare from North Tethys or

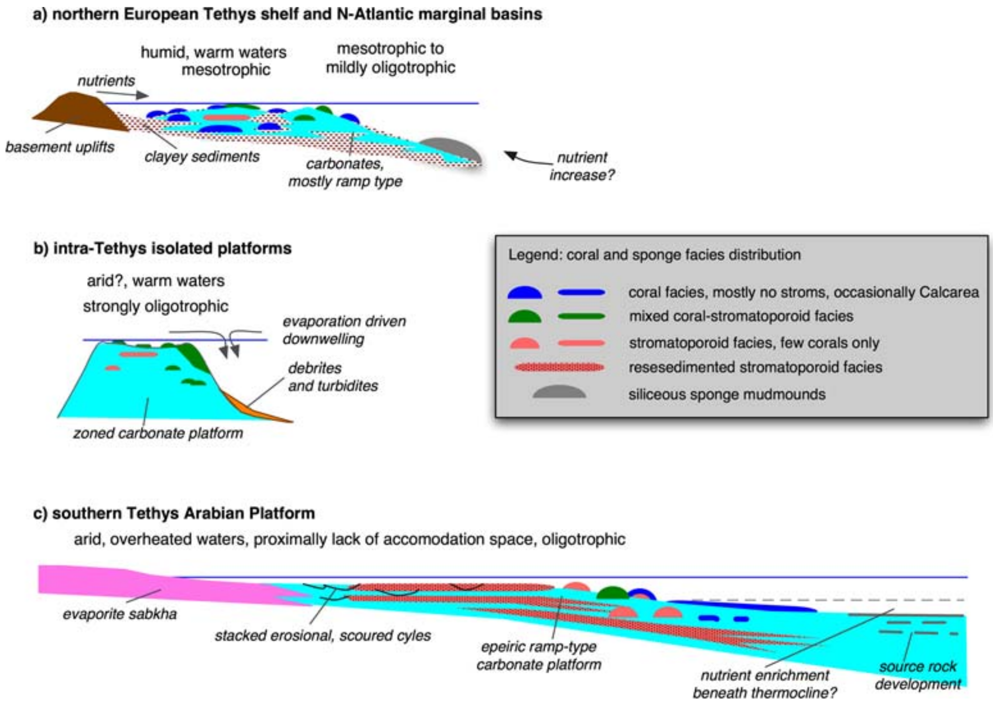


Fig. 21 Sketches of basic platform configurations with Upper Jurassic stromatoporoid (incl. chaetetid) facies (reefs and lagoons). **a** Carbonate platforms in an archipelago of basement uplifts and humid climate. Waters are frequently mesotrophic, carbonate platforms small, surrounded by, and associated with, terrigeneous clays. Mostly microbialite coral reefs develop, stromatoporoids occur subordinate. Shallow lagoons might show stromatoporoid dominated facies. **b** Intra-Tethys open ocean carbonate platforms typically exhibit a pronounced platform margin and well-developed facies belts. Coral-stromatoporoid reefs occur typically, mostly with both high numbers of coral and stromatoporoid taxa, both in platform interior and the marginal upper slope. Open ocean position at about 15–30°N suggests evaporation driven downwelling. **c** Broad epeiric arid platform: The extensive, more than 1000 km broad Arabian carbonate platform developed in an arid setting, possibly exhibiting overheated waters. *Cladocoropsis* meadows and other stromatoporoid associations, both adapted to overheated waters, strong abrasion, and probably oligotrophic waters occurred widespread. Corals occur scattered, coral facies develops on "drowning" stromatoporoid reefs and, rarely, as extensive meadows, in deeper, probably cooler, and nutrient enriched waters

Atlantic occurrences, which is a strong argument for separately developing taxa in palaeogeographically different areas.

Differences in the distribution patterns of stromatoporoid species are even more distinct. As discussed earlier, many stromatoporoid genera have their maximum species number on the Intra-Tethys regions, and much less few genera or species occur at either side of the Tethys. As shown above, multivariate analysis of co-occurrence patterns of stromatoporoid species (R-mode analysis) yield several similarity clusters which are typical of distinct regions. Likewise, cross-comparing the nine representative regions selected for this study using Q-mode analysis yields convincing clusters of close similarities between overall stromatoporoid species patterns from Algarve, Lusitanian Basin, and Celtiberian Basin on the one hand, and from the South/Intra-Tethys regions on the other. As to the latter category, Arabia, Israel, and Turkey form one subcluster, Croatia, Slovenia (Dinaric Platform), and Austria (NCA Platform) another subcluster, with Austria being relatively independent.

The Dinaric-Apulian microplate which housed the probably isolated Dinaric-Adriatic, NCA, and other isolated shallow-water carbonate shelves, was positioned around 15–35° palaeonorth (Ziegler 1988; Stampfli et al. 1998; Dercourt et al. 2000; Leinfelder et al. 2002). According to plate tectonic interpretations, their distance from siliciclastic basement uplifts must have been considerable (see Golonka 2002). All palaeoceanographic interpretations suggest westward oriented flow from the eastern Tethys (cf. Leinfelder 1993; Price et al. 1995; Golonka 2002; Leinfelder et al. 2002) all of which must have resulted in strong oligotrophy of surface waters. Vertical water mixture might have been possibly driven by evaporation, transferring hot, slightly more saline waters down, again not providing nutrients (Fig. 21b). As a countermovement, slight upwelling might have occurred along the northern margin of the Tethys (see Leinfelder 1994a).

The vast carbonate platform of Arabia was positioned around the palaeoequator (Fig. 11). Its extreme width of up to 1000 km and its predominantly very shallow character must have not only decoupled oceanic from shelf circulation systems, but also must have slowed down shelf water exchange considerably, possibly often leading to partial depletion in nutrients. Frequent evaporite intercalations suggest that the climate was not tropically humid but semiarid to arid (see above). Aridity might have triggered partial temperature stratification, which might be also indicated by source rock development in deeper intraplatform basinal parts (Fig. 21c). Source rock development as well as a partially rich microbenthic foraminiferal fauna can be taken as evidence for at least occasional availability of sufficient nutrients. Frequent storm sheet development suggests that storms might have occasionally transported nutrients into the vast carbonate platform either from the Arabian massif or from equatorial upwelling from the Tethys Ocean. On the other hand, the shallowest subtidal marine facies is dominated by *Cladocoropsis* fragments and a dominance of dasycladaceans, with lower proportions of foraminiferans. The trophic state of this huge carbonate platform system is difficult to reconstruct with the data available to date, but considering all the above we suggest partly stratified, overheated, and nutrient-depleted shallow surface waters and somewhat more nutrient-rich distal ramp to intrashelf basinal waters with frequent storm events which mixed up waters to enrich them occasionally with nutrients.

Based on the available data, we therefore assume that whilst most Upper Jurassic corals were strongly mixotrophic and preferred mildly to strongly mesotrophic near coastal waters, some coral taxa became adapted to strongly oligotrophic waters in the South Tethys, particularly on the Dinaric-Apulian microplate. Stromatoporoids, as a whole, avoided strongly mesotrophic clayey settings but lived in carbonate settings ranging from mildly mesotrophic to strongly oligotrophic. This first comparison of stromatoporoid faunas indicates that oligotrophic Intra-Tethys platform taxa were mostly distinct from taxa living in mildly mesotrophic settings, a hypothesis which has to be further tested by additional data and better time resolution.

Alternate concepts

Wood (1999) interpreted the patches of mostly monospecific stromatoporoids, such as the Palestinian Makhtesh Gadol reefs discussed above as owing to rapid colonisation by a single phase of larval spat. Jurassic stromatoporoids, seen as sponges, are clonal organisms, which owing to their clonal structure not only regenerate rapidly but also may spread very fast. Wood thus interprets such reefs as being caused by a single population. In our view, this might be a valid explanation for aggregations of small monospecific stromatoporoid patches within an otherwise more differentiated coral reef, or for similar aggregations within lagoons, but such a mechanism fails to explain the predominance of stromatoporoids within coral-stromatoporoid reefs of the Intra- and South Tethys and would also not explain the differences in composition and frequencies of stromatoporoids in reefs north of the Tethys.

Interpretation could also relate to migration pathways of stromatoporoids. Similar to modern reefs Jurassic reefs might have been compartmentalised into biogeographically different zones. We assume that migration of coral larvae was inhibited from the North to the South Tethys, and stromatoporoid distribution from the South to the North Tethys, by a strong east–west Tethys current, thus explaining the dominance of corals over stromatoporoids in North Tethys and Atlantic epicontinental seas and *vice versa*. A certain argument in favour of this could be that stromatoporoids are more frequent in Spain and Portugal, or even Texas, than in France or Germany, because larvae might have intermixed in the narrowing western European Tethys. Actually, Termier and Termier (1975) suggest such migrational routes. However, the high amount of known coral taxa on intraoceanic microplates is contradictory to such an overall explanation since larvae would have to cross this suggested strong oceanic current. The vast differences in stromatoporoid frequencies in the shelf seas to the north of the

Tethys could be explained by retarded philopatric larval migration. However, since stromatoporoid-rich reefs even predominate in isolated open-ocean carbonate platforms slow, sea-bottom related expansion of stromatoporoids along the South Tethys shelf solely by philopatric larval behaviour is difficult to imagine. We, however, do not exclude the possibility that the observed pattern of species distribution and stromatoporoid abundance might partially reflect 'inequilibrium state' owing to taxa-related differences in migration speed and migration behaviour, although our view on the entire Upper Jurassic (including some Callovian) makes this unlikely.

Conclusions and outlook

Environmental demands of Jurassic stromatoporoids

- As a whole, Jurassic stromatoporoids can occur in a variety of different environments, similar to Jurassic scleractinian corals, but—and again similar to corals—many different taxa clearly may have differing ecological preferences which is far from being fully resolved so far.
- Another obvious result of this first quantitative evaluation is that South and Intra-Tethys Upper Jurassic reefs are actually much richer in stromatoporoid abundance and taxa numbers than North Tethys and North Atlantic reefs.
- Within this area, and based on the selected examples, stromatoporoids (including chaetetids) are more frequent in Iberian coral reefs than in French or German coral reefs. Especially in central and southern Portugal, but to some extent also in other areas, stromatoporoids also settled within distinct horizons in lagoonal environments. Monospecific, mostly reworked *Cladocoropsis* meadows occur both on the epicontinental seas north of the Tethys, particularly in Iberia, France, and Switzerland (Bernier 1984), and on the South and Intra-Tethys isolated platforms. In addition, *Cladocoropsis* was extremely widespread on the Arabian platform.
- Chaetetids appear to be more widespread on the North Tethys/North Atlantic shelves than stromatoporoids *s. str.*, whereas stromatoporoids outnumber chaetetids on the South Tethys and Intra-Tethys shelves. The frequent chaetetid genus *Pseudoseptifer* is particularly widespread in Iberia. However, this must be substantiated by more quantitative data on abundances of stromatoporoid (including chaetetid taxa) in the future.
- The frequently held view that Palaeozoic chaetetids appear to be adapted to high-energy settings holds also true for most Upper Jurassic examples. Most Jurassic chaetetids appear to have liked turbulent water with strong abrasion, where coral diversities have been substantially reduced. The abrasive force of siliciclastic sands must have particularly favoured their partial dominance. However, there were some very few chaetetid specialists (chiefly *Neuropora*) living in somewhat deeper waters together with microsolenid platy corals and even within pure lithistid sponge facies (e.g., Krautter and Hartmann 1999). Also unsolved is the question why chaetetids were not frequent in many other highly abrasive coral reef settings, such as coral-debris-reefs from Switzerland or France. The strong preference of most chaetetids for abrasive settings is very similar to the preferences of modern coralline red algae, some Jurassic solenoporoids, or the Upper Jurassic ancestral coralline alga *Marinella lugeoni*.
- The occurrence of small amounts of stromatoporoids within coral reefs is of no special ecological significance. These organisms appeared whenever encrustable substrates, especially dead corals occurred, but they were in strong competition with other encrusters such as other coralline sponges (inozoans), bryozoans, serpulids, encrusting foraminiferans (*Lithocodium, Koskinobullina*, and others), *incertae sedis* (e.g., *Iberopora, Bacinella*), red algae (solenoporaceans, the gymnocodiacean, or green algae *Thaumatoporella*, the early corallinacean ancestor *Marinella lugeoni*), cyanobacteria (rivulariaceans such as *"Cayeuxia"*), and microbial crusts. They are, in part, favoured by abrasive and resedimentation processes and are more flexible than corals in unstable lagoonal settings provided they are carbonate-prone. A frequent association of such lagoonal stromatoporoids is with miliolids, dasycladacean algae, lituolid foraminiferans (among which *Anchispirocyclina* can be very frequent in late Upper Jurassic examples), all of which indicate that such settings were very shallow. Possibly fluctuations in temperatures and salinities were too severe and excluded corals. Sauropod tracks are known from *Anchispirocylina* facies of central Portugal, pointing to the very shallow character of respective environments (Ramalho 1988).
- Taxonomic composition of stromatoporoid and chaetetid faunas is to a large part due to biogeographical differences, as evidenced by statistical cluster analysis. Analysis was based on selected testing regions comprising Algarve, Lusitanian Basin, Celtiberian Basin, Northern Calcareous Alps of Austria (Apulian Carbonate Platform), Croatia, Slovenia (both Dinaric Carbonate Platform), Turkey, Israel, and the Arabian peninsula. These regions show much higher proportions of stromatoporoids within reefs and are thought to be characteristic representatives. Cluster analysis using the software package PAST has revealed distinct clusters for Iberian, Intra-Tethys, and South Tethys shelf faunal assemblages (R-Mode analysis). Comparing faunal similarities of testing regions by Q-Mode analysis similarities are not at random but are greatest in adjacent regions. However, R-Mode analysis also revealed several faunal assemblages which occur over many or even all testing regions. Among the more pandemic taxa are *Cladocoropsis mirabilis*, *Ptychochaetetes globosus*, or *Astrostylopsis circoporea*. Stromatoporoids also appear to form environment-diagnostic associations, for which we have given a couple of tentative examples above, but closer calibration of these is beyond the scope of this paper. Indicator taxa appear to be relatively rare among

stromatoporoids *s. str.* and chaetetids, but examples are *Cladocoropsis mirabilis* which is typical in shallow lagoons frequently undergoing sediment reworking and resedimentation, or *Ellipsactinia* ssp. and *Sphaeractinia* ssp. which are diagnostic of slightly deeper steep intraocean slope settings next to platform margins. Contrasting, *Pseudochaetetes polyporus* seems to be particularly eurytopic, occurring in a variable set of environments.

- Despite the availability of vast carbonate platform environments, pure Jurassic coral reefs are extremely rare to lacking in palaeoequatorial position. Coral faunas are to a considerable proportion different from settings north of the Tethys, and stromatoporoids prevail. Coral-stromatoporoid reefs are well developed on the Dinaric-Apulian microplate which provided isolated intraocean carbonate platforms situated at about 15–35° palaeonorth. Stromatoporoids are absent in coral reefs from deeper settings or within clayey deposits, except for a very few occurrences.
- The observed pattern of stromatoporoid versus coral abundances, diversities, and taxa distribution both at a local, regional, and global scale together with morphological characteristics of corals, sediment characteristics, and plate tectonic palaeo-constellation allow to conclude that coral reefs thriving in shelf seas to the north of the Tethys were adapted to mildly to strongly mesotrophic settings whereas coral-stromatoporoid reefs from intra-oceanic Tethyan shelves such as the Dinaric and NCA Platforms had already conquered oligotrophic settings (Fig. 21). The strong predominance of stromatoporoids over corals on the Arabian peninsula is interpreted to be due to overheated, slightly hypersaline waters or oligotrophy, or most likely, a combination of both (Fig. 21). For this conceptual study we have not yet incorporated other occurrences but we speculate that even more northwards lying yet isolated Intra-Tethyan settings such as the Stramberg Limestone of Czechia (Vasicek et al. 1994) and the various Upper Jurassic platform limestones of Japan (Yabe and Sugiyama 1927, 1930, 1935) should also have developed under the influence of oligotrophic waters. There are also obvious differences in the distribution of stromatoporoid taxa already within and betweeen adjacent intra-oceanic platforms. As an example, ellipsactiniids are frequent in the Northern Calcareous Alps, the Apennine, and the Dinaric Platform but *Tubuliella* which is frequent in Slovenia and Albania (Gawlick et al. 2004b) is lacking in the Alpine settings. Given these differences it should be worthwile depicting spatial patterns of additional localities at a much higher resolution based on taxonomic revision of the stromatoporoid fauna, in order to depict palaeobiogeographic patterns and, possibly, migrational pathways.

Implications on reef development in the Cretaceous and Cenozoic—a hypothesis

Concluding, we can speculate that the ‘reef window’ (*sensu* Leinfelder and Nose 1999; Leinfelder et al. 2002) started splitting during the Late Jurassic: the Intra-Tethys coral-stromatoporoid reefs of Apulian or Dinaric type are interpreted to be direct predecessors of modern-type oligotrophic tropical to subtropical reefs, whereas the mesotrophic near-coast coral reefs of the Jurassic inhabited mesotrophic environments. Possibly shallow-water mesotrophic coral reefs became replaced by rudist reefs during the Cretaceous and possibly even partially retreated to, and persisted in, deep-water refuges whereas the oligotrophic intra-ocean reefs of the Jurassic developed into the Cretaceous, survived the Cretacous-Tertiary-boundary and evolved into modern oligotrophic coral-coralline algal reefs. This is a speculative hypothesis which should stimulate future deductive research and data aquisition to corroborate, modify, or falsify these interpretations. By doing so, we hope that we can continue a ‘Flügelian’ tradition of motivating different groups for joint ventures and promote future research on the grand theme of Reef Evolution Through Time, to the understanding of which Erik Flügel has contributed so much and everlasting.

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