



JURASSIC REEF PATTERNS—THE EXPRESSION OF A CHANGING GLOBE

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ABSTRACT: Jurassic reef patterns reflect the fulminant global and regional changes initiated by the breakup of northern Pangea. The pattern of reef distribution across the Jurassic reflects a complex mix of (1) different and changing tectonic styles along the continental margins and adjacent shelf seas; (2) sea-level rise and its modulating influence on extrinsic sedimentation; (3) oceanographic and climatic reorganizations related to general sea-level rise and the new plate-tectonic configurations; and (4) evolutionary changes in the ecological demands and abilities of reef biota, which, in part, appear to have been triggered by the extrinsic changes during the breakup of northern Pangea. Rifting and onset of drift in the central Atlantic as well as in the western Tethys resulted in a distinct sea-level rise, which transformed Jurassic shelf seas along the northern Tethys margin from dominantly siliciclastic to dominantly carbonate settings. The opening of the ocean passageway from the Tethys to the Caribbean and Pacific completely reorganized global oceanic circulation patterns. During the Late Jurassic, shelf seas were considerably deep, increasing the areas of settings suitable for development of siliceous sponge mounds on the northern Tethys margin. In contrast, many parts of the southern Tethys margin underwent strong morphological changes due to rift tectonics within the Triassic carbonate platforms, which resulted in a completely different pattern in Jurassic reef distribution relative to the northern Tethys. After the end-Triassic extinction event, Jurassic reefs recuperated gradually during the Early Jurassic, with a first major reef domain developing in Morocco. Their temporal distribution through the Middle Jurassic was more balanced, but reefs occurred in scattered domains often distant from each other (e.g., Portugal, France, Madagascar, Iran). Late Jurassic reefs expanded rapidly in the course of the ongoing sea-level rise and the oceanographic reorganization, resulting in mostly interconnected domains. A pattern of waxing and waning of reef abundance and spatial reef distribution through time is superimposed on this trend. It is again, at least to a large extent, correlatable with sea-level fluctuations of greater magnitude. Jurassic reef growth had peaks during the transgressive episodes of the Sinemurian–Pliensbachian, Bajocian–Bathonian, and Oxfordian–Kimmeridgian, with superimposed higher-frequency peaks. The Jurassic represents the peak not only of development of Mesozoic coral reefs but equally of development of sponge mounds. Sponge mounds represent siliceous sponge–microbolite mud mounds, which expanded enormously during the Oxfordian along the European part of the northern Tethys. A peculiar type of bivalve reefs, the *Lithoththis* reefs, were widespread particularly during the Sinemurian and Pliensbachian, and they might have partially filled a potential reef-growth habitat not occupied by corals, owing to the reduced availability of coral taxa at that time. Bivalve reefs, in particular oyster reefs, also occurred scattered in Middle and Late Jurassic times, mostly representing marginal marine environments. Sea-level rise and tectonic opening of new seaways had a pronounced influence on climate and marine circulation patterns, which were the principal factors in Jurassic reef development. Particularly in the Late Jurassic, coral and stromatoporoid reefs occurred in high paleolatitudinal settings (e.g., Argentina, Patagonia, Japan) evidencing strong climatic equilibration of marine and coastal areas, despite the fact that strong seasonal contrasts should have prevailed in the Gondwana interiors. There are only a few records of low-latitude reef sites, despite the availability of carbonate platforms, which might reflect overheated waters in this area. Humidity was probably higher than previously thought. Siliciclastic influx was partially high during the Kimmeridgian, owing to fluvial runoff and renewed tectonic activity, and reduced the number of reef sites and domains considerably, despite ongoing global sea-level rise. Jurassic, chiefly Upper Jurassic, reefs not only grew within the expanding carbonate settings but also thrived in terrigenously influenced environments. This is particularly obvious in the North Atlantic rift basins, such as the Lusitanian Basin of west-central Portugal, but it is also discernible in many other Jurassic reef domains. Occurrence of coral associations in fine siliciclastics, ratios of skeletal low-density vs. high-density banding, morphological adaptations towards sedimentation, high proportions of bioerosion, and overlap of many coral domains with proposed upwelling areas suggests that there was a considerable stock of Jurassic zooxanthellate corals with a distinct heterotrophic proportion of feeding, thus living in mesotrophic settings. In contrast, reefs on the isolated, oceanic shallow-water Apulia–Adria platforms differ considerably, being dominated by stromatoporoids, chaetetids, and corals. We propose the theory that these oceanic faunas might have already had a more advanced photosymbiotic relationship than the other forms and thus could thrive in presumably strongly oligotrophic settings. Such associations, which might have occurred similarly on oceanic platforms in the Pacific, are thought to have been the stock for Cenozoic development of coral reefs into superoligotrophic settings, whereas the more nutrient-tolerant reefs along the continental margins vanished in the course of latest Jurassic and Berriasian sea-level drop. Sediment-stressed, nutrient-rich shallow-water settings might then have been reconquered by rudist bivalves in the course of the Cretaceous.

Jurassic reefs not only constitute widespread and important hydrocarbon reservoir rocks; their manifold characteristics and related dependence on basin tectonics, sea-level change, and ecological parameters makes them valuable basin-analysis tools for potential hydrocarbon plays.

INTRODUCTION

The Jurassic Period was both a time of unidirectional evolutionary gradational change with no major extinction events affecting Jurassic organisms and a time of fundamental regional and global changes in the course of the breakup of Pangea, reshaping shelf structures, initiating considerable sea-level rise and causing significant oceanographic, climatological, and other environmental changes.

Many reef organisms, particularly corals, suffered a distinct extinction pulse at the end of the Triassic (Flügel, this volume) and had to start from near zero. They diversified in a changing world, giving rise to a great variety of different reef settings and related reef types, including coral reefs, siliceous sponge reefs, bivalve reefs, microbial reefs, or mixtures of them. Owing to the "coevolution" of Jurassic reef organisms and the Jurassic globe, Jurassic reefs should track these general environmental and structural changes in the breakup phase of Pangea.

This paper attempts to integrate previous comparative studies of Jurassic reef organisms and reefs from our own working group (e.g., Leinfelder, 1993a, 1994a; Leinfelder et al., 1993a; Leinfelder et al., 1993b; Leinfelder et al., 1994; Leinfelder et al., 1996) into a global scale. We intend to test, modify, and further develop previous, more qualitative views on Jurassic reef distribution (Beauvais, 1980; Beauvais, 1984; Flügel and Flügel-Kahler, 1992; Leinfelder, 1994b), by integrating latest results on Jurassic reef research (e.g., Nose, 1995; Nose and Leinfelder, 1997; Krautter, 1997; Schmid, 1996; Insalaco et al., 1997; Bertling and Insalaco, 1998; Insalaco, 1999; Leinfelder, 2001) and by attempting to quantify results using the exhaustive reef data base provided by, and updated for, Kiessling and Flügel (this volume).

Definition of time slices for the paleoreefmap project is based on supersequences (Haq et al., 1987). This paper encompasses the Upper Absaroka III and Lower Zuni I–III supersequences (time slices 19–22) (Fig. 1). The abundance of reefs in the Jurassic and a fairly good biostratigraphic resolution allows, however, a much finer resolution of reef patterns based on stages.

We are aware of the fact that the reef database includes many reef sites with insufficient data (e.g., on faunal composition or diversity) and sites of no true reefal character. We are also conscious that notations of algae, cyanobacteria, and microbes, or hydrozoans, stromatoporoids, and certain corals might be in part synonymous. We assume that the frequently used term red algae, for the Jurassic, refers exclusively to solenoporacean algae but might include some misinterpretations of porostromate cyanobacteria (based on strong similarities between, e.g., *Cayeuxia* sp. and *Solenopora cayeuxiformis*; see Leinfelder, 1986). As many references as possible were cross-checked, but considering the enormous wealth of literature we have to apologize for some possible misinterpretations of the reef database or the reference database used. We nevertheless believe that using numerical data of the reef data base will strongly substantiate trends and conclusions drawn from Jurassic reef patterns.

OVERVIEW OF JURASSIC REEF TYPES AND ECOLOGY OF REEF ORGANISMS

The Jurassic, unlike modern and many other Phanerozoic time periods, was a time not only of widespread reef growth but also of completely different reef types, particularly in terms of compositional types. Conclusions drawn from patterns of reef distribution must therefore focus strongly on the great variability of reef types with completely different environmental demands owing to the variable ecological necessities and abilities of the reef organisms involved.

Compositional Types of Jurassic Reefs

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

- (1) coral reef types
- (2) siliceous sponge reef types, and
- (3) pure microbolite reef types.

Additionally, bivalve reefs of various types as well as red algal reefs occur. Although normally only of subordinate importance, lithotid bivalve reefs were common throughout parts of the Early Jurassic.

Coral Reefs.—

There is a wealth of recent literature particularly on Upper Jurassic coral reef types (e.g., Lauxmann, 1991; Leinfelder, 1993a, 1994a, 1994b; Leinfelder et al., 1996; Nose, 1995; Insalaco, 1996a, 1996b; Bertling and Insalaco, 1998; Helm and Schülke, 1998; Insalaco et al., 1997; Nose and Leinfelder, 1997); therefore only a short review of coral reef types is given here. The dominant fauna of these reefs are scleractinian corals which may or may not be preserved in life position. If preserved *in situ*, they may, in rare cases, build true framestones with massive corals growing on top of each other. Coral bushes forming bafflestones, however, are more frequent and, in rare instances may grow up to four meters. In general, dimensions are from a few decimeters height up to stacked reefs attaining the cumulative thickness of 100 m and more. Most common are coral reefs with thicknesses in the range of several meters up to 15 m. Jurassic coral reefs can be typified by their faunal composition, dominance and frequency of coral species, their sedimentological characteristics, and their general shape and dimensions. In general, medium-diversity to high-diversity coral reefs with 30 and more coral species in one coral association should be distinguished from low-diversity coral reefs. (Turnšek et al., 1981, recorded 109 species of corals, hydrozoans, and chaetetids in a barrier-type reef complex of Slovenia, but this appears to be a bulk number from all reef bodies.) Medium-diversity to high-diversity coral reefs comprise coral-debris pile reefs, coral-microbolite-debris pile reefs, marly coral-microbolite reefs, coral mud mounds, and coral-microbolite bioherms and biostromes. Low-diversity coral reefs encompass low-diversity coral-debris pile reefs, *Amphiastrea* patch reefs, various types of marly coral meadows, and coral-stromatoporoid mud mounds (Leinfelder, 2001).

Siliceous Sponge Reefs.—

These reefs are either of biostrome type or exhibit a mound character due to the large contribution of fine-grained carbonate, part of which corresponds to the precipitating and binding activity of microbes (Fritz, 1958; Leinfelder and Keupp, 1995; Keupp et al., 1996; Leinfelder et al., 1996). Siliceous sponges comprised various proportions of hexactinellid sponges and "lithistid" demosponges. Although siliceous sponges were the most characteristic element of these reefs, they often did not dominate volumetrically over microbial crusts and calcareous mud. Mud mounds may range from a few decimeters up to several tens of meters in height. Larger mounds are often composed of stacked, smaller mounds (Leinfelder, 1993a; Leinfelder, 2001). Siliceous sponge-

VALANGINIAN	Early	137.0 *	7.2	CRETACEOUS	Time slice 22 Lower Zuni III
	Late				
BERRIASIAN	Middle	141.8 (+2.5 -1.8 Ma)	6.2	LATE	Time slice 21 Lower Zuni II
	Early				
	Late				
TITHONIAN	Middle	148.0 *	4.0	MIDDLE	Time slice 20 Lower Zuni I
	Early				
	Late				
KIMMERIDGIAN	Early	152.0 *	4.5	EARLY	Time slice 19 Upper Absaroka III
	Late				
	Middle				
OXFORDIAN	Early	156.5 (+3.1 -5.1 Ma)	3.9	MIDDLE	Time slice 18 Upper Absaroka II
	Middle				
	Late				
CALLOVIAN	Early	160.4 (+1.1 -0.5 Ma)	5.6	EARLY	Time slice 17 Upper Absaroka I
	Middle				
	Late				
BATHONIAN	Early	166.0 (+3.8 -5.6 Ma)	8.0	MIDDLE	Time slice 16 Upper Absaroka
	Middle				
	Late				
BAJOCIAN	Early	174.0 (+1.2 -7.9 Ma)	4.0	EARLY	Time slice 15 Upper Absaroka
	Middle				
	Late				
AALENIAN	Early	178.0 (+1.0 -1.5 Ma)	5.6	MIDDLE	Time slice 14 Upper Absaroka
	Middle				
	Late				
TOARCIAN	Early	183.6 (+1.7 -1.1 Ma)	7.9	EARLY	Time slice 13 Upper Absaroka
	Middle				
	Late				
PLIENS-BACHIAN	Carixian	191.5 (+1.9 -4.7 Ma)	5.0	EARLY	Time slice 12 Upper Absaroka
	Domerian				
SINEMURIAN	Early	196.5 (+1.7 -5.7 Ma)	3.1	EARLY	Time slice 11 Upper Absaroka
	Late				
HETTANGIAN	Early	199.6 (± 0.4 Ma)	3.1	EARLY	Time slice 10 Upper Absaroka
	Middle				
	Late				

FIG. 1.—Jurassic time scale (after Pálfy et al., 2000a, Pálfy et al. 2000b, and *Golonka and Kiessling, this volume) and correlation with the time slices used in this paper.

microbolite mud mounds normally are of medium to high diversity in terms of sponge taxa, although a great deal of work is still to be done to determine sponge associations in a quantitative way at the species level (Leinfelder et al., 1993a; Krautter, 1997). Besides the various types of sponge mud mounds, there are a lot of sponge biostromes, which, in the case of the Oxfordian sponge beds from eastern Spain, may stretch across more than 70,000 km² (Krautter, 1995). Sponge biostromes or sponge meadows are variable and mostly of low faunal diversity (e.g., Krautter, 1997). Marly meadows dominated by vase- and tube-shaped sponges are distinguished from calcareous biostromes dominated by dish-shaped sponges. Somewhat muddier, thick-bedded biostromes have less frequent sponges but contain a lot of micro-

bial crusts (e.g., the Treuchtlingen limestone of southern Germany; Kott, 1989).

Microbolite-Dominated Reefs.—

Reefs that are composed almost completely of microbolite (*sensu* Riding, 1991) were widespread in some areas during the Late Jurassic and are also known from the Early Jurassic. Microbolite crusts, dominated by clotted, thrombolitic fabric, may form a true framework, building up bioherms from a few decimeters up to 30 m in height (Leinfelder et al., 1993a; Leinfelder et al., 1993b). Stromatolitic and leiolitic fabrics may prevail in certain reef types (cf. Schmid, 1996), the term “leiolitic” referring

to microbolites with a dense microstructure (Braga et al., 1995). A classification regarding both macrostructure and microstructure allowing genetic clues was proposed by Schmid (1996); see also Leinfelder and Schmid (2000).

Macrofauna in this reef type is either virtually absent or confined to narrow levels, or, in rare cases, scarcely scattered irregularly throughout the reefs in miniature forms. Faunal elements are mostly siliceous sponges, chiefly of the hexactinellid type. Serpulids, terebellid worms, and *Tubiphytes* may be common in some cases. An interesting feature is that such pure microbolite horizons may also occur in a repetitive, stacked manner within some coral reefs. A totally new Jurassic reef type has been discovered in cores from Alabama, where hitherto undescribed *Renalcis*-like calcimicrobes are the only faunal element in mounds that are composed of microbioherms or "microherms" (Kopaska-Merkel and Schmid, 1999).

Bivalve Reefs and Additional Reef Types.—

Apart from the above-mentioned main reef-builder groups, bivalves were important Jurassic reef builders. In the Early Jurassic, some genera of the *Lithotis* (s.l.) group formed extended biostromes and reef mounds up to several tens of meters thick along the whole southern Tethys margin (e.g., Geyer, 1977; Buser and Debeljak, 1996; Dresnay, 1977; Yin and Wan, 1998) and, more rarely, in the eastern Pacific in Oregon and farther south in Peru and Chile (Nauss and Smith, 1988; Hillebrandt, 1971). From the Middle Jurassic onwards oysters began to develop remarkable bioherms and biostromes. Large structures extending for several kilometers exist in the Middle Jurassic of Scotland (Hudson, 1963a, 1963b) and Poland (Hoffmann and Krobicki, 1989) and in the Upper Jurassic of Portugal (Fürsich, 1981; Werner, 1986). In addition to these bivalves with a high potential to construct true mounds, the data base also records bivalve assemblages that represent pure coquina accumulations without any distinct reefal character. Examples are the Gryphaeid banks from the Lower Jurassic (e.g., Poulton, 1988), the *Paradiceras* "biostromes" of the Upper Jurassic of Crimea (Baraboshkin et al., 1996), and the *Buchia* banks of the Berrasian (Poulton, 1989a).

According to the database, stromatoporoids contribute significantly to Upper Jurassic reefs, especially in the Tethys and Pacific realm. In most cases, corals, chaetetids, and, possibly, hydrozoans are the other constituents of such reefs. Calcareous sponges are rarely recorded as the main biota. Only in the Early Jurassic, stylothalamids of Triassic affinity interacted with corals in reefal settings of Peru (Senowbari-Daryan and Stanley, 1994) and Italy (Zempolich, 1993). In the Kimmeridgian of Portugal, coralline sponges, together with corals, occasionally formed extended biostromes, which are locally accompanied by small microbial bioherms (Fürsich and Werner, 1991).

Although calcareous algae were frequently associated with Late Jurassic reefal communities, they never represented the main reef-building organisms, except for solenoporacean biostromes and patch reefs developed in the Kimmeridgian of Northern Germany and the Celtiberian range of eastern Spain (Fezer, 1988; Nose, 1995; Helm and Schülke, 1998, 1999).

Another unusual reef type of marginal marine settings are serpulid reefs recorded from the uppermost Jurassic of Germany (ten Hove and van den Hurk, 1993).

The Reef Players: Capacities and Environmental Necessities of Jurassic Reef Organisms

Reef organisms are strongly dependent on each other and thus play many different roles in reef systems. Reef organisms

can be described as belonging to different guilds, such as: constructors, cementers, decomposers and recyclers, water filterers, and so on (e.g., Fagerstrom, 1987; Leinfelder and Ginsburg, 1998). In order to accomplish their tasks for the entire system, reef organisms have very special capacities but also very distinct environmental necessities. The great variety of compositional reef types in the Jurassic makes it particularly important to uncover the abilities and demands of Jurassic reef organisms in order to elucidate the factors controlling the growth and distribution patterns of Jurassic reefs.

The Dominant Constructors: Jurassic Reef Corals and Their Ecological Characteristics.—

The major constructors of modern reefs are zooxanthellate scleractinian corals, varying in growth rates, shapes, and fragilities. However, scleractinian evolution during the Jurassic was still a young feature and was particularly influenced by the end-Triassic extinction (Flügel, this volume). Therefore, environmental demands of Jurassic reef corals might have been considerably different from modern reef corals, and must be calibrated and evaluated with great care. Across the stages of the Jurassic, scleractinians had a high, generally increasing taxonomic overall diversity. During the Middle and, particularly, the Late Jurassic, coral associations generally appeared in large-scale, shallowing-upwards successions in a broad variety of environments whose parameters can, in many cases, be determined by criteria independent of corals. One of the key questions is whether Jurassic reef corals already had a photosymbiotic relationship with algae, which in modern reef corals is paramount in determining the environmental necessities and physiological abilities of corals, and, in particular, allows them to grow fast. Nose and Leinfelder (1997) have presented clues that many Late Jurassic corals already had photosymbiotic algae. Among the clues are:

- (1) skeletal growth banding of low-density and high-density bands,
- (2) restriction of coral facies to the upper parts of shallowing-upwards successions,
- (3) horizontal flattening of morphovaryable taxa towards deeper water,
- (4) predominance of highly integrated coral taxa such as thamnasterioid and meandroid forms, and
- (5) partial, though not unequivocal, indication of zooxanthellae by stable isotopes (see Stanley and Swart, 1995; Leinfelder, 2001, for discussion).

The efficiency of the photosymbiotic relationship probably was still, however, much lower in Jurassic scleractinians than in their modern counterparts (Nose and Leinfelder, 1997). Despite showing distinct growth bands, overall linear extension rates of Jurassic corals were about 60–70% lower than those of modern zooxanthellate corals. Additionally, the ratios of partly light-controlled low-density to high-density bands are considerably lower in Jurassic corals than in extant scleractinians (Nose and Leinfelder, 1997). Another important argument is that the highest species diversities of Late Jurassic coral associations appear in settings with a reduced yet noticeable siliciclastic influx rather than in pure carbonate settings. All of this indicates that the photosymbiotic relationship was less effective, so that these corals were not yet adapted to strongly oligotrophic settings, and

moderately oligotrophic to mesotrophic sites were preferred for at least some Late Jurassic coral associations (Nose and Leinfelder, 1997; Leinfelder, 2001).

In contrast to the above-mentioned positive effect of a very low terrigenous influx, strongly elevated sedimentation rates were just as much a threat to Jurassic corals as they are to modern ones (Rogers, 1990; Riegl, 1995). Nevertheless, coral growth forms and calical types may be adapted to sedimentation to a variable degree (Hubbard and Pocock, 1972; Leinfelder, 1986, 1994a). However, corallum shapes are multifunctional and may represent a best-fit compromise towards different adaptations. The dominantly platy shapes of many microsolenid associations, interpreted as a low-light adaptation in deeper or turbid settings, are an example. (Errenst, 1990, 1991; Leinfelder et al., 1993a; Leinfelder et al., 1996; Bertling, 1993a, 1993b, 1995, 1997b; Insalaco, 1996a). Microsolenids have been compared with the modern zooxanthellate tabular deep-water form *Leptoseris fragilis* (Leinfelder, 1994a; Insalaco, 1996a; Schlichter, 1992; Morycowa and Roniewicz, 1995).

Besides general growth and calical forms of corals, additional criteria are necessary to estimate the degree of sedimentation in a Jurassic coral association, particularly because many modern corals show active behavioral responses to cope with sedimentation (e.g., mucus secretion, ciliary action, hydrostatic inflation), which have no direct expression in the morphology (Lasker, 1980). Other useful criteria are:

- (1) Corals may show step-like ragged undersides or margins accompanied with non-enveloping growth bands, demonstrating that corals became partially buried while growing (Nose and Leinfelder, 1997; Nose, 1999). Remarkably, scleractinian corals exhibiting non-enveloping growth bands and ragged margins are to date only known from the Late Jurassic (Nose, 1995, 1999; Laternser, 2000).
- (2) Thick microbial crusts with frequent microencrusts on coral surfaces are good indicators of strongly reduced background sedimentation (cf. Leinfelder et al., 1993b).
- (3) Very low diversities of coral associations point strongly to sedimentation stress, if other stress factors such as great water depth, strong abrasion, or abnormal salinities can be ruled out (cf. Nose and Leinfelder, 1997; Leinfelder, 1997).

The hydraulic regime in which a scleractinian reef occurs is one of the most dominant determinants of its character and exerts a primary control on the zonation along the reef front (Hubbard, 1997). The dominance of a distinct morphology in comparable hydraulic settings is not compatible between Jurassic and modern corals. Jurassic high-energy settings are dominated by massive hemispherical rather than branching forms as in modern coral reefs. In the Jurassic, branching forms were largely restricted to lower-energy settings. Some species of *Calamophylliopsis*, *Stylosmilia*, and *Dermosmilia* do occur, however, in higher-energy reefs of Portugal and Lorraine (France), which could indicate strategies similar to modern acroporoids, using a rapid regeneration potential after storms (cf. Nose, 1995). However, Jurassic branching corals apparently did not rely on breakage as a method of reproduction like modern acroporoids (Bertling and Insalaco, 1998). Flat encrusting forms, which may occur in modern, highly abrasive settings, are not similarly developed in Jurassic reefs because such environments were normally unsuitable for colonization. Loaf-shaped, broad, non-encrusting morphologies are, however, a typical element of unstable, sand-ground, high-energy reefs and prob-

ably represent stabilization strategies by a broad, lower resting surface. A few Jurassic coral taxa were very euryhaline. *Amphiastrea piriformis*, for instance, formed small, monospecific reef bodies up to one meter large in an oyster-*Isognomon* association within delta embayments in Kimmeridgian and Tithonian rocks of Portugal (Fürsich, 1981; Fürsich and Werner, 1986; Leinfelder, 1986; Yin et al., 1995). In the Callovian succession of the Kachchh basin (northwestern India), low-diversity *Amphiastrea* meadows developed in a restricted shallow-water setting under elevated siliciclastic input (Fürsich et al., 1994b). Nearly all modern shallow-water coral reefs are enclosed in the 20° isochryme, which demonstrates that water temperature is the main factor for their global distribution and zonation pattern (e.g., Hubbard, 1997). Diversity of reef corals decreases in a marked and tight regression along north-south coastlines, as for example along Japan and Australia (Veron, 1995; Paulay, 1997). Reefs extended to considerably higher latitudes during several time periods in the Phanerozoic; this could have been due to (1) subtropical waters reaching farther poleward at those times (Adams et al., 1990; Copper, 1994) or (2) a generally equilibrated climate during high sea-level stands. The latter situation is valid especially for Late Jurassic times (Leinfelder, 1993a, 1994b). Coral reefs with high diversity may occur in fairly high paleolatitudes. Low coral diversities of southern Argentinian Oxfordian coral associations are interpreted as the result of siltation stress (Morsch, 1989). Lowered temperature in this high-paleolatitude setting can be ruled out, because coral colonies are large and co-occur with dasycladacean algae and calcareous oolites (Morsch, 1989; Legarreta, 1991). Also, the reef localities and the paleoclimatic indicators in southern England (paleolatitude 35° N) demonstrate the equilibrated climate at least during the Late Jurassic. Sedimentary evidence as well as floral characters (e.g., growth rings in fossil wood) indicate a warm Mediterranean-type climate in this region (Francis, 1984). Besides temperature, competition with macroalgae is thought to be another important factor for the latitudinal restriction of modern and probably also fossil zooxanthellate scleractinians. In the low-productivity environments typical of reefs, the efficient recycling capabilities of animal-plant symbioses allow for the successful competition with macroalgae, whereas the latter take over where productivity is higher (Birkeland, 1988).

Jurassic sponges—

In Jurassic coral reefs, stromatoporoid and chaetetid sponges (e.g., Wood, 1987) as well as other calcisponges (Calcarea) are common elements and occasionally even dominate to form meadows (e.g., Fürsich and Werner, 1991). Nearly all of them are restricted to shallow water. Siliceous sponges are rare in Jurassic coral reefs but are the dominant element in the sponge reefs, being associated with microbolites. There may be either a dominance of lithistids with additional hexactinellid elements or a dominance of hexactinellids without lithistids. The two groups differ considerably in their biology and physiology (Krautter, 1997). As the abundance of free bacteria rapidly diminishes in greater water depths (cf. Rheinheimer, 1980), sponges have to compensate for this by enormous pumping activity or by additional forms of energy uptake. Many sponges of the demosponge group cultivate enormous numbers of bacteria or cyanobacteria. Hexactinellid sponges have a completely different structure and feed largely on dissolved and colloidal organic matter by osmotrophy. These substances are enriched in deeper water, which makes deeper settings the preferential site of hexactinellid growth. Whereas modern sponges generally live in nearly all water depths, most modern siliceous sponges (lithistid

demosponges and hexactinellid sponges) are restricted to deeper waters, down to bathyal depths (Reid, 1968; Krautter, 1997). Only a few localities are known where rigid hexactinellid sponges occur in deep-shelf mud mounds (Krautter et al., 2001).

Sponges, like any other fixosessile organism, are vulnerable to elevated sedimentation rates, but they have a variety of adaptations that are also recognized in fossil examples. Development of a tube shape is one of the primary adaptations to sedimentation. Dish-shaped sponges are completely unprotected. Demosponges, however, have multipurpose cells that can transport unwanted particles away, although this mechanism is hindered in lithistid demosponges by the denseness of their spicular skeleton. Consequently, this group is largely restricted to clear waters. Hexactinellid sponges have the ability to let particles migrate through their tissues, although the process, and especially the limitations of it, are not yet fully understood (Krautter, 1997). The fossil examples show, however, that hexactinellids are often the only sponges appearing in clayey deposits. Another important feature with paleoenvironmental implications is the restriction of modern hexactinellid sponges to water temperatures colder than 15°C (Mackie et al., 1983; Dayton et al., 1994), although this might be an evolutionary adaptation and not necessarily transferable to the ancient examples. Water energy is another factor that may control the occurrence of sponges. Although the siliceous sponge skeleton itself is a rigid structure, some modern hexactinellids are physiologically very sensitive to higher water energy, so even the turbulence produced by scuba divers' air bubbles may be sufficient to cause the death of these sponges (Mehl, 1992). Therefore, modern hexactinellids are restricted to low-energy environments. The growth rates of sponges, though poorly known and apparently very variable, appear to range around an average of 2 cm/yr for modern siliceous sponges (Krautter, personal communication). Some Late Jurassic siliceous sponges of more than 2 m in diameter thus should have attained an age of several hundred years, making growth rates and individual life spans comparable to scleractinian corals.

Bioeroders in Jurassic Reefs.—

In Jurassic reefs, bioeroding organisms similar to modern counterparts were active, namely boring bivalves, "worms", and sponges (Bertling, 1999). Boring bivalves, being widespread from shallow to mid-ramp settings, often mined massive skeletons to their complete destruction, but they are also found in microbial crusts. Bertling (1997a) demonstrated that taxonomic composition and intensity of the boring fauna was also related to the degree of sedimentation. Although boring sponges were not yet as important in Mesozoic reefs as in Neogene reefs (Bertling, 1997a), the boring haplosclerid sponge *Aka* was widespread in deeper sponge-reef settings (Reitner and Keupp, 1991). Some case studies showed that boring sponges were more abundant in reefs with a high proportion of microbial crusts, the latter probably supplying additional nutrients (Bertling and Insalaco, 1998; writers' own observations). However, these observations cannot yet be generalized. Boring microbes were ubiquitous in coral reefs and back-reef sands, as evidenced by cortoids and reef biomorpha showing the typical microcrystalline rims with an irregular inner margin. Even the oldest boring foraminifer, *Troglotella incrustans*, is known from the Jurassic, though it did not contribute much to general bioerosion (Schmid and Leinfelder, 1996). Regular echinoids are common in many Jurassic reefs, mainly in those containing microbial crusts. As in modern reefs, these grazers appear to have had the task of keeping growth of microbial films under control. In rare cases, scratch marks from sea urchins on bivalve shells are known from the Upper Jurassic

(Leinfelder, 1986), providing evidence for the existence of soft algal turfs or microbial coatings on these shells. Regular Late Jurassic echinoids can also be used as valuable indicators of specific environmental factors. Analysis of their constructional morphology (based on shape and thickness of test, morphology of spine mammillae, and characteristics of ambulacral pore system) particularly allows for the interpretation of water energy, oxygen availability, and water depth (Baumeister and Leinfelder, 1998; Leinfelder, 2001). To date, it is impossible to calculate mass-balance budgets of reef construction versus reef destruction in Jurassic reefs, although bulk accretion rates can be determined in some cases. Nevertheless, the patterns show that bioerosion was an important factor in Jurassic reefs as well.

Jurassic Binding and Cementing Reef Organisms.—

Binding and cementing organisms are extremely important in the reef ecosystem, because they fix loose surplus material that cannot be stored in reef cavities or exported from the reef. Much of the material is produced by bioerosion, but in exposed reefs a large proportion of additional debris is generated by waves and storms. We propose that binding and cementing organisms, or the lack of many of these, greatly influence which type of reefs can be built, and therefore they are of major influence on the Jurassic reef patterns. Although calcareous red algae did exist in Jurassic reefs, they did not play important roles in reef stabilization as they do today, except for a very few cases where solenoporacean bindstones cover coral reefs (Nose, 1995; Helm and Schülke, 1998; Schmid, 1996). A direct ancestor to the coralline algae, *Marinella lugeoni*, inhabited Late Jurassic coral reefs sporadically but was of no importance for reef stabilization (Leinfelder and Werner, 1993). The most important stabilizers in Jurassic reefs were microbial mats, which calcified as microbial crusts (Leinfelder et al., 1993b). Microbial calcification in modern reefs is largely restricted to cavities (Reitner, 1993; Montaggioni and Camoin, 1993; Reitner et al., 1996). The occurrence of Jurassic microbolites at different water depths, including shelf settings about 400 m deep (Jansa et al., 1989; Dromart et al., 1994) as well as their prolific development in Jurassic reef caves (Schmid, 1996) shows that microbolites were potentially aphotic and hence are not solely of cyanobacterial origin. Obviously, microbial films and mats composed of cyanobacteria and/or eubacteria or other microorganisms can result in the same typical, clotted peloidal microfabric generating a thrombolitic mesofabric. Thrombolitic types were common from shallow to deep water, whereas stromatolites were largely restricted to shallow water. Reduced sedimentation is the most important prerequisite for the development of microbial crusts, a fact which is corroborated by the common occurrence of microbolites at hiatuses and condensation levels. Microbial films may also grow under elevated background sedimentation, but then they trap and baffle sediment, resulting in arborescent, digitate growth forms. Consequently, occurrence and fabric patterns of microbolite crusts are a useful tool for sequence stratigraphic interpretation (Leinfelder, 1993b; Nose, 1995). Kempe (1990), Kempe and Kazmierczak (1994), and Kempe et al. (1996) argued that vast development of microbolites during earth history should be indicative of strongly increased sea-water alkalinity, which, in turn, may be associated with ecosystem collapse and mass appearance of calcareous microbolites. The alkalinity model alone, however, cannot explain the co-occurrence of pure thrombolite reefs and macrofauna-rich reefs. Microbolites also occur as a typical element of Jurassic coral reefs (Leinfelder et al., 1993b; Schmid, 1996; Bertling and Insalaco, 1998; Dupraz and Strasser, 1999), presumably ranging from oligotrophic to mesotrophic. It appears plausible, however, that nutrients had a

positive influence on microbolite development, inasmuch as reefal microbolite crusts are often better developed in areas with reduced though noticeable terrigenous influx compared to pure carbonate settings. Finally, the exclusion of reefal macrofauna for distinct time intervals in certain areas is probably often due to strong eutrophication. This can be proven, however, only in cases where oxygen impoverishment occurred, which is highlighted by an association of pure microbolite reefs, bacterial framboidal pyrite, richness in authigenic glauconite, and the occurrence of dysaerobic or poikiloaerobic pectinid bivalves (Leinfelder, 1993a; Leinfelder et al., 1996). This makes pure microbolite development a good indicator of eutrophication/oxygen depletion in low-sedimentation regimes, at least for water depths at which other limiting factors such as salinity fluctuations can be ruled out. Microbolites are therefore important tools for paleoceanographic reconstructions. A wealth of encrusting microorganisms lived on the surfaces of Jurassic microbolite crusts. Many of these were considered earlier as enigmatic, alga-type organisms but are now in part interpreted as foraminifers (Leinfelder, 1986; Schmid, 1995, 1996; Schmid and Leinfelder, 1996). Some of these, such as the Loftusiid foraminifer *Lithocodium aggregatum*, the miliolid foraminifer *Tubiphytes morronensis*, or the enigmatic *Bacinella irregularis*, may, in some cases, contribute to binding and construction of reefs. These and other encrusters such as bryozoans are often valuable indicators of environmental factors. *Lithocodium* and *Bacinella* are both restricted to shallow settings, the porostromate cyanobacteria *Giroanellaminuta* is common in coastal settings, and *Tubiphytes*, though eurybathic, is nevertheless a good dipstick because the thickness of its outer wall changes with light availability, although low-light cave settings must be taken into consideration (Schmid, 1996; Leinfelder and Schmid, 2000). Using microencruster associations rather than indicator species allows for an even more refined paleobathymetric interpretation (Leinfelder et al., 1993b).

Other Jurassic Reef Organisms and Their Role in the Reef System.—

Sponges are assisted in water filtering by an enormous wealth of other organisms. It would be beyond the scope of this paper, however, to discuss them all. Among the most common are pectinid, ostracean, and pteriacean bivalves, serpulids (occasionally forming serpulid reefs), crinoids, bryozoans, and brachiopods. Bivalves also produced various reef types, amongst which the *Lithiotis* reefs were particularly successful, covering wide areas during the Early Jurassic. Deeper sponge mounds might also contain burrowing bivalves, including rare nuculids and pholadomyids, parts of which were sediment feeders. Gastropods, including nerineids, were also widespread, but their life habit is largely unknown. Belemnite and ammonite taxa, belonging to the predators and, possibly, scavengers, were common in sponge reefs, and several taxa definitely lived within the reefs. Crustaceans and many other reef organisms with a poor preservation potential can exceptionally be found in lithographic limestones developing in close proximity to reefs, such as the Solnhofen or Nusplingen limestones of southern Germany. Many of the organisms mentioned above provide additional clues to the special settings of Jurassic ecosystems. Cementing bivalve taxa change along a water-depth gradient (Werner et al., 1994), burrowing bivalves allow for the recognition of soft muds within reef systems, crinoid types may indicate energy levels, and the general abundance of filter feeders and sediment feeders gives insight into the trophic situation. Comparative paleoecological analysis allows evaluation of differences in these patterns. Very obvious is, for example, the general occurrence of "true"

(i.e., non-cyanobacterial) calcareous algae, such as dasycladaceans, in shallow-water coral reef settings but not in sponge reefs. Additionally, certain taxa of dasycladaceans, foraminifers, nerineids, and ammonoids allow for paleotemperature analysis, biogeographic comparison, or biostratigraphic correlation.

PATTERN OF JURASSIC REEF DISTRIBUTION THROUGH TIME AND SPACE: EVALUATION

Jurassic Reef Domains

Reef domains *sensu* Kiessling and Flügel (this volume) are geographically restricted areas yielding a large number of reefs. As further stated by these authors, it is necessary to distinguish between the number of reef domains and the intensity of reef growth; e.g., reefs can be concentrated within only a few domains and at the same time occur worldwide with isolated records. In the Jurassic, the various reef domains can be assigned to four large realms: northern Tethys, southern Tethys, North Atlantic, and Pacific realms (Table 1, Figs. 2–8). During the Early Jurassic, reefs were mainly in the westernmost Tethyan realm and in the western part of the northern Tethyan shelf. Some reefs also occurred along the southern Tethyan margin and along the coast of western Pangea. In the Middle Jurassic, this pattern of reef distribution remained more or less the same. In the Late Jurassic, reefs rapidly became globally distributed, mainly in the western and northern Tethyan realm. Reefs were also common in the North Atlantic area. Towards the eastern Tethyan margin, reef distribution became more scattered. Apart from that, reefs were also found in southernmost America, Japan, and Sakhalin. High-paleolatitude reefs occurred in Japan, Argentina, and Antarctica (the latter representing a methane-seep limestone and thus a very special reef type).

Lower Jurassic Reef Pattern (Fig. 2)

General Distribution and Characteristics.—

The Early Jurassic as a whole was a period not very favorable for the development of reefs. The database actually records 51 entries: 4 Hettangian, 10 Sinemurian, 26 Pliensbachian, and 7 Toarcian reefs. The stratigraphic age of four reefs is not known exactly. Most reefs, especially those with coral and/or sponge contribution, occur in the northern hemisphere (up to 41° N); only two Sinemurian coral reefs (Peru: Senowbari-Daryan and Stanley, 1994; Stanley and Beauvais, 1994) and some bivalve reefs are situated south of the equator. The rare Hettangian reefs occurred in moderately high paleolatitudes between 34° N and 41° N (coral reefs in France, England, and the Russian Far East; Elmi and Mouterde, 1965; Beauvais, 1976; Krasnov, 1997), and there was a *Gryphaea* bank at 58° N in Canada (Poulton, 1989b) (but see remarks above). In the Sinemurian, the four reefs with significant coral contribution occurred widely scattered, mostly in the western hemisphere: at 17° S in outer-slope environments of Peru, in British Columbia at 5° N (Stanley *vide* Flügel, personal communication), on the Stikinia terrane at 31° N (Stanley and Beauvais, 1994; Stanley and McRoberts, 1993), and farther east at 25° N in Morocco. Here, sponge mud mounds also existed (Dresnay, 1977). Apart from the slightly isolated Moroccan domain, no coral, sponge, and/or microbial reefs have yet been recorded from the Sinemurian of the Tethys realm. Lithiotids began to establish reefs north of the equator between 7° N and 34° N in the western and middle part of the Tethys (Morocco, Spain, Switzerland, Iran) (Dresnay, 1977; Geyer, 1977). The Pliensbachian represents the climax of reef development during the Early Jurassic

TABLE 1.—Reef domains of the Jurassic (see also Fig. 8).

EARLY CRETACEOUS	BERRIASIAN / EARLY VALANGINIAN	Atlantic, Bahamas, Hungary, Montenegro, S France, Swiss Alps, Texas, Turkmenistan, Ukraine, W Canada
LATE JURASSIC (undifferentiated): Karakorum, Sakhalin, Tibet, Yemen/Somalia	TITHONIAN	Antarctica, Argentina, Atlantic, Caucasus, Czechia, E Canada, England, Japan, Lower Austria/Northern Alps, Lusitanian Basin (Portugal), Morocco, N Germany, Romania, S France, S Germany, S Italy, Serbia/Montenegro, Sicily, Swiss Alps, Tunisia, Ukraine, Yemen
	KIMMERIDGIAN	Algarve (Portugal), Algeria, Atlantic, Bosnia/Montenegro, Caucasus, Celtiberian Basin (Spain), Colombia, French Jura, Lusitanian Basin (Portugal), Mexico, Northern Alps, Oman, Poland, S France, S Germany, Saudi Arabia, Eastern Africa, SE Asia (Thailand/Sumatra), SE USA, Southern Alps, Tadjikistan, Turkmenistan, Ukraine
	OXFORDIAN	Algarve (Portugal), Argentina, Atlantic, Caucasus, Corsica, Czechia/Slovakia, E Canada, England, French Jura, Swiss Jura/Swiss Alps, French W Alps, Iran, Israel/Lebanon, Japan, Lorraine, Lusitanian Basin (Portugal), Eastern Africa, Madagascar, Morocco, N Germany, NW France, Montenegro, Poland, Romania, S Germany, Spain, Saudi Arabia, SE USA, Slovenia, Southern Alps, Tadjikistan, Tunisia, Ukraine, Uzbekistan/Turkmenistan
MIDDLE JURASSIC (undifferentiated): Thailand/Burma, Tibet, Oman	CALLOVIAN	French Jura, India, Iran, Israel, Madagascar, Poland, Saudi Arabia, Somalia, Tunisia, Ukraine
	BATHONIAN	Atlantic, Egypt, England, French Jura, India, Iran, Madagascar, NW France, Poland, Romania, S France, Spain
	BAJOCIAN	Chile, French/Swiss Jura, Hungary, Morocco, Spain, Tadjikistan, W USA
	AALENIAN	Morocco, Thailand, W Alps
EARLY JURASSIC (undifferentiated): Nepal, Timor, US eastcoast)	TOARCIAN	Chile, Lusitanian Basin (Portugal), Morocco, Northern Alps/Germany, Southern Alps/Italy
	PLIENSBACHIAN	Algeria, Morocco, Oman, Slovenia, Southern Alps/Italy, Spain, Tibet, W USA
	SINEMURIAN	Iran, Morocco, Peru, Spain, Switzerland, W Canada
	HETTANGIAN	France, England, Far East, NW Canada

if one considers the number of reefs (26 reef sites). Only the lithiotid facies, however, extended from the western hemisphere (Oregon: Nauss and Smith, 1988) to Algeria/Morocco (Dresnay, 1971, 1977; Scheibner and Reijmer, 1999) and into the western, middle, and eastern Tethys (e.g., Geyer, 1977). All other Pliensbachian reef sites are concentrated in a relatively small area between 24° N to 32° N and 4° W to 19° E (western Tethys: Spain, Slovenia, Italy; North Atlantic: Portugal). Apparently the Moroccan domain was the center of reef development not only in the Pliensbachian but also in the entire time span of the Early Jurassic. Wide platforms of the High and Middle Atlas with marginal nearshore environments, extended intra-platform areas, and platform edges along rift zones and marine troughs provided favorable conditions for sponge mud mounds, coral reefs, and *Lithiotis* facies (e.g., Dresnay, 1971, 1976, 1977, 1979). Apart from Spain (Turnšek et al., 1975), no coral, sponge, and/or microbial reefs are known from the Pliensbachian of the northern Tethys, the eastern Tethys, and the Pacific. The Toarcian reef record (seven reef sites)

is affected by a strong decline in reef development at the end of the Pliensbachian. Only a few coral and lithiotid reefs persisted in Morocco from the Sinemurian into the Early Toarcian (Beauvais, 1986; Dresnay, 1977), and they became extinct at the end of the Early Toarcian because of the drowning of the Moroccan platforms (Dresnay, 1979; Blomeier and Reijmer, 1999; Scheibner and Reijmer, 1999). An additional few reef records from deeper-slope areas such as microbial mud mounds of Portugal at 30° N (Duarte, 1997), an atypical siliceous-calcisponge association from Italy (Beccarelli-Bauch, 1988), and a deep-water massive red limestone facies from the Northern Calcareous Alps of Germany (Mathur, 1975) point to the scarcity of favorable shallow-water habitats. In the western hemisphere, sites with *Lithiotis* facies are known from marginal marine environments in Peru and Chile (Hillebrandt, 1971, 1981; Hallam, 1983). Two coral-reef sites from shallow intraplatform and shelf-margin areas of Morocco are listed in the database for the Toarcian-Aalenian time span (cf. Beauvais, 1986; Park, 1983). Detailed stratigraphic study is needed, however, to

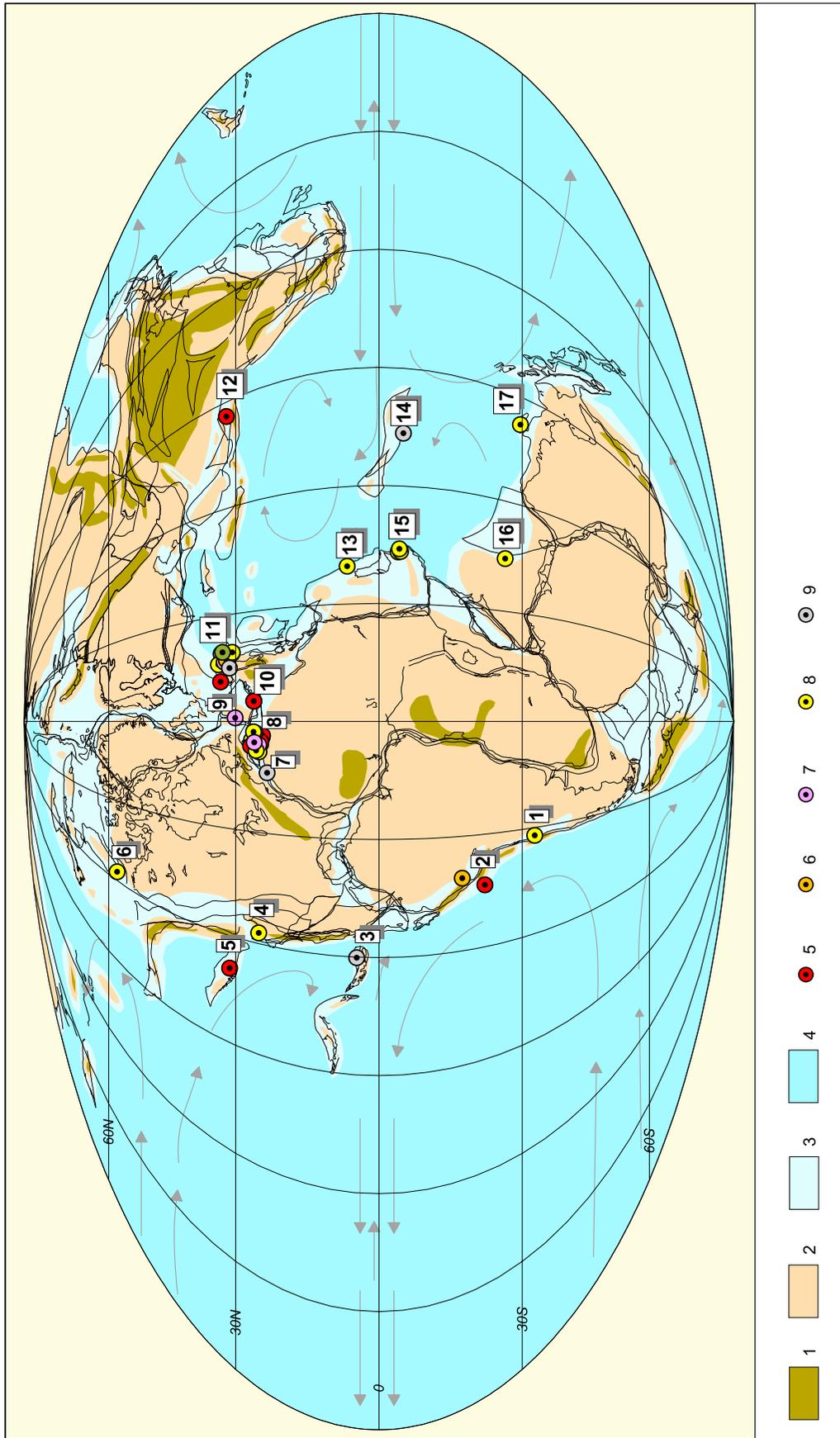


FIG. 2.—Global distribution of Lower Jurassic reefs, indicating probable current systems and dominant reef biota. 1, mountains; 2, land; 3, shelf; 4, deep water; dominant biota: 5, corals; 6, coralline sponges; 7, siliceous sponges; 8, bivalves; 9, others/unknown; reef sites (numbers in rectangles): 1, Chile; 2, Peru; 3, Waddington, British Columbia, Canada; 4, Oregon, U.S.A.; 5, Telkwa Range, British Columbia, Canada; 6, Yukon, Canada; 7, Georges Bank, Atlantic; 8, NE Morocco; 9, Lusitanian Basin, Portugal; 10, southern Spain; 11, southern Alps, Italy, and southern France; 12, SE Pamir, Tadjikistan; 13, Zardeh Kuh, Iran; 14, Nyalam, Tibet; 15, Oman; 16, Koma, Nepal; 17, West Timor, Indonesia. Map provided by Wolfgang Kiessling.

confirm whether the new episode of coral-reef development already started in the Early Jurassic.

Biota.—The Early Jurassic reef biotas were dominated by corals and bivalves. Sponges and microbial associations played a subordinate, mostly regional role. The coral reefs of the Early Jurassic, especially those of the Hettangian, Sinemurian, and to a lesser degree also the Pliensbachian, were generally characterized by a rather low to moderate diversity, the dominance of branching (mostly phaceloid) and solitary corals, and a subordinate presence of colonial forms (Beauvais, 1980, 1986; Dresnay, 1977; Turnšek et al., 1975). In this context, the reef builders can be attributed rather to the baffling than to the constructor type. The coral fauna at the genus and species level shows Triassic affinities and consists of taxa that are generally regarded as ahermatypic. They were able to survive the collapse of the Triassic platforms and the end-Triassic mass extinction in settings rather unfavorable for reef growth (cf. Leinfelder, 1994b, Flügel, this volume). Especially the phaceloid morphotype (e.g., the *Retiophyllia* type and *Stylophyllipsis* type) seems to have coped with higher sedimentation rates (Leinfelder et al., 1994) and therefore was well adapted to such conditions typical of Early Jurassic environments. From the Pliensbachian onward, Triassic faunal elements became extinct whereas new typical Jurassic forms developed. The Early Jurassic corals represent a transitional stage between the Triassic and the Jurassic coral fauna (Turnšek et al., 1975; Beauvais, 1986). The scarcity of potentially framework-building corals at the beginning of the Early Jurassic may be an essential reason for the scarcity of reefs in the Hettangian and Sinemurian (see Leinfelder, 1994b, for discussion). Coral reefs were restricted to shallow platform areas, shelf or platform margins, and upper-slope settings (e.g., Dresnay, 1977; Beauvais, 1980, 1986; Scheibner and Reijmer, 1999). Additional faunal elements to a varying degree were pharetronid sponges (also of Triassic affinities, cf. Flügel, this volume), solenoporacean red algae, stromatoporoids, spongiomorphids, bivalves, and gastropods. From Spain, a unique coral-bryozoan and a hydrozoan-rich association have been described (Turnšek et al., 1975). Bioerosion is rarely documented. Compared to the Middle and Late Jurassic, sponges played a minor role in reef building during the Early Jurassic. Only in Morocco did they develop large mounds in slope or deeper shelf environments (Dresnay, 1979; Crevello and Harris, 1984; Hauptmann and Warne, 1990), which served as base for the younger coral reefs (Dresnay, 1977). In some examples lithistids prevailed over hexactinellids (Evans and Kendall, 1977), but a hexactinellid dominance also occurred (Dresnay et al., 1978). Additional faunal elements occasionally were brachiopods, crinoids, and bivalves. An important contribution of microbial crusts is also recorded. An unusual association of dictyids with pharetronid sponges (*Stylothalamia*), corals, brachiopods, thin-shelled bivalves, crinoids, and radiolarians in the Toarcian of Italy is explained by upwelling effects at an outer platform edge (Beccarelli-Bauck, 1986, 1988). Pure microbial reefs are recorded only from the Pliensbachian of Portugal, where they interdigitate with organic-rich shales of outer shelf areas; they represent phases of lowered sedimentation rates (Dromart, 1991). Reefs with a significant contribution of microbial crusts are the above-mentioned sponge microbial mud mounds of Morocco and a sponge-rich mound facies from the Toarcian of Portugal (Duarte, 1997; Duarte et al., 2000). Microbial activity is not documented in any of the coral reefs of the Early Jurassic recorded in the database. Because the binding capacity of microbes is regarded as an important factor for the building of true reef frameworks in the Jurassic (Leinfelder et al., 1993b; Leinfelder, 1994b), the scarcity of microbial contribution may also be a main factor for the scarcity

of Early Jurassic reefs and reflect generally unsuitable conditions for the formation of microbial mats, e.g., elevated sedimentation rates (cf. Leinfelder, 1994b). A characteristic feature of the Lower Jurassic and restricted to this stage are lithiotid banks, biostromes, and reefs. The first reefs occur in the Sinemurian, but the climax period was the Pliensbachian, with a nearly continuous distribution belt in warm, low-latitude areas (PL = paleolatitude 34° N to 30° S) along the southern Tethys margin from Spain and Algeria/Morocco in the west, passing the Apulia-Adria polygon (Italy, Slovenia) to Oman, Iran, Tibet, Nepal, and Timor in the east. The migration through Central America by the Hispanic corridor allowed the establishment of *Lithiotis* reefs in Oregon during the Pliensbachian. Later on, in the Toarcian, after the extinction of *Lithiotis* in North America, *Lithiotis* facies developed in the southern part of the western hemisphere (Nauss and Smith, 1988; Hillebrandt, 1971; Geyer, 1977). The common usage of the genus name *Lithiotis* (s.l.) comprises different genera (e.g. *Lithiotis* s.str., *Cochlearites*, *Lithopedalion*, *Opisoma*). Each of these genera preferred different low-energy and high-energy settings, partly intertidal subenvironments on intraplatform and marginal marine settings. These often unfavorable biotopes were sometimes protected from normal open-marine conditions by coral reef barriers (Buser and Debeljak, 1996; Dresnay, 1977). A recent study from Morocco (Scheibner and Reijmer, 1999) regards *Lithiotis* reefs as the main stabilizing structure of platform edges. The *Lithiotis* (s.l.) reefs generally are of low diversity and are occasionally enriched by a few additional faunal elements (e.g., other bivalves, branching corals, stromatoporoids, and gastropods). Bioerosion has not been recorded.

Eastern Pacific Realm: North America, Peru, Chile.—In the eastern Pacific realm, few coral reefs developed in both hemispheres. Stanley and Beauvais (1994) and Stanley and McRoberts (1993) describe a coral reef 44 m thick with colonies up to 5 m high from the Late Sinemurian of British Columbia (Stikinia terrane, PL 31° N, 69° W). Despite the few, mostly branching (phaceloid, dendroid) coral species responsible for the reef structure, a variety of other organisms (brachiopods, bivalves, gastropods, echinoids, sipunculids, fishes) contributed to the moderate diversity of the whole reef association. Biostromes of lower diversity are reported from lower latitudes (PL 4, 56° N) in British Columbia (personal communication, Stanley *vide* Flügel). In Peru, during the Sinemurian, baffling corals could form low-diversity biostrome complexes extending over 5 km on an open marine shelf (Stanley and Beauvais, 1994; Wells, 1953). Their thickness reaches more than ten meters. In contrast to most other Lower Jurassic coral reefs, they show a clear vertical succession with a bivalve shell substrate at the base, baffling corals dominating in the middle part, and a pervasive framework on top. Another Early Jurassic reef association of moderate diversity (pharetronid sponges and corals) grew in an outer-shelf environment probably more than 50 m deep (Senowbari-Daryan and Stanley, 1994). In contrast to the Tethys, *Lithiotis* facies rarely occurred in the eastern Pacific realm. Nauss and Smith (1988) report bioherms from the Lower Pliensbachian Robertson Formation of east-central Oregon (PL 25° N, 57° W). Only after the extinction in North America, the genus had its first appearance farther south in Peru and Chile during Toarcian time (Nauss and Smith, 1988; cf. Geyer, 1977; Hillebrandt, 1971). The *Lithiotis* reefs and biostromes of the western hemisphere include also the reefs of *Plicatostylus*, which is a junior synonym of *Lithiotis* (Lupher and Packard, 1930; Cox, 1969; cf. Nauss and Smith, 1988).

Moroccan Domain: Morocco, Algeria.—Morocco played a major role in Early Jurassic reef development. Numerous localities with

sponge-microbial mud mounds, coral reefs, and/or lithiotid bioherms are recorded from the Middle and High Atlas region (e.g., Beauvais, 1986; Dresnay, 1971, 1977; Park, 1983; Crevello and Harris, 1984; Hauptmann and Warme, 1990; Morabet, 1974; Scheibner and Reijmer, 1999). The three reef-building groups may have occurred separately from each other, such as siliceous sponge mud mounds up to 150 m high in slightly deeper basin positions (Dresnay et al., 1978; Evans and Kendall, 1977), pinnacle coral reefs growing on conglomerates of Paleozoic boulders (Jebel Bou Mokhta: Dresnay, 1971), or isolated bivalve banks in the middle of coastal platforms (Dresnay, 1977). More often, a genetic relationship existed between these reef biotas: Early Liassic (mostly early to late Sinemurian) sponge mud mounds generally are the base of Late Sinemurian and Pliensbachian coral bioherms and biostromes. On the other hand, the lithiotid associations (s.l.) flourished in the shallowest, partly intertidal environments protected from open-marine conditions by a coral reef barrier, but they also could interfinger with coral facies (e.g., Dresnay, 1977). A different interpretation concerning the relationship between coral and lithiotid biofacies was recently presented, at least for the Jebel Bou Dahar, by Scheibner and Reijmer (1999). For this oval-shaped, 35-km-long isolated platform situated at the margin of the Liassic High Atlas trough, Dresnay (1979) assumed an atoll-like zonation with a barrier of Pliensbachian coral reefs, an inner protected platform with lithiotid biostromes, and an island formed by Paleozoic basement near the center. According to Scheibner and Reijmer, the lithiotids lived on the morphological top of the platform margin and stabilized this edge by baffling sediment, whereas the corals lived in a slightly deeper position on the upper slope. In siliceous sponge-microbial mud mounds, hexactinellids (e.g., Dresnay et al., 1978) or lithistids (Evans and Kendall, 1977) may have been the dominant poriferan groups. In any case these reefs show all the characteristics of an origin below the wave base (almost no debris, micritic matrix, virtual absence of vertical and horizontal zonation, boring activity not recorded). Only a few taxa of higher systematic order (brachiopods, crinoids, bivalves) may complete this low-diversity mound biofacies (Dresnay et al., 1978). Size and morphology of Moroccan coral reefs vary from small patches (e.g., Meknes, Park, 1983; Tazzeke, Dresnay, 1979) to large reef complexes, up to 100 m thick and with wide lateral extent, forming reef belts extending more than 150 km. They can be found scattered on littoral platforms or on platform margins on both sides of marine troughs (e.g., High Atlas Trough) (Dresnay, 1971, 1977; Morabet, 1974; Beauvais, 1986; Scheibner and Reijmer, 1999). The structure-controlled position is more pronounced in the Middle Atlas than in the High Atlas. The pattern of these reef structures correlates with fracture zones of the Paleozoic basement and paleo-shoals and mirrors the early Jurassic synrift tectonics in this region (Dresnay, 1977, 1979; Leinfelder, 1994b). Branching and solitary corals prevail in the generally low-diversity to moderate-diversity associations, but highly diverse communities with hermatypic corals may also occur in complex reef bodies (e.g., atoll-like reef of Jebel Bou Dahar; Dresnay, 1977). Additional faunal elements are solenoporacean red algae, spongiomorphids, stromatoporoids, and gastropods; destruction by macroborers is also a common feature. The database records two Late Toarcian coral reefs (Midelt, Touissite; Park, 1983) which should represent a new beginning of reef development in the Early Jurassic after the extinction event at the end of the Early Toarcian. However, the information about the stratigraphic position of these reefs is very poor. The *Lithiotis* (s.l.) facies is represented in Morocco by biostromes tens of meters thick (Park, 1983) and mounds more than 100 m high, which may extend laterally over one kilometer (Lee, 1983; Monbaron et al.,

1984; Agard and Dresnay, 1965). The bivalves have formed monospecific or low-diversity associations, but reefal associations with phaceloid corals, stromatolites, gastropods, and solenoporaceans also existed (Lee, 1983; Dresnay, 1977). The facies may be associated with pure carbonates, bird's-eye facies, and spherical oncoids (Lee, 1983). Debris-rich biostromes also occur.

North Atlantic: Portugal, U.S. East Coast.—In an outer-shelf position in the northern part of the Lusitanian Basin, small microbial reefs and biostromes are intercalated in organic-rich shales of the Lower Pliensbachian (Dromart, 1991). They are reliable markers for third-order marine flooding maxima, when lowered sedimentation rate favored growth of microbial mats. Similar but sponge-rich microbial mud mounds also grew in deeper-slope settings near Coimbra at 30° N in Toarcian time (Duarte, 1997; Duarte et al., 2000). Only from seismic evidence, an Early Jurassic reef ridge is inferred from Georges Bank (U.S. east coast; Austin et al., 1980).

Northern Tethys: France, England, Spain.—There are only few Lower Jurassic reef records from the northern Tethys. In the Ardèche region (France, 34° N, 11° E) low-diversity coral associations formed dome-shaped bioconstructions up to 25 m thick. Dominant biota of these poorly known Hettangian reefs are branching corals ("*Thecosmilia*"/?*Retiophyllia* type) (Elmi and Mouterde, 1965; Elmi, 1987, 1990). Farther north, in Dorset, England, phaceloid, solitary, and to a lesser extent massive colonial corals lived in scattered communities rather than in compound biostromes or reefs (Beauvais, 1976, 1980). From Murcia in Spain (26° N) Turnšek et al. (1975) report a succession of coral-bryozoan biostromes, brachiopod biostromes, and hydrozoan biostromes from a Pliensbachian outer platform environment; laterally, *Lithiotis* biostromes also occur. The coral-bryozoan biostromes of relatively high diversity are composed of 24 coral species (phaceloid, solitary, meandroid, and other hermatypic forms), a rich encrusting fauna (the bivalve *Placunopsis*), brachiopods, gastropods, crinoids, sponges, and fishes. The *Lithiotis* biostromes are embedded in a micritic matrix, and hence are regarded as bioconstructions of low-energy settings. The database records another, moderately diverse *Lithiotis* reef a few meters thick from a Sinemurian shallow intraplatform setting in Spain. Corals, stromatoporoids, microborers, and macroborers are other faunal components; the high micrite and low debris contents reflect a low-energy environment (Geyer, 1977).

Southern Tethys: Apulia-Adria-Polygon, Oman, Iran, Tibet, Nepal, Timor.—A common reefal element in low-latitude platform environments along the southern Tethys margin were lithiotid biostromes and reefs. They are recorded from the Sinemurian and Pliensbachian of the Apulian-Adria polygon comprising localities in Switzerland, northern Italy, and Slovenia (Geyer, 1977; Göhner, 1981; Buser and Debeljak, 1996), Oman (Glennie et al., 1974; Geyer, 1977; Pratt and Smewing, 1990), Iran (Geyer, 1977), Nepal (Fuchs, 1967; Geyer, 1977), Tibet (Yin and Wan, 1998), and Timor (Krumbeck, 1923; Geyer, 1977). The *Lithiotis* facies generally occurs on very shallow intraplatform settings and is characterized by low diversity, high micrite content, a rather low debris content, large extent of belts (e.g., 25 km in Slovenia; Buser and Debeljak, 1996), and biostrome thicknesses reaching from some centimeters to 10 m, rarely up to 75 m. Occasionally associated faunal elements are few, mostly branching corals, other bivalves, and stromatoporoids. According to the available data, reefs with pronounced coral participation are restricted to the western part of the southern Tethys realm and can be found in rather untypical

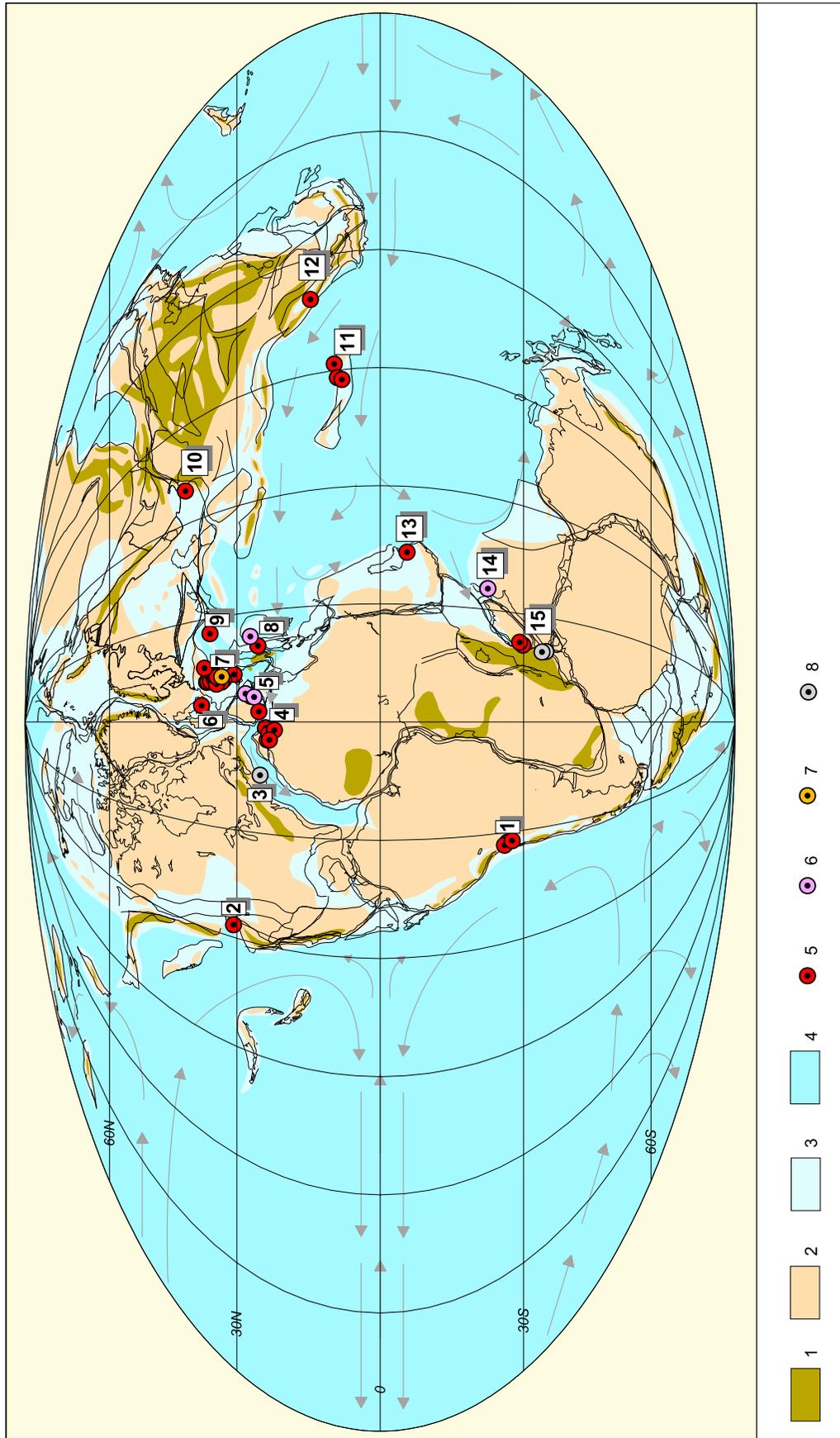


FIG. 3.—Global distribution of Bajocian and Bathonian reefs, indicating probable current systems and dominant reef biota. 1, mountains; 2, land; 3, shelf; 4, deep water; dominant biota: 5, corals; 6, siliceous sponges; 7, stromatoporoids; 8, others/unknown; reef sites (numbers in rectangles): 1, Chile; 2, Idaho; 3, Georges Bank, Atlantic; 4, Morocco; 5, southern and eastern Spain; 6, England; 7, Luxembourg, France, and southwestern Germany; 8, Montenegro and Hungary; 9, Dobrogea, Romania; 10, Tadzhikistan(?); 11, Tibet; 12, Thailand–Burma; 13, Oman; 14, Kachchh, India; 15, Madagascar and Mozambique. Map provided by Wolfgang Kiessling.

associations. A coral patch reef 5 m thick and 35 m long grew on the Dinaric Platform (Slovenia, loc. Gornja Brezovica) within a lithotid biostrome of Pliensbachian age (Buser, 1965; Buser and Debeljak, 1996). In northern Italy (Monte Grappa, PL 32° N) pharetronid sponges (*Stylothalamia*) were main constructors of highly diverse Upper Pliensbachian patch reefs together with solitary and colonial corals, stromatoporoids, and solenoporaceans (Zempolich, 1993; Broglio Loriga et al., 1991). The reefs, 15 meters thick and tens of meters wide, grew in a shallow intraplatform environment with variable energy conditions (mudstones with grainstone intercalations). A unique biostrome composition of siliceous (dictyid) and calcareous sponges (*Stylothalamia*) is described from the Upper Pliensbachian to Lower Toarcian micritic Misone limestone in northern Italy (PL 32° N) (Beccarelli-Bauck, 1986, 1988; Broglio-Loriga et al., 1991). The co-occurrence of the main baffler organisms with some solitary corals, brachiopods, thin-shelled bivalves, crinoids, and radiolarians as well as the moderate diversity of the fauna is interpreted as representing a situation of a mud mound or still-water bioherm on a marginal platform with upwelling (Beccarelli-Bauck, 1988). Siliceous sponge-microbial mud mounds are not yet recorded from the southern Tethys realm. From the Northern Calcareous Alps (PL 33° N) a massive red limestone facies with mudstones and wackestones (ammonites, sponge spicules, crinoids, echinoids), stromatactis, and slumps is interpreted as a deeper-water mud mound (Mathur, 1975). This upper Liassic facies crops out as massive complex 3 km long and 5 to 45 m thick and grades continuously into Middle Jurassic nodular red limestones.

Middle Jurassic Reef Pattern (Fig. 3)

General Distribution and Characteristics.—

Despite the availability of shallow seas and extensive shelves in the subtropical and tropical belts, Middle Jurassic reefs have a scattered distribution. Reefs reveal a global paleolatitudinal range from about 37° N to 30° S. Remarkably, reefs in the northern hemisphere are mainly located higher than 30° N (e.g., central European reef localities). Aalenian reef sites have been reported only from the southern Tethys shelf (Morocco; PL 21–24° N), Thailand (PL 14° N), and the western Alps (Préalpes Romandes, central Penninikum, PL 30° N) (Dresnay, 1971; Septfontaine and Lombard, 1976; Beauvais, 1986; Bassoullet, 1986). Because of the maximum peak of platform development, Bajocian–Bathonian reefs reveal a much wider distribution and have been described from the northern Tethys shelf (Spain, England, France–southwestern Germany–Luxembourg, Romania, Poland; PL 25–39°) (e.g., Beauvais, 1972; Hallam, 1975; Beauvais and Negus, 1975; Palmer and Fürsich, 1981; Lathuilière, 1982; Draganescu and Beauvais, 1985; Beauvais, 1985; Geister, 1989; Geister and Lathuilière, 1991; Ernst, 1991; Deusch et al., 1991; Friebe, 1995), the southern Tethys margin (Montenegro, Hungary, Morocco, PL 22–27° N) (Turnšek, 1968; Pisera, 1993; R.G. Stanley, 1981), Oman (PL 5° S) (Watts and Blome, 1990), India (Kachchh, PL 22° S) (Pandey and Fürsich, 1993), Madagascar (PL 29° S) (Alloiteau, 1958; Collignon, 1959), Tibet (PL 7–9° N) (Liao, 1982), U.S. west coast (Idaho, Pacific, PL 30° N) (Stanley and Beauvais, 1990), U.S. east coast (Georges Bank, Atlantic, PL 24° N) (Ryan and Miller, 1981) and Chile (PL 25–27° S) (Hillebrandt et al., 1986; Prinz, 1986, 1991). Callovian reefs, in part initially developing already in the Bathonian, have been reported from the northern Tethys shelf (France, PL 34° N; Poland, PL 39° N) (Beauvais, 1972; Garcia et al., 1989), Ukraine (Crimea, PL 37–38° N), Egypt (PL 6° N), Tunisia, Iran (PL 32° N) (e.g., Farag, 1959; Flügel, 1966; Mikhailova, 1968; Beauvais,

1985; Klikushin, 1996; Schairer et al., 2000), and the southern hemisphere (Saudi Arabia, India, Madagascar, Somalia; PL 1–31° S) (e.g., Alloiteau, 1958; Barnes, 1976; Beauvais, 1985; El Asa'ad, 1989; Pandey and Fürsich, 1993; Fürsich et al., 1994b). Middle Jurassic reefs, dominated by scleractinian corals, usually stem from shallow platform settings within open shelf environments, with exception of the coral reefs of Chile, which presumably formed in slightly deeper settings below fair-weather wave base. The Madagascar and Morocco examples developed along the platform margins. Reefs dominated by siliceous sponges normally grew in deeper platform positions below storm wave base (e.g., sponge facies of Spain; Deusch et al., 1991; Friebe, 1995), except for the siliceous sponge reef facies of northwestern France (Normandy), which is considered to have formed above storm wave base but still below normal wave base (Palmer and Fürsich, 1981). Taking into account that many reefs lack diversity evaluations, most reefs exhibit low to moderate diversities. Generally, low-diversity associations are a characteristic feature of stressed reefs, as exemplified by the Callovian coral meadows of Kachchh, India, which grew despite an elevated siliciclastic influx (Fürsich et al., 1994b). According to the database only the Bathonian reefs of Kachchh, India, as well as the British reefs are characterized by a high-diversity coral fauna (Beauvais and Negus, 1975; Pandey and Fürsich, 1993). The size of Middle Jurassic reefs varies from small and/or thin reef structures (e.g., sponge biostromes of the Normandy, France; Palmer and Fürsich, 1981) with thicknesses of less than 10 meters and lateral extents of less than 100 meters to huge buildups with cumulative thicknesses of more than 100 meters and lateral extents of more than 500 meters (e.g., Madagascar; Alloiteau, 1958). Maximum lateral extents up to 250 km are mentioned from Madagascar. Reef belts in the Middle Jurassic of France and Morocco still extended to about 100 km, whereas the Indian (Kachchh) reef sites as well as some localities in France (Normandy, Provence) and Madagascar exhibit only short reef belt lengths (1–8 km).

Biota.—Primary or secondary reef builders in the Middle Jurassic were, in decreasing importance, scleractinian corals, siliceous sponges, coralline demosponges (stromatoporoids and chaetetids), red algae, microbes, bivalves, calcareous sponges, serpulids, and encrusting foraminifera. Many reef structures in the Middle Jurassic were clearly dominated by scleractinian corals, often representing the only constituent of the reef fauna (e.g., Chile, Madagascar, Iran, Egypt). However, the overall diversity and the reef-building potential of corals appear to be still lower than in the Late Jurassic (Lathuilière, 2000a, 2000b). Coral reefs are quite often associated with red algae, coralline demosponges (chaetetids), foraminifera, and microbes (e.g., Morocco, Thailand) or bivalves and stromatoporoids (e.g., Tibet, Tunisia, India). Pure coralline sponge reefs developed at the southern margin of the Tethys in southern Israel, including monospecific aggregations of branching and domal stromatoporoids (Wood, 1999). Mixed coral–siliceous sponge reef types are reported only from the Middle Jurassic of southern France (Ile de Crémieu; Lathuilière, 1982). Reef structures dominated by siliceous sponges were commonly associated with serpulids, bryozoans, brachiopods, and crinoids. Microbial crusts occurred within the biostromes and bioherms but are obviously less common constituents than Upper Jurassic siliceous sponge mounds (e.g., siliceous sponge facies of eastern Spain; Deusch et al., 1991; Friebe, 1995). Siliceous sponge reefs of northwestern France (Normandy) are characterized by the co-occurrence of bivalves, calcisponges, and serpulids (Palmer and Fürsich, 1981).

Northern Tethys: Spain, England, France–Luxembourg–Southern Germany, Western Alps (Préalpes), Poland, Romania, Ukraine, Iran, Thailand, Tadzhikistan.—Most reefs on the northern Tethys shelf developed within Bajocian and Bathonian time, which represents the maximum development of carbonate platforms in the Middle Jurassic. The succession in eastern Spain is characterized by the development of siliceous sponge reef facies, which suddenly colonized extensive areas (Deusch et al., 1991; Friebe, 1995). Reef facies mainly include small lens-like bioherms (thickness up to 7 m, diameter 10–15 m) as well as biostromes (thickness 0.5 m). Reefs are generally composed of hexactinellid and lithistid sponges, brachiopods, serpulids, bryozoans (*Stomatopora*, “*Berenicea*”), and subordinate peloidal microbial crusts. During the Bajocian, the composition of siliceous sponge fauna varied between hexactinellid dominance and lithistid dominance, probably reflecting deepening and shallowing trends (Friebe, 1995; cf. Leinfelder et al., 1993a). Generally, siliceous sponge reefs of Spain are interpreted to have been built in the oligophotic zone (Friebe, 1995). Siliceous sponge reefs are also known from northwestern France (Normandy). Here, sponge reefs, reaching a height of 2–3 meters, are clearly dominated by the lithistid sponge *Platychonia magna*. Remarkably, successive generations of the sponges settled on conspecific adults and firmly cemented themselves to form a rigid reef structure (Palmer and Fürsich, 1981). In contrast to the majority of Upper Jurassic siliceous sponge mounds from southern Germany (Swabian and Franconian Alb), these reefs lack microbial crusts and are considered to have grown in much shallower water above storm wave base (Palmer and Fürsich, 1981). Siliceous sponges are very rare in the Middle Jurassic of southern Germany (Franz and Müller, 1988), however, without forming a siliceous sponge reef facies. Coral reefs on the northern Tethys shelf are especially reported from the France–Luxembourg–southern Germany–northern Switzerland reef province (eastern Paris Basin). During the Bajocian there was an extensive reef development on the eastern margin of the Paris Basin (e.g., Lorraine), being the first time in earth history that scleractinian corals almost exclusively formed reefs over an entire carbonate platform (Geister and Lathuilière, 1991). Besides the Lorraine localities, Bajocian coral reefs also developed in Luxembourg (“Calcaire d’Audun-le Tiche”; Hary, 1970). Generally, coral reefs occur within two distinct reef-bearing limestone complexes (“lower coral limestone”, “upper coral limestone”). The reefs have an irregular shape; the morphology of individual reef bodies includes small lens-shaped patch reefs a few meters in diameter, dome-shaped bioherms up to 10 meters thick, and 10–20 m broad and large buildups up to 20 m thick and extending laterally for more than 100 meters. The reefs formed no barrier reef system along a steepened platform margin but reveal a patchy distribution with no zonation trends across the shelf (Geister and Lathuilière, 1991). Especially the smaller reefs in the “lower coral limestone” obviously grew despite increasing sedimentation rates indicated by argillaceous overlapping inter-reef sediments. These reefs are interpreted to have formed below wave base, whereas the larger reef structures were embedded in bioclastic, oolitic, and oncolitic crossbedded limestones, which prove a position well above wave base (Geister and Lathuilière, 1991). Generally, the coral fauna of Bajocian coral reefs from Lorraine is of low to moderate diversity with platy and massive growth forms prevailing. It is clearly dominated by the genus *Isastrea* (up to 70%); additional taxa are *Kobyastrea*, *Periseris*, and the branching forms *Stylosmilia*, *Thecosmilia*, and *Dendraraea*. A similar facies situation is documented from southern Germany (Kandern, Upper Rhine Valley), where in the Upper Bajocian small mid-shelf coral patch reefs with *?Isastrea*, *?Thamnasteria*, and *Cladophyllia* developed within ooid–bioclastic bars presum-

ably not far from the eastern margin of the Burgundy platform (Ernst, 1991). In northern Switzerland (Aargau area) at least one Bajocian platform-margin coral reef is described by Wullschlegel (1966). Bajocian biostromes and meadows composed mainly of massive reef corals are known also from Moutier (Jura of Bern) and the valley “Val de Travers” near Neuchâtel (J. Geister, personal communication, 2000).

Despite the predominantly siliciclastic development of the Middle Jurassic succession in Germany, coral reef facies are known not only from the Upper Rhine Valley (see above) but also from Franconia (southeastern Germany). Low-relief coral meadows and patches developed in the early Bajocian. Besides relatively low-diversity structures dominated by solitary corals (*Montlivaltia*), moderately diverse coral patches and meadows occurred. The latter are composed mainly of colonial corals (*Thamnasteria*, *Dimorphastrea*, *Isastrea*, *Latimeandra*, *Thecosmilia*). Today, the reefs are situated within a restricted area of 5–6 km east–west and 1.5 km north–south (Schmidtill, 1951).

Bajocian coral-dominated facies also occur in southern France (Ile de Crémieu) and include coral biostromes bearing siliceous sponges, with thicknesses of about 15 meters. The reefs are characterized by framestones, bindstones, and bafflestone fabrics. The fauna is of moderate diversity and comprises 10 coral genera. Remarkably, boring lithophagid bivalves are quite abundant on nonreefal hardgrounds, but they rarely affected the reef-building fauna within the reef facies of Lorraine and Luxembourg (Lathuilière, 1982). Although still existent, coral facies on the eastern margin of the Paris Basin became more restricted in the Late Bajocian. In the earliest Bathonian biostromal units occurred which are extremely rich in *Chomatoseris*, a solitary mobile coral (Gill and Coates, 1977; Geister and Lathuilière, 1991). Bathonian coral reefs are also known from southern France (Barre de Cuers, Provence), where small coral patch reefs up to 4 m in height associated with bryozoans and bivalves developed (Beauvais, 1972; Arnaud et al., 1982).

Middle Jurassic reef facies are also known from the Swiss and French Alps within the allochthonous nappe units of the “Préalpes Romandes”. The upper Aalenian “calcaire rosé coralligène” of the “Nappe de Préalpes Médiannes” is characterized by biotrititic and oolitic, massive to crudely bedded limestones with stromatoporoid coral boundstones. In the so-called *Mytilus* beds, coral reefs developed during the ?Callovian with coral biostromes, composed of a moderate-diversity to high-diversity “Kimmeridgian-type” coral fauna (e.g., *Adelocoenia*, *Stylina*, *Diplocoenia*, *Latomeandra*, *Ovalastrea*), partly dominated by branching forms (*Latomeandra*) (Renz, 1935; Beauvais, 1975). The shallow-water platform development of the “Préalpes Médiannes” is related mainly to the Briançonnais high within the Penninic Ocean (Septfontaine and Lombard, 1976). Beauvais and Negus (1975) and Beauvais (1985) mentioned coral reefs from the Middle Jurassic (Middle Bathonian) of England (“Fairford coral beds”). Although situated in fairly high paleolatitudes (37° N), these reefs are composed of a highly diverse coral fauna associated with molluscs, echinoderms, brachiopods, and serpulids. Remarkably, these reefs are rich in binding organisms, such as encrusting corals, stromatoporoids, and algae, and reveal considerable amounts of bioclastic debris.

In the external Subbeticum of Spain, the existence of a Middle Jurassic (Bajocian–Bathonian) shallow-water platform associated with coral bioherms as well as oolitic and oncolitic lagoonal limestones was stated by Molina et al. (1984). Middle Jurassic coral reefs also existed in the carbonate platform developments of southern Portugal (Praia da Mareta) (e.g., Rocha, 1976) and Romania (Draganescu and Beauvais, 1985). If of high-energy character these inner ramp coral reefs mostly represent the coral-

debris sand type. Widespread are low-energy bafflestones and framestones in protected or slightly deeper positions. The Romanian reefs, Bathonian in age, developed under a constant siliclastic input, allowing only for the growth of generally small, short-lived coral faunas within three distinct, successive assemblages. Remarkably, corals grew especially in tranquil muddy inner-platform environments, whereas exposed, agitated platform settings showed only subordinate coral growth (Draganescu and Beauvais, 1985).

In Poland (Balin), Middle Jurassic (Late Bajocian–Early Callovian) marly coral meadows presumably developed in somewhat deeper-water environments, judging by the occurrence of predominantly wedge-shaped and plate-shaped microsolenid corals (*Dimorphastrea*, *Dimorpharaea*). The moderately diverse coral fauna is additionally composed of *Latiphyllia*, *Thamnosseris*, and *Montlivaltia* (Beauvais, 1972).

In the eastern part of the northern Tethys shelf, besides the Polish and Romanian localities, reefs are also reported from Ukraine and Iran. The Ukraine localities (Shchebetovka, Sudak) partly represent large shelf-margin reefs of Late Callovian age with a high-diversity coral fauna additionally composed of red algae (solenoporacean, including rhodolites), microbolites, and calcareous sponges. Reefs at the Shchebetovka locality are characterized by a lumpy, cavernous, and partly recrystallized fabric with large coral and algal nodules. Cryptobiotic crinoids are fairly common. Generally, reefs accumulated to 50 up to 200 meters thickness with lateral extents reaching more than 100 meters (Mikhailova, 1968; Klikushin, 1996). Iranian reefs are also dominated mainly by corals and developed in a platform-margin position (Kuh-E-Birk) and as shallow-ramp to deep-ramp reefs (Qal'eh Dokhtar). The platform-margin bioherms with cumulative thicknesses up to 100 meters and lateral extents of more than 100 meters exhibit a moderate-diversity fauna composed mainly of corals (e.g., *Thamnasteria*) and red algae. The reefs at Qal'eh Dokhtar occurred in the so-called "middle siltstone member" of the Qal'eh Dokhtar formation and comprise shallow-ramp nonrigid coral–calcareous sponge patch reefs, up to 8 m thick, and small, deep-ramp microbolite patch reefs, only 1 m thick. The shallow-ramp reefs reveal a dense but relatively low-diversity coral fauna (e.g., *Epistreptophyllum*, *Microsolena*, *Comoseris*, *Actinastrea*, *Stylina*) together with calcareous sponges (e.g., *Eudea*, *Cylindroporella*) and bivalves (oysters, limids, pectinids). Further characteristics are the dominance of branching coral morphologies and a high mud content. The reef-bearing carbonate strata developed during a transgressive pulse on an overall storm-influenced siliclastic ramp system (Flügel, 1966; Schairer et al., 2000).

Baratov (1976) mentioned Bajocian "reef-like" coral-bearing limestones (Mamazairskaya and Chakobaiskaya formations) intercalated in an overall plant-rich continental succession from Tadzhikistan. In the easternmost part of the northern Tethys margin, transitional to the Western Pacific realm, reefs are documented from Thailand. The reefs include biostromes dominantly composed of corals, red algae, coralline demosponges, foraminifera, and microbial crusts (Bassoulet, 1986).

Southern Tethys Margin: Hungary, Morocco, Tunisia, Israel, Egypt, Oman, Saudi-Arabia, India, Madagascar.—On the southern Tethys shelf, reef domains were largely restricted to stable shelves in the direct vicinity of the Gondwana mainland. During the Middle Jurassic, no true siliceous sponge reefs developed on the southern Tethys shelf, except within the Bajocian to Callovian succession of southern Hungary, which most likely was part of the southern Tethys margin (Pisera, 1993) and siliceous sponge meadows in the Bathonian–Callovian Patcham Formation from northwestern India (Kachchh basin; Fürsich et al., 1994b). Coral reefs, however,

were widespread along the southern Tethys margin. Within the Morocco domain, reefs occurred from Aalenian to mid-Bajocian time in the course of the second platform development, after the Sinemurian to Domesian platform has been drowned and covered with pelagic sediments (Dresnay, 1979; Warme, 1988). The moderate-diversity reefs included shelf-margin reefs (Jebel Mechkakour, Jebel Klakh), atoll-like pinnacle structures (Jebel Assameur), and shallow intraplatform buildups (Dresnay, 1971; R.G. Stanley, 1981) with thicknesses of 10 to 100 meters and lateral extents of 20 to more than 100 meters. The fauna is composed mainly of scleractinian corals, red algae, coralline sponges, bryozoans, and bivalves. In Tunisia, shallow-water coral reef facies still occurred in the Callovian, representing bioherms with up to 20 meters cumulative thickness and a lateral extent of 20 to 100 meters. Colonial corals, bivalves, and rare stromatoporoids are the main constituents (Busson, 1965). Coral colonies are generally of small size, most probably because of the restricted intrashelf shallow-marine environment (Beauvais, 1985).

Other reef domains existed farther east, comprising Israel, Oman, Egypt, and Saudi Arabia. Although situated close to the paleoequator, Callovian reefs in Saudi Arabia are of low diversity, forming relatively small patch reefs with thicknesses of up to 15 meters and lateral extents of up to 50 meters as well as low-relief biostromes. Reefs do not constitute a major barrier-reef system, but rather a series of isolated bioherms and biostromes within an extensive sheet of pure limestone (20–40 m thick) stretching for more than 1000 km along strike in central Saudi Arabia (e.g., Al Majma'ah; El Asa'ad, 1989). In Oman, the existence of Middle Jurassic shelf-margin reefs can be only assumed from coral-bearing calcirudites and megabreccia forming a base-of-slope apron along a block-faulted platform margin (Watts and Blome, 1990). Reefal facies in Egypt (Maghara Massif) refer to relatively thick, mainly Callovian coral biostromes extending laterally for up to 100 meters. The reefs, of moderate diversity, developed in a shallow intraplatform setting (Farang, 1959; Alloiteau and Farang, 1964; Beauvais, 1985). Besides reefal units composed of colonial reef corals like *Thamnasteria*, *Chomatoseris*, and *Meandראה*, biostromes with dominance of solitary corals (*Montlivaltia*) also exist (Farang, 1959).

Although Middle Jurassic reefs along the southern Tethys margin were built mostly by corals, Middle to Upper Callovian reefs in southern Israel (Makhtesh Gadol) are exceptionally characterized by the dominance of coralline demosponges. These reefs formed low-relief patch reefs and thickets within a shallow, fairly open, low-energy environment. The reef fauna is composed mainly of monospecific aggregations of branching and massive stromatoporoids (*Promillepora*, *Shuqraia*, *Parastromatopora*, *Actostroma*). Reefs in more agitated areas, associated with oolitic shoals, are composed of domal stromatoporoids (*Dehornella*, *Promillepora*) and somewhat smaller coral heads (Wood, 1999). The reef occurrences in India grew within a pericratonic rift basin at the western margin of the Indian plate. Shallow marine conditions became established in the Bajocian and persisted into the Early Cretaceous. Because sedimentation was characterized predominantly by terrigenous fine-grained and coarse-grained siliclastics, carbonates are rare and reefs developed only within two levels representing the acme of Jurassic coral reef development in the Kachchh basin. However, general conditions were still unsuitable for intensive coral growth. The first level is formed by Upper Bathonian–Lower Callovian coral meadows with a high-diversity coral fauna (*Microsolena amorpho*–*Montlivaltia frustriformis* association), interfingering with bioclastic wackestones. Massive and flat morphotypes are prevalent. Corals successfully colonized a soft to firm substrate in a low-energy, possibly poorly lit environment with a moderate sedimentation

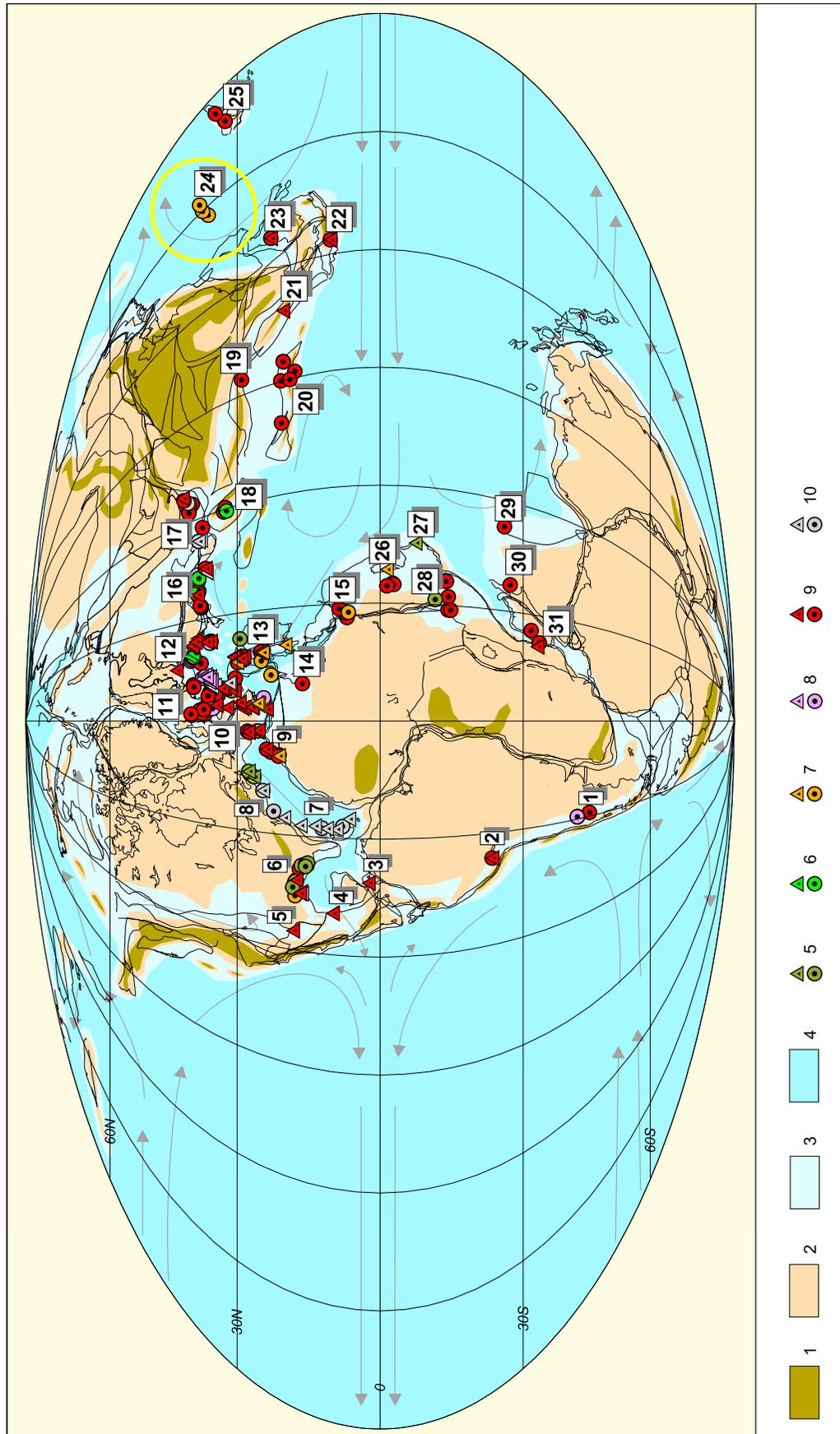


FIG. 4.—Global distribution of Callovian to lower Tithonian reefs, indicating probable current systems and dominant reef biota. 1, mountains; 2, land; 3, shelf; 4, deep water; dominant biota: 5, microbes; 6, algae; 7, coralline sponges; 8, siliceous sponges; 9, corals; 10 others/unknown; circles: Callovian–Oxfordian reefs, Triangles: Kimmeridgian–early Tithonian reefs; reef sites (numbers in rectangles): 1, Neuquén Basin, Argentina; 2, Peru; 3, northern Colombia; 4, eastern Mexico; 5, Chihuahua, Mexico; 6, northeastern Florida to southern Texas; 7, Atlantic margin of eastern U.S.A.; 8, off Nova Scotia, Atlantic; 9, Morocco; 10, Portugal and Spain; 11, England; 12, Central Europe to Black Sea; 13, southern Europe; 14, Tunisia; 15, Egypt, Israel, and Lebanon; 16, Crimea, Ukraine to Caucasus, Russia; 17, Turkmenia, Uzbekistan, Tadzhikistan; 18, Iran; 19, Denchin, Tibet; 20, southern Tibet; 21, Klu Tho, Thailand; 22, Sumatra, Indonesia 23, Sarawak, Borneo, Malaysia; 24, Japan (yellow circle indicates the uncertain paleo-position); 25, Sakhalin, Russia (paleo-position hypothetical); 26, Saudi Arabia; 27, Oman; 28, Somalia, Ethiopia, and Yemen; 29, Karakorun; 30, Kachchh, India; 31, southern Tanzania and southwestern Madagascar. Map provided by Wolfgang Kiessling.

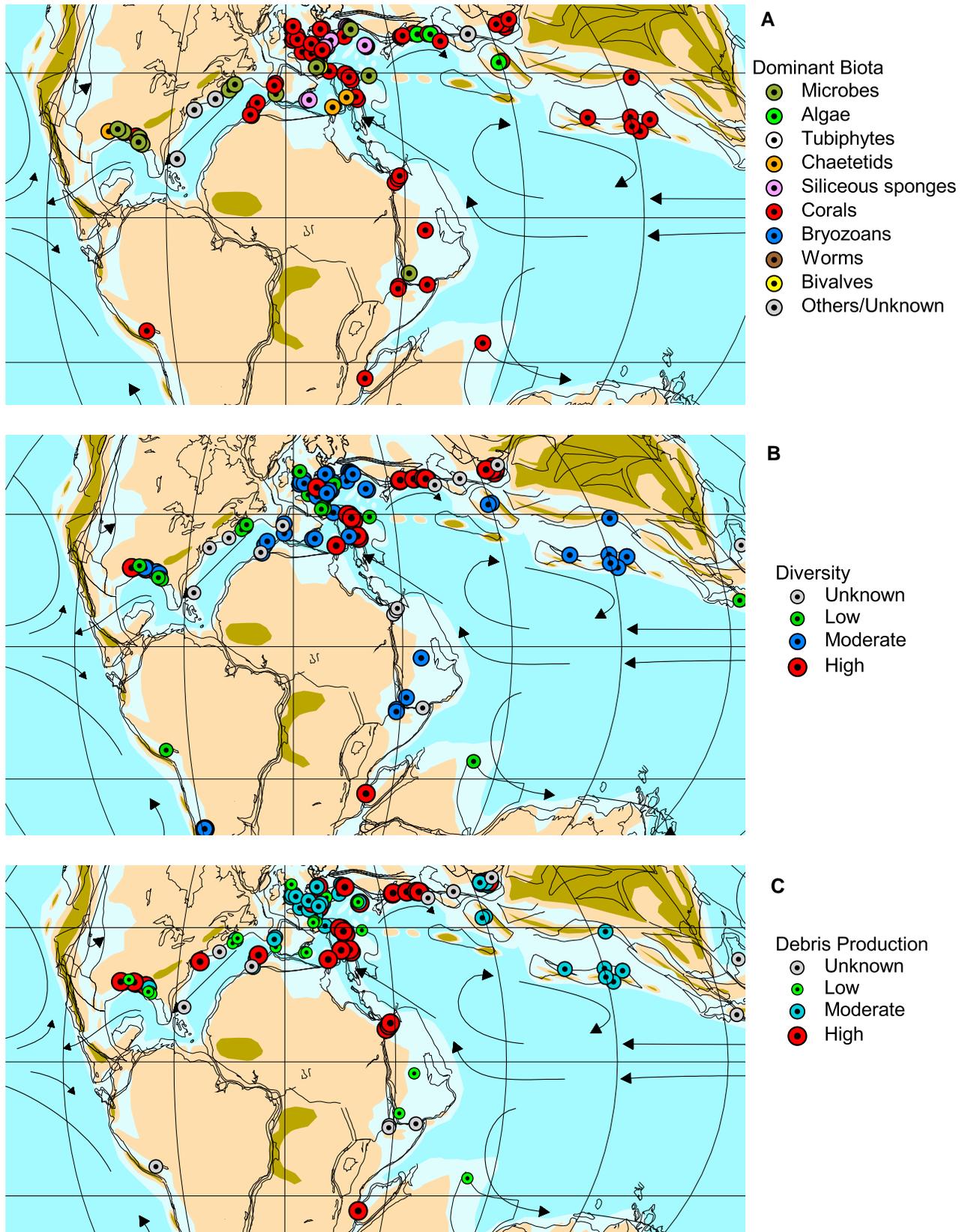


FIG. 5.—Detail of Oxfordian reef distribution and circulation pattern between the Caribbean and Tibet for A) dominant reef biota, B) diversities, and C) debris production.

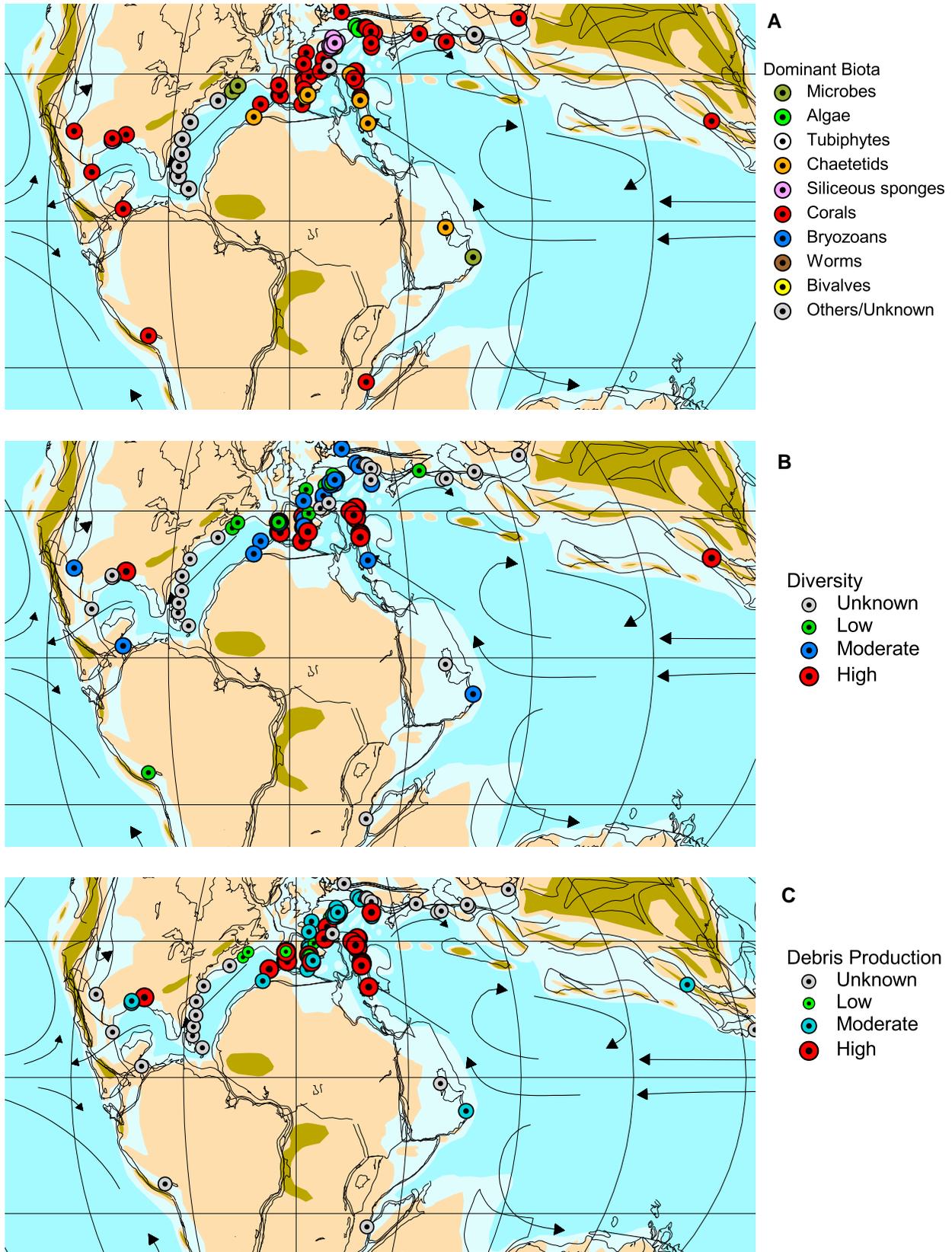


FIG. 6.—Detail of Kimmeridgian reef distribution and circulation pattern between the Caribbean and Tibet for A) dominant reef biota, B) diversities, and C) debris production.

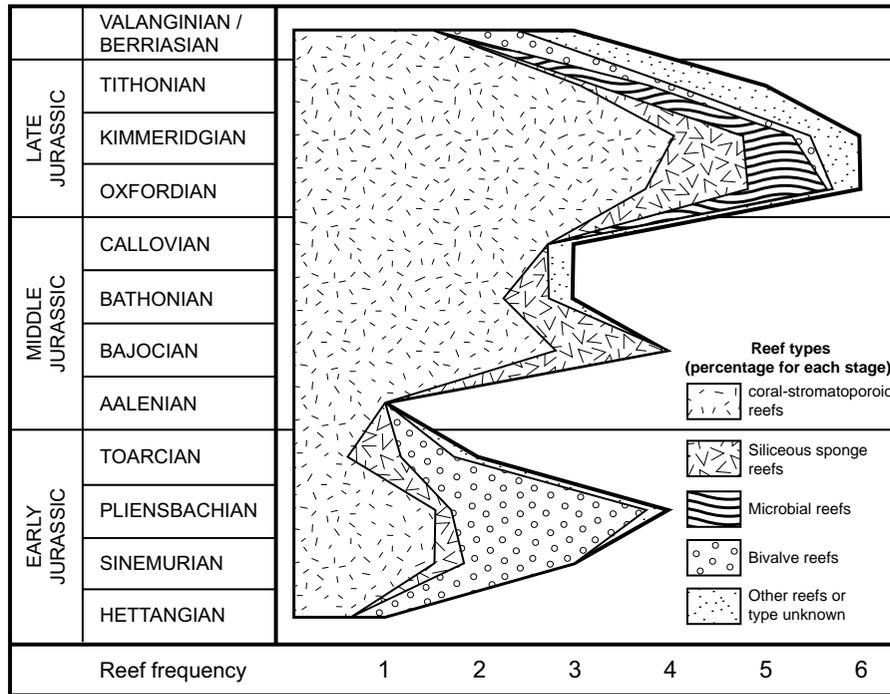


FIG. 7.—Fluctuations in the abundance of Jurassic reef types through time. Frequency of reefs and intensity of reef growth are classified into six categories considering the number of records and the geographical distribution: 1, Extremely rare (very few records, regionally very restricted); 2, very rare (few records, regionally restricted); 3, rare (some records but occurring in different regions); 4, common (common records, regionally expanded); 5, abundant (many records, regionally widely expanded); 6, very abundant (abundant records, regionally widely expanded). Reef types are also indicated in five categories, each stage representing 100 percent.

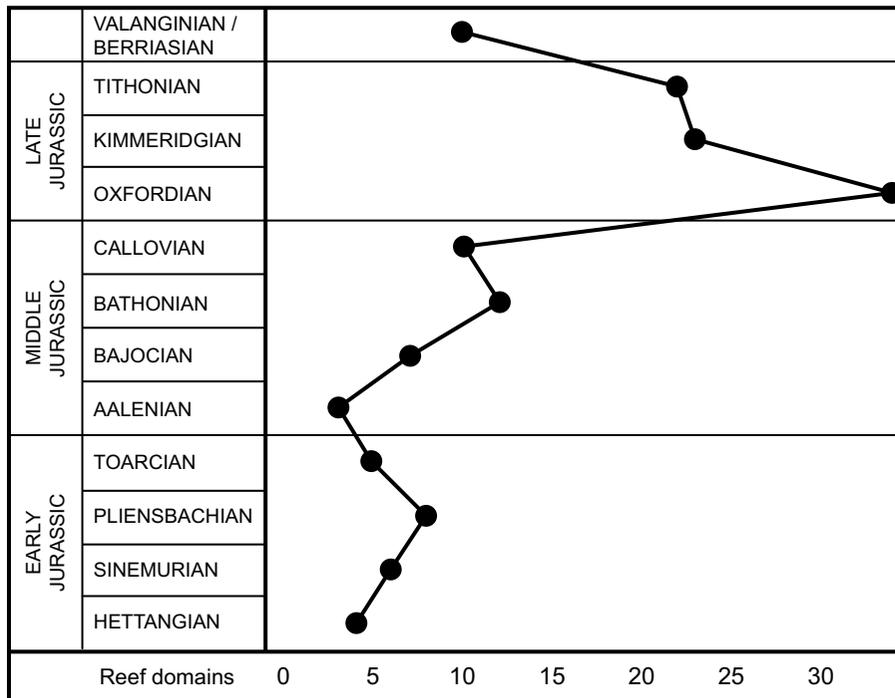


FIG. 8.—Reef growth intensity exemplified by the number of Jurassic reef domains per stage. Reef domains are geographically limited regions yielding a large number of reefs. Note that the number of reef domains must not necessarily coincide with reef abundance (cf. Fig. 7).

rate. The second level comprises a Callovian low-diversity coral bed dominated by *Amphiastrea piriformis*. *A. piriformis* is considered to have tolerated elevated sedimentation rates, intermittently mobile substrates, and fluctuating salinity (Fürsich et al., 1994b; cf. Yin et al., 1995). The Madagascar reefs (Ankotoboka) developed in the Bathonian and Callovian across a narrow embayment at the platform margin or as shallow intraplatform structures. The Bathonian, partly atoll-like reefs with a cumulative thickness of more than 100 meters and lateral extents of more than 500 meters belong to the largest Middle Jurassic buildups worldwide. Collignon (1959) stated a reef belt length of more than 10 km and compared the Madagascar reef system with the modern Great Barrier Reef off northeastern Australia. The reefs exhibit a rich coral fauna of moderate diversity (e.g., *Stylina*, *Microsolena*, *Collignonastraea*, *Isastrea*, *Diplocoenia*) partly dominated by branching morphotypes (Alloiteau, 1958; Collignon, 1959; Beauvais, 1985). Middle Jurassic (Callovian) reefs of Somalia, located in a transitional position between India and Madagascar in respect to paleolatitudes, were characterized by a moderately diverse coral fauna. The relatively small biostromal reef bodies grew in a marginal marine coastal setting on a siliciclastic shelf (Latham, 1929; Barnes, 1976). Besides reef domains from the circum-Tethyan margin, Middle Jurassic reefs are also known from Tibet, which was part of the Lhasa plate forming an isolated terrane within the eastern Tethyan Ocean. Tibetan reefs developed as shallow-water low-relief biostromes in intraplatform environments. The moderately diverse fauna, composed mainly of branching corals and bivalves, reveals affinities to the fauna of Kachchh in northwestern India (Liao, 1982).

North Atlantic and Pacific Realm: U.S. West Coast and East Coast, Chile.—Our knowledge of Middle Jurassic reefs from the North Atlantic realm stems from only a few localities off eastern North America, in contrast to the extensive shallow reef-bearing platform development in the Late Jurassic, which extended from the southwestern Grand Banks to Florida (Eliuk, 1989). The subordinate occurrence of reefs is due mainly to the Middle Jurassic early rift-basin stage with predominantly nonmarine or pre-oceanic marine sedimentary infill, tectonically disturbed during the continental breakup (cf. Ryan and Miller, 1981; Eliuk, 1989). The onset of carbonate deposition took place not before the Middle Bathonian, and carbonate sedimentation was again interrupted during the Callovian transgression, when mainly marine shale was deposited (Jansa and Wade, 1975; Jansa, 1981). Within this Middle Bathonian “carbonate deposition window” a platform with a later, mostly eroded, shallow-water barrier reef complex developed, today located beneath Georges Bank (Ryan and Miller, 1981). Exposed at today’s surface is only the Lusitanian Basin of west-central Portugal, which provides the case example for Atlantic marginal basins. In the large carbonate ramp systems of the Bajocian–Bathonian local coral (Ruguet-Perrot, 1961) and siliceous sponge facies (M. Klingel, personal communication, 1998) occurred, but it was only during the Late Jurassic, as in the U.S. east coast example, that extensive shallow-water reef development took place (e.g., Leinfelder, 1994a; Nose, 1995). In the Eastern Pacific realm, two reef domains are reported from the western American margin. The Chilean reef domain, located in relatively high paleolatitudes in the southern hemisphere, includes lower to middle Bajocian patch and fringing reefs within an intrashelf, partly siliciclastic setting (Cerro Jaspe, Quebrada Guatacondo, Cerro Azabache). Owing to the active continental-margin situation, reefs and carbonate deposition are limited and are characterized by relatively short-lived environments suitable for coral growth. Moreover, contemporaneous volcanism temporarily led to the death of growing coral meadows (Prinz, 1991). The low-

relief, mud-rich reef structures are composed almost exclusively of corals with a low to moderate diversity (*Actinastrea*, *Isastrea*, *Microphyllia*, *Latomeandra*) partly associated with some mollusks and echinoid remains. Baffling morphotypes prevail. The corals are frequently bored by lithophagid bivalves (Hillebrandt et al., 1986; Prinz, 1986, 1991). At the western margin of North America, Middle Jurassic reefs were widespread from Alaska down to California. Many of these reefs are situated on exotic terranes, and some of them may not have been locked at the western North American margin during the Middle Jurassic. However, at least some “reef-bearing” terranes were fairly close to the North American craton, and many reef sites also developed in the Western Interior embayment (Stanley and Beauvais, 1990). In Middle Bajocian time, Pittsburg Landing (Idaho) was part of the Wallowa terrane, situated close enough to the North American craton for faunal exchange with the Western Interior embayment. Reefs developed as high-energy biostromal units in a shallow intraplatform setting. The contemporaneous reef belt extended for approximately 40 km. Autochthonous reef facies occurred in laterally restricted lenses 1–3 meters thick. The low-diversity coral fauna (only two taxa: *Thecomeandra*, *Coenastraea*), embedded in wackestones to packstones, occur close to the top of a series of volcanic conglomerates within a transgressive marine sequence. Besides the heavily bored corals (“*Lithophaga*”), rare gastropods and abundant bivalves occurred (Stanley and Beauvais, 1990).

Late Jurassic Reef Pattern (Figs. 4–7)

General Distribution and Characteristics.—

Oxfordian.—Reefs were widespread in Middle and Late Oxfordian times (Figs. 4, 5). As for the Early Oxfordian, there are no precisely dated reef records in the database. Apparently, no larger reefs existed in the Early Oxfordian, but only nonreefal benthic communities or very small initial patch reefs. It has to be added, however, that the Early Oxfordian was a time of nondeposition in most areas and is therefore often represented by a hiatus. From Middle Oxfordian times on, coral reefs were widely distributed in shallow-water settings of the northern Tethys realm, the corals often being associated with stromatoporoids. Microsolonid coral reefs were clearly restricted to slightly deeper settings. Siliceous sponge reefs were common in deeper shelf settings, extending from Portugal to Spain, France, southern Germany, Poland, and Romania to the Caucasus. A special feature of the North Atlantic is the high microbolite percentage in the reefs in the Gulf Coast region, which might hint at partly steepened platform margins (Leinfelder, 1992, 1994a). Morocco and Portugal are mainly characterized by the occurrence of coral reefs and mounds. Compared to the northern Tethys, reefs in the southern Tethys were not very abundant and restricted to certain areas. Large coral–stromatoporoid barrier reefs developed on the Apulia–Adria polygon. Near the paleoequator, conditions for reef growth were apparently quite unfavorable, so that only a few small coral reefs are found there. The only high-latitude reefs in the Oxfordian are found in the Pacific realm. These reefs may have a high diversity, being dominated mostly by corals. In Japan, stromatoporoids are abundant; in Argentina, coral reefs occur in the same reef belt as siliceous sponge reefs. These are the only occurrences of siliceous sponge reefs outside Europe, apart from the sponges (mostly coral–sponge limestones) that occur along the North American Atlantic coast.

Kimmeridgian.—In the Kimmeridgian (Figs. 4, 6), the northern Tethys underwent a fundamental change from siliceous sponge

facies to coral facies. The only exception to this supraregional development is the southern German reef domain, where siliceous sponge–microbial mud mounds reached their maximum distribution ever. A variety of reef types occurred in the North Atlantic, including sponge reefs (the only occurrences outside Europe), mixed sponge–coral reefs, and bivalve reefs, reflecting mainly bathymetric control. On the southern Tethyan margin, reefs were scarce. Stromatoporoid–coral reefs continued to grow on the Apulia–Adria polygon, but apart from that, only some small- to medium-size coral–stromatoporoid reefs are found near the paleoequator. No Kimmeridgian reefs are recorded from the Pacific realm. High-latitude reefs are totally absent in the Kimmeridgian.

Tithonian.—Reef distribution in Tithonian times (Fig. 4) appears scattered compared to the Oxfordian–Kimmeridgian. On the northern Tethyan shelf, the rest of the formerly widely distributed siliceous sponge facies grades into shallow-water coral facies. Some special reef types such as *Paradiceras* bivalve biostromes occur, heralding the importance of bivalves as reef builders in the Cretaceous. Only scattered occurrences are reported from the North Atlantic, ranging from coral–oyster to coral–sponge reefs. The same heterogeneous pattern occurs in the southern Tethys, where stromatoporoids and corals were once again the most prominent reef builders; siliceous sponges still occurred in northern Africa, partly together with rudists. As in Oxfordian times, high-latitude reefs are found only in the Pacific realm. Whereas the highly diverse stromatoporoid–coral reefs of Japan do not differ significantly from low-latitude reef types, the bivalve-rich coral reefs of Argentina may reflect somewhat special conditions but certainly still indicate warm water.

Late Jurassic (Undifferentiated, Stage Unknown).—In the northern Tethys, several coral-dominated reefs, which can be dated only as Late Jurassic, are recorded from Tibet. As for the southern Tethys, nothing new is added to the trends already indicated above. The coral–bivalve reefs of Sakhalin formed on the isolated North Japan plate in the middle of the Pacific.

Berriasian to Early Valanginian.—Compared to Late Jurassic times, reefs were extremely scarce in the earliest Cretaceous; high-latitude reefs are not known. On the northern Tethys shelf, corals occurred together with typical Cretaceous reef builders such as rudists and coralline algae. A similar situation existed in the Atlantic, apart from the special occurrence of siliceous sponges. From the southern Tethys, only a stromatoporoid reef is reported. No true reefs but only bivalve banks are described from the Pacific.

Biota.—

Coral Reefs.—Some basic coral morphotypes can be distinguished: massive (e.g., *Isastrea*), branching (e.g., *Thamnasteria*), and platy (e.g., microsolenid) corals. Other framebuilders associated or even dominating in the coral facies were red algae (mainly solenoporaceans), stromatoporoids, chaetetids, and calcisponges. The so-called “spongiomorphids” of some authors actually represent microsolenid corals in most cases (e.g., Hüssner, 1985) or calcareous sponges (e.g., Benke et al., 1981; Kano, 1988). Microbes may have acted as framebuilders (massive growth forms), bafflers (dendroid growth form), or binders (microbial crusts). In any case they were essential for the development of a genuine reef framework. Therefore, pure coral reefs were mostly mere high-energy debris piles or low-energy marly meadows.

Siliceous Sponge and Microbolite Reefs.—Siliceous sponges (hexactinellids and lithistid demosponges) are perhaps the most characteristic reef builders of the Late Jurassic. In most cases, they were associated with microbolites, which were of paramount importance for the development of siliceous sponge reefs; without them, the sponges could form only sponge meadows or biostromes (Leinfelder et al., 1993b). Pure microbolite reefs reflect special settings unfavorable for other reef-building organisms, such as dysoxic conditions (Leinfelder et al., 1993b). The problematic encruster *Tubiphytes morronensis* (interpreted as a sessile foraminifer by Schmid, 1995) was common in both coral and sponge reefs, but in rare cases it could even form independent reefs.

Other Reef Types.—Apart from these large two groups of reef types, which make up the majority of Late Jurassic reefs, there were some additional special reef types. In restricted lagoons, serpulid reefs reflect an environment with frequent changes of salinity and temperature. Oyster patch reefs represent brackish conditions. In Late Jurassic to Early Cretaceous times, bivalves such as *Paradiceras* formed biostromes in some places. From deep basins, two examples of methane-derived cold seep mound occurrences are reported, dominated by special bivalves (see below for details).

Oxfordian—Northern Tethys Realm: Spain, England, Northwestern France, French Jura, Lorraine, French Western Alps, Corsica–Sardinia, Swiss Jura–Swiss Alps, Southern Germany, Northern Germany, Poland, Romania, Ukraine, Caucasus, Iran, Uzbekistan–Turkmenistan, Tadzhikistan.—

In the Oxfordian, reefs occurred all along the northern Tethys shelf (Fig. 4). At the western margin of the northern Tethys, in eastern Spain (PL 24–26° N), siliceous sponge–microbolite biostromes and microbolite-stabilized mud mounds were widespread in the deeper parts of the Celtiberian Basin (Krautter, 1995, 1997) as well as in the Prebetic area, where sponge biostromes probably started to grow as early as in the late Early Oxfordian (*cordatum* subzone; Behmel, 1970). Coral facies did not occur. Farther north, in England (PL 37–40° N), no sponge facies but only coral facies developed during the Oxfordian. In shallow platform-margin settings, moderately diverse coral biostromes grew under partly high local turbidity, but still with up to 80% of corals in growth position (Talbot, 1972; Ali, 1977; Negus and Beauvais, 1979; Beauvais, 1985). Branching and massive growth forms prevailed in this environment. The deeper platform margin was the place where platy microsolenid coral biostromes grew (Ali, 1983; Insalaco, 1996a, 1999). The diversity of these biostromes is low to moderate; bioerosion is documented by bivalve and “worm” borings. In other places, cyanobacteria also participated in the formation of low-diversity shallow-water coral biostromes and bioherms, producing volumetrically significant peloidal crusts, which are also important for reservoir quality (Sun and Wright, 1989; Sun et al., 1992). Vertical successions could occur from laminar *Thamnasteria* and digitate *Thecosmilia* to robust branching *Thecosmilia* and massive *Isastrea*. The northernmost site in this domain is represented by an effectively monospecific *Thamnasteria* reef (Insalaco, 1999). A similar reef type is found in northwestern France (PL 35° N) with an almost monospecific coral mud bank consisting of *Thamnasteria dendroidea* (Beauvais et al., 1974; Beauvais, 1985).

Towards the east, in the French Jura and Lorraine reef domains (PL 33–36° N), coral reef facies was especially widespread during Oxfordian times on the shallow-water carbonate platform

of the eastern Paris Basin. In shallow water, corals formed mounds with moderate diversity (Beauvais, 1964; Beauvais et al., 1980; Beauvais, 1985; Geister and Lathuilière, 1991; Lathuilière et al., 1994). Together with other secondary framebuilders, true reefs such as coral–solenoporacean reefs (Geister and Lathuilière, 1991) and microbial–coral reefs (Bertling and Insalaco, 1998) could emerge. In somewhat deeper settings of the epeiric sea, microsolenid coral biostromes occurred (Rutten and Jansonius, 1956; Menot, 1980; Insalaco, 1996a). The same reef domain stretches into the extant Upper Rhine Valley, where microsolenid coral biostromes grade vertically into coral–microbial biostromes, dominated by branched corals such as *Stylosmilia* and *Aplosmilia* (Kabelac, 1955; Laternser, 2000). This coral facies is continued in the Swiss Jura (see below). Farther south, in the deeper-water environment of the French Jura, a siliceous sponge–microbial mud-mound belt extended over 50 km (Gaillard, 1983). A special reef setting existed in the reef domain of the French Western Alps (PL 31–32° N), where reefs grew in a deep basin of probably some 100 m water depth (e.g., Elmi, 1990). This special, probably aphotic environment allowed only small microbolite mounds to develop (Dromart, 1989). So-called pseudobioherms with a thickness of up to 15 m, extending over 30 km, could be shown by Gaillard et al. (1992) to represent cold-seep mounds dominated by lucinid bivalves (see also Peckmann et al., 1999). Even farther south, on Corsica (PL 30° N), a coral facies occurred in a shallow intraplatform setting, dominated by the baffler guild (Beauvais and Rieuf, 1981). A low-diversity shallow-water coral fauna associated with nerineans and diceratids occurs at the eastern coast of Sardinia (Russo and Sirna, 1986).

The Swiss Jura (PL 35° N) was clearly dominated by coral facies. As in the French Jura, secondary framebuilders helped the corals to form a reef framework; still these reefs produced a lot of debris. Coral–microbolite reefs with a thickness of 20–40 m as well as coral–solenoporacean reefs are described by Pümpin (1965; see also Bolliger and Burri, 1970, and Dupraz and Strasser, 1999). Interestingly, in some of these reefs abundant siliceous sponges occurred in underlying biostromes, mirroring a shallowing-upward trend. Microsolenid coral biostromes can be found in somewhat deeper settings compared to the coral reef facies (Insalaco, 1996a), similar to the French and English examples. In both the Swiss and the French Jura, the deeper shelf was widely colonized by siliceous sponge biostromes and partly also microbial sponge mud mounds in the “Birmenstorfer Schichten” (Gaillard, 1983). In the Swiss Alps, this facies is continued in the Helvetian nappes (Kugler, 1987). In southern Germany (PL 36–38° N), numerous siliceous sponge–microbial mounds extended all along the deeper shelf (Gwinner, 1976; Flügel and Steiger, 1981; Geyer and Gwinner, 1984; Schweizer, 1987; Lang, 1989; Meyer and Schmidt-Kaler, 1990; Selg and Wagenplast, 1990; Hammes, 1995; Nose et al., 1997). The mounds grew in a deeper shelf environment with micritic sedimentation and produced hardly any debris; mound thickness reaches from 1 m to over 100 m. Today, siliceous sponge–microbial mounds are found in numerous outcrops, but there are also subsurface occurrences beneath the Tertiary Molasse Basin (Huber, 1987). In Late Jurassic times, the reef domain of northern Germany (PL 40° N) was separated from the southern German domain by the Rhenish–Bohemian Massif. Despite this paleogeographic situation and the relatively high latitude, at least some of these reefs can be characterized as “Tethyan type” (Helm and Schülke, 1999). Where corals occurred without other framebuilders or binders, they formed debris-rich coral mounds (Bertling, 1993a) or small patch reefs, dominated by massive corals such as *Thamnasteria* (Bertling, 1993a, 1997b). Other corals could occur together with microbolites, which may act as framebuilders and binders to form coral–

microbolite patch reefs of 4 m thickness (Helm and Schülke, 1998). The siliceous sponge facies belt of southern Germany continued farther east to Poland (PL 40° N) where it reached a lateral extent of 110 km. Very similar to southern Germany, numerous siliceous sponge–microbial mounds are situated in this deeper shelf environment (Trammer, 1989; Matyszkiewicz and Felisiak, 1992). Well-developed stromatolite structures are a typical feature in some of these mounds (Matyszkiewicz, 1993). In the central Polish Uplands, moderately to highly diverse coral assemblages including branching and massive growth forms occur (Roniewicz and Roniewicz, 1971). The reefs of Romania (PL 36° N) belong to the Moesia polygon, which can be considered as part of the northern Tethyan shelf. Coral reefs and coral–red algal reefs are found in shallow-water settings, being of moderate diversity with plenty of debris and large numbers of boring bivalves (Turnšek and Barbulescu, 1969; Roniewicz, 1976; Herrmann, 1996). *Solenopora* and micro-encrusters such as *Lithocodium* are secondary frame builders (Herrmann, 1996). In deeper ramp settings, siliceous sponge–microbial mud mounds developed, similar to the sponge facies in southern Germany or Poland. A very particular reef type found nowhere else, however, are atoll-shaped mounds up to 30 m thick formed by microbes and siliceous sponges (Herrmann, 1996). A coral–red algal reef of probable Oxfordian to Kimmeridgian age is known only from exotic limestone blocks (Pana and Nimigean, 1981). Reef facies continued farther east in the Ukraine (belonging to the Eurasian plate; PL 38° N). Coral reefs in a shallow shelf-margin setting, exhibiting moderate diversity, extended for over 50 km (Baraboshkin et al., 1996). In the Upper Jurassic of Crimea, coral reefs occur intercalated in coastal conglomerates (Dobrovolskaya et al., 1983). Situated near to the Ukraine but belonging to the Scythian plate was the reef domain of the Caucasus (PL 38–39° N), including Armenia. Highly diverse red algal–coral reefs with calcisponges are found on the shallow margins of huge carbonate platforms with a bulk thickness of up to over 1000 m (Mikhailova, 1968; Bendukidze, 1977, 1980; Papoyan, 1977; Makkevich et al., 1980). Another reef type in the same setting is represented by a coral–bryozoan–microbolite reef, zoned with a cyanobacterial bindstone at the base and masses of almost monospecific corals at the top (Kuznetsov, 1993). Siliceous sponge–microbial mud mounds with a thickness of 60–80 m and an extent of 50 km are once more found in deeper water (Kuznetsov, 1993). The Iran reef domain (PL 32° N) lay on an isolated plate (the Lut Block) that was incorporated into the northern Tethyan shelf. Here, thick and very broad algal reefs with corals exhibited a moderate diversity (Flügel, 1966). Some distance farther north, being part of the Eurasian plate, lay the reef domain of Uzbekistan–Turkmenistan (PL 40–41° N). With few exceptions (see Preobrazhensky, 1995a), these reefs are subsurface occurrences, being the host rocks of a giant gas field. A first subgroup of reefs in this domain was formed by shallow shelf-margin barrier reefs, extending over 160 km. These shelf-margin reefs had a high diversity and can be characterized as coral–red algal reefs and coral–stromatoporoid dominated reefs (Saidusmanov, 1974; Iljin, 1981; Fortunatova et al., 1986; Khusanov, 1987). The thickness of these reefs reaches from 100 to 250 m, the data probably representing bulk platform thickness, owing to the lack of detailed outcrop data. The second subgroup of reefs represents isolated intrabasin dome-like coral–stromatoporoid reefs, which also grew in shallow water and had a high diversity. These structures may reach a thickness of up to 265 m. Cyanobacteria were found only as a minor constituent in one reef (Iljin, 1981; Fortunatova et al., 1986). Considering the scarcity of binding and encrusting organisms, it is not astonishing that most of the reefs in this domain produced large amounts of debris. This reef domain so far represents the only known ex-

ample of continuous reef development across the Callovian–Oxfordian boundary (Iljin, 1981; Preobrazhensky, 1995a). Reefs in Tadjikistan (PL 36° N) are mentioned by Akhmedova (1987) and Baratov (1976) but not further described.

Oxfordian—North Atlantic Realm: Southeastern U.S.A., Eastern Canada, Atlantic, Morocco, Algarve (Portugal), Lusitanian Basin (Portugal).—

During the Late Jurassic, the North Atlantic was still a narrow proto-ocean with a connection to the Tethys. In the western part of the North Atlantic, reefs occur in the subsurface along the Gulf Coast (Texas, Arkansas, Louisiana, Mississippi, Alabama, Florida), forming the reef domain of southeastern U.S.A. (PL 15–18° N). Small but broad microbial reefs in a shallow marginal marine setting are described by McGraw (1984). Microbial stromatolite mounds with a lateral extent of 5–10 km are described from the shallow platform margin; at least partly, reef-building macroorganisms such as corals, lithistid sponges, calcisponges, and red algae occur (Baria et al., 1982; Harris and Crevello, 1983; Crevello and Harris, 1984). A very special reef type occurs in a core from Alabama, where small microbial deeper-water mounds are formed by previously unknown enigmatic tubular organisms; probably, these microbioherms or “microherms” (up to 0.3 m thick) combined with micritic sediment to form a decameter-scale mound (Kopaska-Merkel and Schmid, 1999). Another reef type is characterized by a framework formed by *Tubiphytes* and stromatolitic cyanobacteria, but some corals (mainly *Actinastrea*) and stromatoporoids are also present (Crevello and Harris, 1984; Crevello et al., 1985). Similar reefs and mounds, which are dominated by corals, are rich in debris (Baria et al., 1982; Crevello and Harris, 1984), thus confirming the important binding function of microbial crusts lacking here. The same is true for highly diverse stromatoporoid-dominated reefs with corals, the reef framework being formed by stromatoporoids and corals with only some microencrusters (Cregg and Ahr, 1983). To summarize, the high microbial content of these shallow-water reefs seems quite unusual compared with all the other Oxfordian reefs. Because all reef descriptions from the Gulf Coast have to rely on subsurface data only, however, it cannot be ruled out that reef-building macroorganisms are just underrepresented in the cores. Compared with outcrop data of probably similar reefs in the Lusitanian Basin (Leinfelder, 1992; see below), the high microbolite content might hint at partly steepened platform margins. A situation somewhat similar to that of the Gulf Coast prevailed along the shelf of eastern Canada (Nova Scotia; PL 27° N). Microbial mud mounds and thrombolite mounds have been described from both inner-ramp and outer-ramp settings (Ellis et al., 1985; Jansa et al., 1989). A microbial mound with a moderately diverse fauna consisting of *Tubiphytes*, corals, stromatoporoids, and sponges has also been described (Jansa et al., 1982; Pratt and Jansa, 1989). In the Atlantic domain (PL 24° N), not much is known from a very thick (platform up to 500 m), mostly eroded supposed barrier reef (Ryan and Miller, 1981). At the eastern coast of the North Atlantic realm, in Morocco (PL 21–23° N), up to 100-m-thick coral reefs with stromatoporoids and oysters occurred in a 30 km belt (Park, 1983; Hüßner, 1985). Small but up to 100 m broad coral-stromatoporoid reefs were described by Park (1983). A special reef type is found in Algarve (southern Portugal; PL 25° N), where a microbial mound of 30 m thickness, consisting of thrombolites with abundant *Tubiphytes* and serpulids, grew in a deeper outer-ramp settings. Because siliceous sponges are restricted to certain levels, the pure thrombolites probably formed under dysoxic conditions (Leinfelder et al., 1993a; Leinfelder et al., 1993b). In the Lusitanian Basin of central Portugal (PL 27–28° N), coral reefs

developed in the Late Oxfordian. Shallow coral reefs on a platform margin as well as various knoll reefs in various slope positions were described by Ellis et al. (1990) and Leinfelder (1994a). A large coral mound with a thickness of > 100 m, rich in binding microbes and micrite, started in a deeper setting, and after a shallowing phase later drowned, the initial drowning stage being characterized by *Tubiphytes* wackestones (subsurface data; Ellis et al., 1990; Leinfelder, 1994a).

Oxfordian—Southern Tethys Realm: Czechia–Slovakia, Southern Alps, Slovenia, Montenegro, Tunisia, Israel–Lebanon, Saudi Arabia, Eastern Africa, Madagascar.—

Situated halfway between the northern and southern Tethys, coral reefs developed in Czechia on an isolated microplate (PL 38° N). These coral patch reefs, extending over 20 km, are dominated by bafflers and are of moderate diversity (Eliás and Eliášová, 1986). Coral-calcisponge reefs of moderate diversity are recorded from the western Carpathians of Slovakia by Misík (1979). In the Southern Alps domain of the Apulia–Adria polygon (PL 29–30° N), large coral-stromatoporoid reefs with a thickness of over 100 m formed at the shallow shelf margin, extending as far as 150 km (Bosellini et al., 1981; Winterer and Bosellini, 1981; Sartorio et al., 1987; Geyer, 1993). These reefs exhibit a high diversity and yielded large amounts of debris. Similar reefs are found on the same plate, in Slovenia (PL 28–29° N), spanning the Oxfordian–Kimmeridgian. These large coral-stromatoporoid reefs with a thickness of over 100 m formed a reef belt 140 km long across Slovenia, extending to Italy and Croatia–Albania. The reefs were well zoned with fore-reef and back-reef zones and produced large amounts of debris. The central reef zone was up to 15 km wide with a parastromatoporoid zone on the back-reef side and an actinostromiid zone on the seaward side (Milan, 1969; Turnšek et al., 1981; Bosellini et al., 1981; Winterer and Bosellini, 1981). Some distance farther south, in Montenegro (PL 25° N), a coral-stromatoporoid reef developed that is obviously equivalent to the Slovenian reefs (Turnšek, 1968). Calcareous demosponge bioherms up to 10 m thick are reported from Tunisia (PL 21° N) (Gautret and Cuif, 1989). Near the paleo-equator, on the Arabian plate, coral reefs developed in the Israel–Lebanon domain (PL 7–8° N). Not much is known about these reefs, which are thinner than 10 m but wider than 500 m in a reef belt up to 150 km in length (May, 1991). Towards the south, in Saudi Arabia (PL 3° S), small coral patches of medium diversity, dominated by bafflers, formed a belt up to 200 km long (El Asa’ad, 1991). In Ethiopia, belonging to the reef domain of Eastern Africa (PL 14° S), a medium-diversity association of corals and stromatoporoids has been described by Wells (1943), with an Oxfordian age suggested. The only reef on the southern Tethyan margin that was positioned relatively far south is found in Madagascar (PL 33° S). This shallow-water coral reef formed at the shelf margin, is thicker than 100 m, and is of high diversity and rich in debris (Pichon, 1969; Beauvais, 1985).

Oxfordian—Pacific Realm: Japan, Argentina.—

During the Oxfordian, it was only in the Pacific realm that reefs developed in high latitudes. In Japan (South Japan plate; PL ?35–50° N, see Fig. 4), small stromatoporoid reefs with corals, algae, and microbes extended over 200 km; a stromatoporoid reef forming an atoll is also known (Tamura, 1961; Mori, 1963). These reefs are of moderate to high diversity. In Argentina (Patagonia terrane; PL 42–45° S), corals could form small reefs with a low-diversity fauna and quite some algae or microbes (Morsch, 1989; Matheos and Morsch, 1990). In spite of the relatively high latitude, however, a

highly diverse coral reef which is less than 10 meters thick but which extended for more than 500 m was described by Legarreta (1991). It is dominated by corals of the constructor guild; red algae, encrusting platy algae, sponges, and serpulid worms are also present. Borings and debris were important. This reef belonged to a reef belt 10 km long. In the same reef belt, siliceous sponge-microbolite mounds with a thickness of 5–10 m are found (Legarreta, 1991). Corals and some calcisponges occurred also.

Kimmeridgian—Northern Tethys Realm: Celtiberian Basin (Spain), Southern France, French Jura, Southern Germany, Poland, Ukraine, Caucasus, Turkmenistan, Tadzhikistan, Southeast Asia (Thailand–Sumatra).—

In contrast to the Oxfordian situation, the Kimmeridgian reefs of the Celtiberian Basin (Spain; PL 27–29° N) are clearly dominated by corals. In the Celtiberian Range, numerous well-exposed coral-microbolite reefs with a thickness of 10 m extend over 30 km (Leinfelder et al., 1993b; Nose, 1995; Baumgärtner and Reyle, 1995). These reefs grew in a mid-ramp setting (below fair-weather wave base); thrombolites dominate at the base, but corals, chaetetids, and stromatopores increase upsection (Nose, 1995; Schmid, 1996; Badenas and Aurell, 1996). In siliciclastic inner-ramp settings, conditions were unfavorable for microbial crusts, so that sandy coral-solenoporacean-chaetetid-debris reefs with a thickness of 10 m developed in this special environment (Nose, 1995). In marly mid-ramp to outer-ramp settings, marly coral biostromes with mainly massive morphotypes associated with a thin coral-stromatoporoid thrombolite bank occurred (Geyer, 1965; Nose, 1995). In the northern part of the Celtiberian Basin, moderately to highly diverse coral-calcisponge bioherms with a thickness of up to 60 m developed in shallow intraplatform settings, forming a series of laterally prograding buildups (Benke et al., 1981; Mas et al., 1997; Benito et al., 1998). In southern France (PL 29–32° N), low-diversity coral biostromes grew in shallow intraplatform settings (Carozzi et al., 1972), whereas microsolenid coral bioherms formed at the platform margin (Bodeur, 1976, 1980). In the Aquitanian Basin, several coral-microbolite reefs with a thickness of 10 m developed in close proximity, so that reef caves could develop where thrombolites joined at the reef base (Lafuste, 1959; Taylor and Palmer, 1994; Schmid, 1996). These reefs are quite similar to the microbolite-rich reefs from Spain (see above). In the French Jura (PL 33° N), moderately diverse coral barrier reefs developed at the shallow platform margin, the coral fauna being dominated by *Stylina*, *Adelocoenia*, *Cryptocoenia*, and *Ovalastraea* (Bernier and Gaillard, 1980; Beauvais and Bernier, 1981; Bernier, 1984; Beauvais, 1985). In another part of the shallow platform margin, a debris-rich coral-stromatoporoid-microbolite reef was found (Fookes, 1995). In contrast to the other northern Tethyan reef domains, siliceous sponge facies persisted throughout the Kimmeridgian in the deeper shelf environment of southern Germany (PL 36–38° N). In southwestern Germany (Swabian Alb), the siliceous sponge-microbolite mounds of up to 100 m thickness formed a continuous belt 140 km long (Gwinner, 1976; Geyer and Gwinner, 1984; Schorr and Koch, 1985; Wirsing, 1988; Selg and Wagenplast, 1990; Leinfelder et al., 1994). The problematic sessile foraminifer *Tubiphytes morronensis* (see Schmid, 1995) became an important constituent of these reefs and could even form *Tubiphytes* mounds with a thickness of over 100 m, being associated with serpulids and bryozoans (Pomoni-Papaioannou et al., 1989). In southeastern Germany (Franconian Alb), siliceous sponge-microbolite mounds occur in several irregular belts up to 50 km long (Meyer, 1975, 1977; Brachert, 1986; Meyer and Schmidt-Kaler, 1990; Flügel et al., 1992; Koch et al., 1994). It was only at the end of Kimmeridgian times that shallow-water areas emerged because of extensive reef growth, allowing

the development of coral mounds, rising above a mixed siliceous sponge-coral facies (see Tithonian for details) (Paulsen, 1964; Meyer, 1977). In the Kimmeridgian of Poland (PL 40° N), the Oxfordian siliceous sponge facies was totally replaced by shallow-water red algal-coral reefs with dominating solenoporaceans and mainly solitary corals (Golonka, 1970, 1978; Roniewicz and Roniewicz, 1971). The northernmost European in-place occurrence of coral facies is reported by Roniewicz (1977), describing a medium-diversity association from an outcrop in Pomerania. Branching corals (*Thamnasteria concinna*) from erratic boulders that are found on the south Baltic coast are described by Roniewicz (1984). In the Ukraine (PL 39–40° N), coral facies were more extensive than in the Oxfordian. Coral reefs and coral-red algal reefs with a thickness of partly more than 100 m extend over 250 km (Kalik, 1986; Izotova and Popadyuk, 1993, 1996). Many of these reefs are known from subsurface data only, being of some importance as host rocks for gas. In the Upper Jurassic of Crimea, coral reefs occur intercalated in coastal conglomerates (Dobrovolskaya et al., 1983). Large coral-calcisponge reefs show a continuous development since Oxfordian times in the Caucasus (PL 39–40° N) (Bendukidze, 1977, 1980; Makkevich et al., 1980). The Kimmeridgian-Tithonian reefal shelf margin in Turkmenistan (PL 38° N) reaches a thickness of up to 300 m, being known from both outcrops and subsurface data (Grachevskiy et al., 1982; Pätz and Kulke, 1994; Preobrazhensky, 1995a). Reefs in Tadzhikistan (PL 37° N) are mentioned by Akhmedova (1987) and Baratov (1976) but not described further. In the far east, on the Burma-Malaya plate, lay the reef domain of southeast Asia (Thailand-Sumatra; PL 20° N). From Thailand, a coral mound with a highly diverse coral fauna, including meter-size coral colonies, associated with microbes and bryozoans was described by Beauvais et al. (1985) and Fontaine (1986). (For the Sumatra reefs, see "Late Jurassic undifferentiated".)

Kimmeridgian—North Atlantic Realm: Colombia, Mexico, Southeastern U.S.A., Atlantic, Algarve (Portugal), Lusitanian Basin (Portugal).—

Near the paleoequator, in Colombia (PL 2° N), medium-diversity coral biostromes are dominated by branching baffling scleractinians (J. Geister, personal communication, 2000; see also Geyer, 1973). Farther north, in Mexico (PL 7° N), shallow intraplatform coral patch reefs were reported by Wilson (1990); corals are also mentioned by Wells (1946) and Reyeros de Castillo (1974). In the southeastern U.S.A. (PL 16–17° N), Kimmeridgian-Tithonian reefs are restricted to Texas (subsurface data). Positioned within the shelf area, moderately large coral reefs are found in a belt 130 km long (Montgomery et al., 1999a; Montgomery et al., 1999b). These reefs are rich in microbial crusts and occasionally contain siliceous sponges. A different reef type is found near the shelf margin on a distally steepened ramp, where cement-rich coral-sponge-microbial boundstones are of high reservoir quality (Montgomery et al., 1999a; Montgomery et al., 1999b). Some of these reefs may show a pronounced deepening trend from corals to siliceous sponges and microbolites at the top, capped by shallow-water facies. Shirley (1998) mentions another reef representing a producing gas reservoir (seismic data only). From the Atlantic U.S. coast (PL 21–22° N), very debris-rich coral barrier reefs are reported by Gamboa et al. (1985) and F.O. Meyer (1989). In the Algarve (southern Portugal, PL 24–25° N), different reef types occurred in a narrow zone, because of a steep ramp gradient. In the shallow inner ramp, highly diverse coral-stromatoporoid reefs 100 m thick are found, rich in debris (Leinfelder et al., 1993a). Lithistid sponges at the base reflect the shallowing-upward trend. In slightly deeper settings below fair-weather wave base, the vertical development spans from lithistid biostromes to microsolenid boundstones at the

top (Leinfelder et al., 1993a). In the western Algarve, large coral biostromes with bivalves thrived in a coastal siliciclastic shelf environment (Rosendahl, 1985). Numerous different reef types occur in the Lusitanian Basin of central Portugal (PL 25–28° N). Oyster patch reefs developed in brackish lagoons and bays (Werner, 1986; Fürsich and Werner, 1986). Reef types occurring on coastal siliciclastic shelves include low-diversity *Calamophylliopsis* biostromes, coral–bivalve biostromes (Werner, 1986), small coral patch reefs dominated by *Amphiastrea* (Ellis et al., 1990), and coralline sponge–coral biostromes (Fürsich and Werner, 1991). In some cases, highly diverse coral–microbolite patch reefs could emerge despite intermittent influx of terrigenous mud and silt (Nose, 1995). In Ota, a modern-type coral–microbolite barrier reef dominated by massive corals (*Thamnasteria*, *Microsolena*, *Stylina*) developed on a shallow platform margin, large amounts of debris being bound by microbial crusts with *Tubiphytes* and other encrusting organisms or exported down the steep margin (Leinfelder, 1992, 1994a). Where microbial crusts were lacking, coral–chaetetid–debris reefs occurred in high-energy environments (Nose, 1995; Leinfelder et al., 1993a). Mixed coral–siliceous sponge reefs grew in deeper mid-ramp settings (Andrade, 1934; Leinfelder, 1994a). The outer ramp is represented by microbolite–coral–siliceous sponge biostromes with crinoids (Leinfelder et al., 1993a; Nose, 1995).

Kimmeridgian—Southern Tethys Realm: Northern Calcareous Alps, Southern Alps, Bosnia–Montenegro, Algeria, Saudi Arabia, Oman, Eastern Africa.—

In the Northern Calcareous Alps, which were part of the Apulia–Adria polygon (PL 31° N), debris-rich coral–stromatoporoid–chaetetid reefs grew in shallow intra-platform environments (Fenninger, 1967; Fenninger and Holzer, 1972; Steiger and Wurm, 1980). The stromatoporoid *Ellipsactinia* is the dominant reef builder in some other reefs (Steiger and Wurm, 1980). In the Southern Alps (PL 30° N), reef growth continued on the Friuli platform, where a stromatoporoid–coral reef (with an *Ellipsactinia* facies at the deeper shelf margin) reached a thickness of more than 500 m and extended over 200 km (Winterer and Bosellini, 1981; Bosellini et al., 1981). On the same plate, in Bosnia–Montenegro (PL 25° N), highly diverse, debris-rich stromatoporoid–coral reefs occurred (Gorican, 1994; Turnšek, 1968), which are also documented as allochthonous reefal debris in Croatia (Milan, 1969). In Algeria (PL 24° N), two biostromes representing a highly diverse coral association are described by Caratini and Beauvais (1969). Near the paleoequator, some coral reefs are reported from the Arabian plate. In Saudi Arabia (PL 1° S), coral–stromatoporoid bioherms up to 30 m thick occur on a high-energy inner-ramp shoal (Sun et al., 1996). Farther south, in Oman (PL 7° S), small microbial coral–stromatoporoid mounds were described by Pratt and Smewing (1990). In Eastern Africa (PL 14° S), a low-diversity association of corals occurs in Tanzania (Weissermel, 1900; Dietrich, 1926). In Ethiopia, a low-diverse association of corals and stromatoporoids has been described by Zuffardi–Comerci (1932).

Kimmeridgian—Pacific Realm.—

No Kimmeridgian reefs are recorded from this realm.

Tithonian—Northern Tethys Realm: Southern France, England, Swiss Alps, Southern Germany, Northern Germany, Romania, Ukraine, the Caucasus.—

Tithonian reefs in southern France (PL 29° N) are represented only by the very special type of monospecific (*Neoteutloporella*) dasycladacean patch reefs (Bodeur, 1980, 1995, 1996). Another

peculiar reef type occurs in England (PL 35° N), where bivalve–solenoporacean–bryozoan patch reefs thrived in a shallow intraplatform setting (Fürsich et al., 1994a). Coral–sponge patch reefs from the Helvetian nappes of the Swiss Alps are mentioned briefly by Mohr and Funk (1995). In the Tithonian of southern Germany (PL 35–37° N), the siliceous sponge facies partly continued. Siliceous sponge–*Tubiphytes* reefs or almost monospecific *Tubiphytes* reefs with a thickness of 20–30 m occur in the Lower Tithonian (Trauth, 1986; Pomoni–Papaioannou et al., 1989). In other cases, a vertical reef development from siliceous sponge facies to mixed siliceous sponge–microsolenid coral facies to massive coral facies can be observed (Paulsen, 1964; Laternser, 2000), thus mirroring the general though nonlinear shallowing-upward trend. For the same time interval, coral–thrombolite reefs with abundant shell debris and bioerosion can be found (Barthel et al., 1971; Joachimski and Scheller, 1987; Flügel et al., 1993); these grew on elevations in shallow-water settings. In northern Germany (PL 38–39° N), a very special reef type is represented by serpulid worm and serpulid–stromatolite structures, extending over 5 km (ten Hove and van den Hurk, 1993). According to the authors, these reefs probably formed in a restricted lagoon with fluctuating salinities and temperatures. A similar setting has been assigned to a horizon of stromatolites whose cores are often made up of serpulid colonies (Merz–Preiß, 1997). These environmental interpretations are corroborated by the occurrence of the same reef type in a Holocene restricted lagoon from Tunisia (Davaud et al., 1994). From Romania (Moesia polygon, PL 23° N), a highly diverse, debris-rich coral–red algal reefal facies with dominating bafflers was described by Bucur (1978). A special Late Tithonian reef type is recorded from the Ukraine (PL 37° N) with *Paradiceras* bivalve biostromes which formed on a shallow shelf margin (Baraboshkin et al., 1996). In the Upper Jurassic of Crimea, coral reefs occur intercalated in coastal conglomerates (Dobrovol'skaya et al., 1983). In the Caucasus (PL 38° N), the coral-reef development described above continued into Early Tithonian times, the reefs being mostly dolomitized (Bendukidze, 1977, 1980; Makkevich et al., 1980; Kuznetsov, 1993). Within the backreef complex of these large barrier reefs, gold mineralization took place (Boiko, 2000).

Tithonian—North Atlantic Realm: Atlantic, Eastern Canada, Morocco, Lusitanian Basin (Portugal).—

In the Atlantic domain of the U.S. coast (PL 23° N), a thick, mostly eroded shelf-margin barrier reef was recorded by Ryan and Miller (1981). Offshore eastern Canada (PL 26° N), coral mounds more than 100 m thick with lithistid sponges and binding microbial crusts occur (Jansa et al., 1982; Pratt and Jansa, 1989), similar to those occurring in the same position during the Oxfordian. In Morocco (PL 21° N), shallow coral reefs with calcisponges, microbial crusts, and *Tubiphytes* are recorded only from reworked clasts (Steiger and Jansa, 1984). In the Lusitanian Basin of Portugal (PL 26° N), meter-size coral patch reefs, partly rich in oysters with additional calcisponges, stromatoporoids, and the red alga *Marinella lugeoni*, developed in a siliciclastic–carbonate setting. The patch reefs are dominated by massive corals such as *Amphiastrea piriformis*, whereas *Calamophylliopsis*, *Dermosmilia*, and *Actinastrea* prevailed in bafflestone areas (Geyer, 1955; Leinfelder, 1986, 1994a).

Tithonian—Southern Tethys Realm: Czechia, Lower Austria–Northern Calcareous Alps, Swiss Alps, Serbia–Montenegro, Southern Italy, Sicily, Tunisia, Yemen.—

The reef domain of Czechia (PL 37–38° N), today part of a tectonic nappe, is characterized by coral facies occurring at the

shallow shelf margin. Small coral–stromatoporoid mud mounds, rich in debris, were described by Eliás and Eliášová (1986, 1995). Besides small coral reefs, a large coral–red algal reef complex with a thickness of more than 100 m and abundant debris occurs also (Eliášová, 1981a, 1981b; Eliás and Eliášová, 1986). In the northern part of the Apulia–Adria polygon, representing Lower Austria (PL 29° N), a thick coral–stromatoporoid reef with high diversity was reported by Bachmayer and Flügel (1961). In the Northern Calcareous Alps (PL 31° N), stromatoporoid biostromes occurred in a lagoonal inner-platform setting (Darga and Schlagintweit, 1991). Massive coral reef limestones and stromatoporoid reefs have been reported but not further described from the Penninic nappes of the Swiss Alps (Weiss, 1949). Farther south on the same plate, in Serbia–Montenegro (PL 22–25° N), numerous debris-rich, highly diverse stromatoporoid–coral reefs developed at the shelf margin (Turnšek, 1968; Turnšek and Mihajlovic, 1971), continuing the trend from the Oxfordian and Kimmeridgian. In the western part of the same plate, in southern Italy (PL 23° N), a debris-rich coral–*Ellipsactinia* reef, more than 100 m thick, extended over 30 km, the corals being abundant on the reef flat and reef front, whereas the stromatoporoid *Ellipsactinia* occurs in the external margin zone (Mattavelli and Pavan, 1965; Morsilli and Bosellini, 1997). On the Sicily polygon (PL 20° N), low-diversity *Cayeuxia* (cyanobacterial) biolithites were found in a shallow intraplatform setting, surrounded by coralgall debris; corals and red algae formed debris-rich reefs at the shelf margin (Catalano et al., 1974). On the Northeast Africa plate, in Tunisia (PL 17° N), siliceous sponges were still important in Tithonian to Berriasian reefs. Small but up to 100 m broad siliceous sponge reefs with corals, bryozoans, and microbes developed on a broad inner ramp; the reef top is dominated by corals (Ouribane et al., 1996). On the inner platform, debris-rich red algal reef with rudists and lithistid sponges are found (Ouribane et al., 1996). Farther south, only one reef occurrence is reported from Yemen (PL 14° S), where microlite boulders form a bed 3 m thick (Howarth and Morris, 1998). In our view, however, because these boulders of presumed microbial origin contain only ammonites, their reefal nature has yet to be proven.

Tithonian—Pacific Realm: Japan, Argentina, Antarctica.—

On the South Japan plate, reefs occurred in paleolatitudes as high as 35–50° N (see Fig. 4). From a marginal-marine shelf with plenty of siliciclastic input, a 70–80 m thick stromatoporoid–coral mud mound with moderate diversity was described by Kano (1988) and Kano and Jiju (1995); bafflers dominated in this micrite-rich reef, whereas solenoporaceans were also important. The northernmost Tithonian reefs were debris-rich coral–stromatoporoid–chaetetid reefs with a high diversity; 28 scleractinian genera were described by Yabe and Sugiyama (1935). In the southern hemisphere, in Argentina (Patagonia) high-latitude reefs occurred at 55° S. These were small debris-rich coral–oyster reefs with thick branching corals, oysters, bivalves, and stromatoporoids (Ramos, 1978). The same author also described an atoll-type, shallow-water coral–stromatoporoid reef with bivalves, rich in debris. Both reef types are of moderate diversity. Even farther south, on the West Antarctic Peninsula (PL 70° S), cold-seep mud mounds 3 m thick are found in a deep basin (>200 m); the methane-seep limestone yields laminated crusts of probably bacterial origin, gastropods, and bivalves (Kelly et al., 1995). Apart from this site, cold-seep reefs have been reported only from the Bathonian to Oxfordian of the French Western Alps (Gaillard et al., 1992; Peckmann et al., 1999; see above).

Late Jurassic (Undifferentiated, Stage Unknown)—Northern Tethys Realm: Tibet, Southeast Asia (Thailand, Burma, Malaysia, Sumatra, Philippines).—

The reefs of the Tibet domain belong to the Lhasa plate (PL 29°); only one reef is positioned on the adjacent Qiang Tang plate (PL 29° N). The latter represents a baffler-dominated, medium-diversity coral reef of unknown type (Liao, 1982). Several similar reefs also occurred on the Lhasa plate, including coral–stromatoporoid biostromes or mounds with microbes, the corals partly showing affinities to European faunas (Liao, 1982; Yue and Liao, 1986; Liao and Xia, 1993).

From the Philippines and Sumatra, low-diversity faunas have been described by Beauvais (1983), the Philippines fauna being dominated by stromatoporoids. The Late Jurassic reefs of Sumatra are positioned on the Burma–Malaya plate, belonging to the domain of southeastern Asia (PL 18° N). These reefs, which are about 10 m thick and 3–4 km wide, were characterized as coral–calcsponge mud mounds by Beauvais (1989b) and Beauvais et al. (1989). The same is true for the buildups occurring in the frontier region between Thailand and Burma (Beauvais 1988a, 1988b). The coral limestones of Malaysia are also similar to the Sumatra examples (Beauvais 1990).

Late Jurassic Reefs (Undifferentiated, Stage Unknown)—Southern Tethys Realm: Swiss Alps, Sicily, Israel–Lebanon, Yemen–Somalia, Karakorum.—

From the Penninic nappes of the Swiss Alps, Oxfordian to Tithonian coral limestones and stromatoporoid reefs have been reported but not further described (Heinz and Isenschmid, 1988). On the northern Sicily polygon (PL 23° N), a thick coral–stromatoporoid reef developed at the shallow shelf margin, with intercalations of massive *Ellipsactinia*–coral–calcsponge framework (Crevello and Harris, 1984).

In the reef domain of Israel–Lebanon (PL 8° S), medium-size debris-rich coral reefs occurred in a belt 150 km long at the shelf or platform margin (Beydoun, 1977; May, 1991). The reef domain of Yemen–Somalia is positioned on the adjacent Arabian and Somalian Plates (11–14° S). Moderately diverse microbial mud mounds with corals and stromatoporoids were found in the shallow inner platform of Yemen (El-Anbaawy and Al-Thour, 1989). In Somalia, merely a single coral (*Stylina lortphilippsi*) has been recorded by Latham (1929).

Farther south, in the Karakorum domain on the India plate (PL 26° S), a low-diversity coral biostrome with mostly bafflers in marly matrix is described by Fantini-Sestini (1965).

Late Jurassic Reefs (Undifferentiated, Stage Unknown)—Pacific Realm: Sakhalin.—

The reefs of Sakhalin developed in the North Pacific on the isolated North Japan plate in a moderate paleolatitude (PL 33–35° N). Baffler-dominated coral–bivalve reefs grew on the shelf margin, extending over 300 km (Krasnov et al., 1975).

Berriasian—Northern Tethys Realm: Southern France, Swiss Alps, Hungary, Ukraine, Turkmenistan.—

Only very few reefs are found on the northern Tethyan shelf compared to Late Jurassic times. In southern France (PL 29° N), low-diversity *Monopleura* rudist clusters occur in a shallow intraplatform setting (Gili et al., 1995). In the Helvetic nappes of the Swiss Alps, small bioherms with corals and stromatoporoids are mentioned briefly by Mohr and Funk (1995). In Hungary, being

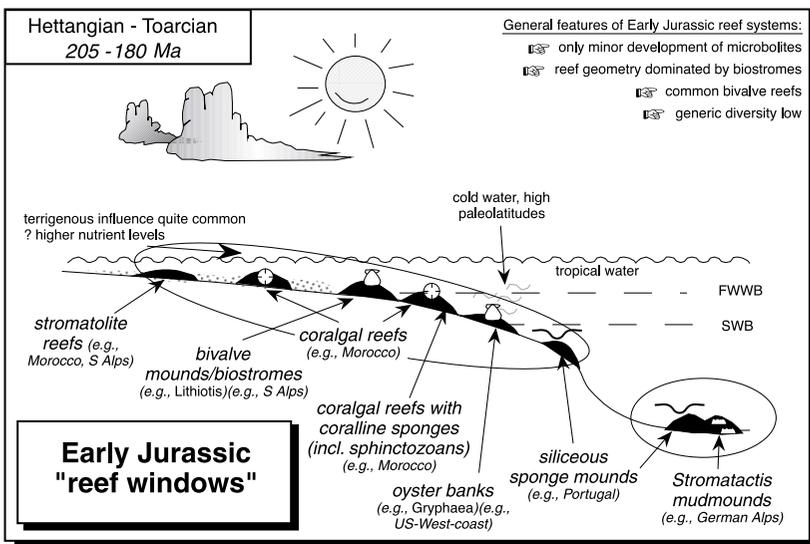
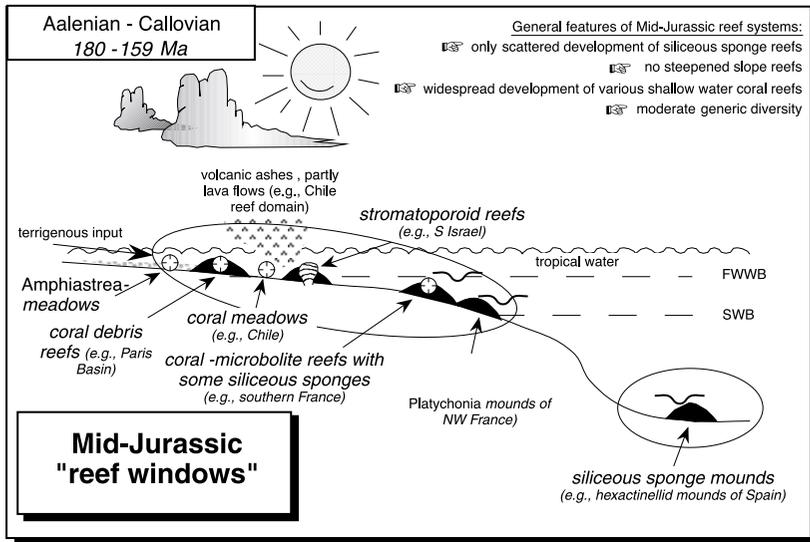
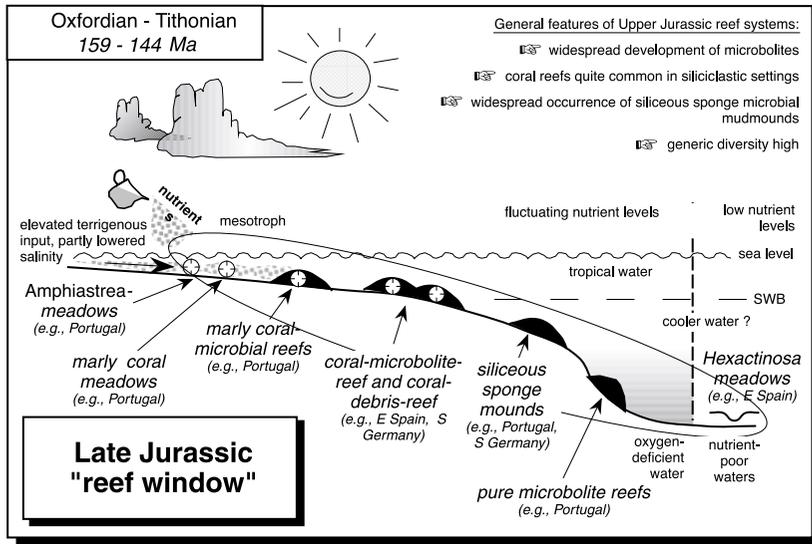


FIG. 9.—Jurassic “reef windows” change in the course of the Jurassic, owing to evolution and associated change of environmental capacities of reef organisms. See text for explanation. Late Jurassic “reef window” from Leinfelder and Nose (1999), modified. Basic data for Late Jurassic: e.g., Nose (1995); Leinfelder et al. (1996); Leinfelder (1993a); Schmid (1995); Krautter (1997); Leinfelder et al. (1993a); Leinfelder et al. (1993b); Middle Jurassic: e.g., Pandey and Fürsich (1993); Fürsich et al. (1994b); Deusch et al. (1991); Friebe (1995); Geister and Lathuilière (1991), Wood (1999); Early Jurassic: e.g., Mathur (1975), Göhner (1981), Poulton (1988), Duarte (1997), Scheibner and Reijmer (1999), Blomeier and Reijmer (1999).

part of the Dinarides polygon (PL 26° N), atoll-type coral–chaetetid–stromatoporoid buildups developed on volcanoes, associated with coralline algae, rudists, and ostreids (Császár, 1996; Császár and Turnšek, 1996). Farther east, in the Ukraine (Crimea peninsula, PL 37° N), corals of different morphotypes formed small bioherms in a shallow intraplatform setting (Arkadiev and Bugrova, 1999). In Turkmenistan (PL 38–39° N), shallow micritic coral biostromes are associated with mollusks and brachiopods (Bugrova, 1986; Preobrazhensky, 1995a, 1995b). The Kimmeridgian–Tithonian reefal shelf margin reaches a thickness of up to 300 m, being known from both outcrops and subsurface data (Grachevskiy et al., 1982; Pätz and Kulke, 1994; Preobrazhensky, 1995a, 1995b).

*Berriasian—North Atlantic Realm:
Bahamas, Texas, Atlantic.—*

Near the paleoequator, in the Bahamas domain (PL 7° N), debris-rich algal mounds with corals and rudists extended over 30 km in a shallow intraplatform setting (Freeman-Lynde et al., 1981). In Texas (PL 15° N), quite large and broad coral–stromatoporoid reefs with microbes exhibit a high diversity, with sponges being restricted to the fore-reef in this outer-ramp environment (Finneran et al., 1984; Scott, 1988). In the Atlantic domain of the U.S. east coast (PL 21–22° N), the barrier reefs of the Tithonian were followed in the Berriasian by a deep-marine fauna with hexactinellid sponges, partly under siliciclastic influence (Gamboa et al., 1985; Meyer, 1989).

Berriasian—Southern Tethys Realm: Montenegro.—

In the Montenegro part of the Apulia–Adria polygon (PL 23° N), the once extensive reefs of the Late Jurassic were reduced to a thick but reworked stromatoporoid debris reef of high diversity, being associated with chaetetids, *Tubiphytes*, and coralline algae (Gorican, 1994).

Berriasian—Pacific Realm: Western Canada.—

In two different terranes of western Canada (PL 37–38° N), *Buchia* bivalve banks and coquinas up to tens of meters thick are recorded by Poulton (1989a); true reefs, however, do not occur in the Pacific realm.

**PATTERN OF JURASSIC REEF DISTRIBUTION
THROUGH TIME AND SPACE: INTERPRETATION**

The main scope of this paper is to interpret temporal and spatial Jurassic reef patterns in order to deduce their major controlling factors. An earlier discussion of the temporal evolution of reefs throughout the Jurassic period was given by Leinfelder (1994b), who stressed the fact that the abundance of reefs has generally increased with time, although there are considerable differences in the trend between sponge reefs and coral reefs and differences between the northern and southern Tethys shelf. According to Leinfelder (1994b) tectonic setting and tectonic evolution as well as sea-level development exerted major controls on reef development. The PaleoReef database, together with the greatly increased number of Jurassic reef studies, allow corroboration of patterns hitherto deduced from qualitative data only, and to refine them to much greater detail.

We will attempt to demonstrate that both biological adaptation and evolution, and global environmental changes have had strong feedbacks on the evolution of reef patterns, and that Jurassic reef distribution was, to a great extent, governed by mechanisms different from modern reefs.

Biological and Evolutionary Control of Reef Patterns

Ecological Evolution and the “Reef Window”-Concept.—

Recently, Reitner (1998) introduced the concept of modularity in reef systems. According to Reitner, modules are defined as metabolic systems related to trophic, structural, and productive aspects. Taking up the modularity concept of Reitner (1998), Leinfelder and Nose (1999) focused on the development and distribution of reef-building modules (also termed reef-building blocks) through time. Reef-building blocks are modules responsible for biogenic or biogenically induced carbonate production within reefs. Generally, maximum modular complexity in ecological structure and carbonate productivity increases towards modern reefs. Except for the coralline red algae reef-building block, evolving major importance in reef construction not before the Late Cretaceous, all reef-forming modules present in modern reefs already existed in Jurassic times, although the metazoan photosymbiosis was still young. In any given time slice, however, not all reefs had the maximum potential modular complexity, as exemplified by the Jurassic reefs, comprising at least three intergrading basic reef types (coral reefs, siliceous sponge reefs, microbolite reefs), which differ in their modular complexity (Leinfelder and Nose, 1999).

Reef-building blocks together with the ecological demands and capabilities of reef organisms determine the actual character and the ecological position of the reefs. All potential reef environments of all reef types in a given time slice can be described and illustrated by one or more “reef windows”, i.e., the environmental spread in which organisms are capable of forming reefs (cf. James and Bourque, 1992; Leinfelder and Nose, 1999; Leinfelder, 2001).

Because reefs are biological constructions, nearly all parameters of reef patterns are biologically controlled at first hand. To name but a few, this is true of depth distribution, nutrient demands, substrate and sediment influx tolerance, or water temperature, all of which are determined by the demands and abilities of reef organisms involved. Tolerances of reef organisms along gradients at a given time interval define the general width of the “reef window”, and the threshold of opening and closing the “reef window” through time. A “reef window” may wax and wane or split into several coeval ones throughout Earth history, depending on the ecological evolution of reef organisms. In conclusion, actualistic concepts have to be critically tested with fossil reefs, because demands and abilities even of apparently similar reef organisms may have changed drastically in the course of evolution. A good example are scleractinian corals, many taxa of which apparently required more particulate nutrients during the Jurassic (Nose and Leinfelder, 1997; Leinfelder and Nose, 1999; Leinfelder, 2001). It is also the biology of organisms which determines how large a reef may be at a given time slice, whether it can grow up to high-energy levels to build up barrier reefs, or form mud mounds in deeper settings. Hence, the biology of reef organisms in a given interval determines in which general environmental setting reefs may develop.

Jurassic “Reef Windows” (Fig. 9).—

The Jurassic reef examples demonstrate that the “reef window” was relatively wide, especially in the Late Jurassic. This is mainly because of its transitional position. Many marginal, “stressed” reefs (reefs in siliciclastic settings, brackish-water reefs, various deep-shelf reefs, dysaerobic reefs) existed, owing to the widespread occurrence of the “conservative” reef organisms

(sponges, microbolites) together with the newly established adaptive strategies, particularly within corals. It was the time of change towards photic algal symbiosis in scleractinian corals, with corals thriving both in mesotrophic and in increasingly oligotrophic environments (Leinfelder et al., 1996; Nose and Leinfelder, 1997; Leinfelder, 2001).

According to the main reef-building organisms and their paleoecological demands, the Jurassic "window" of reef growth can be further differentiated into "reef windows" for the Early, Middle, and Late Jurassic (Fig. 9). Comparing the positions and structures of reef sites in all three epochs, some trends, differences, and similarities between Early, Middle, and Late Jurassic reef systems become visible.

- (1) The importance of benthic microbial communities in reef formation, forming rapidly lithifying, mainly thrombolitic microbial crusts, seems to have increased in the course of the Jurassic. This assumption is substantiated by the rare occurrence of true bioherms in the Early Jurassic, taking into account that microbial crusts are considered to be essential in the formation of reefs with a considerable positive relief (Leinfelder et al., 1993b).
- (2) Generally, three basic intergrading reef types existed throughout the Jurassic: (a) siliceous sponge reefs, (b) microbolite reefs, and (c) scleractinian coral reefs. However, the occurrence pattern and the detailed composition could differ considerably in the Early, Middle, and Late Jurassic. Because of the apparent lack of Lower and Middle Jurassic reefs at deeper slope settings, which were occupied by coral-siliceous sponge-microbial reefs during the Late Jurassic, there is a spatial gap in reef distribution, so that both the Early and the Middle Jurassic are best characterized by two coeval "reef windows". Moreover, some additional reef types developed only in either the Early, Middle, or Late Jurassic "reef windows". Low-diversity bivalve reefs formed by *Lithiotis* or other bivalve taxa are a typical feature of Early Jurassic reef systems, although oyster reefs are a common reef type also in very shallow Late Jurassic shelf settings. Pure stromatoporoid reefs from Slovenia (Turnšek, 1969) and southern Israel (Wood, 1999), or small solenoporacean patch reefs (northern Germany; Helm and Schülke, 1998) are to date known only from the Middle Jurassic or the Late Jurassic.
- (3) Many reef settings in all three epochs were influenced by fine siliciclastics. Because siliciclastic input is often combined with elevated particulate nutrient levels, this may reflect the greater importance of heterotrophic nutrition within scleractinian corals, as suggested by Nose and Leinfelder (1997).
- (4) Bivalve reefs in the Early Jurassic partly outcompeted scleractinian corals as reef-building organisms, possibly even in high-energy platform-margin environments (cf. Scheibner and Reijmer, 1999). Corals were still recovering from the setback at the end of the Triassic. Moreover, the reef-building potential of Early Jurassic scleractinians might have been lower compared with the large and thick-shelled bivalve communities. This assumption can be deduced from (a) the dominance of low-relief reef structures, (b) the still young and imperfect coral-zooxanthellae symbiosis, important for enhanced carbonate production (cf. Nose and Leinfelder, 1997; Leinfelder, 2001) and (c) the restricted availability of framebuilders among corals after the Triassic-Early Jurassic extinction (Leinfelder, 1994b).

Diversity Through Time (Fig. 18).—

Diversity is one of the key features of reef ecology. General change in diversity is used to demonstrate possible adaptations of reefs along latitudinal gradients (e.g., Grigg, 1982; Hopley, 1982; Hubbard, 1997; Paulay, 1997) but also to prove the frequent variation of physicochemical factors, such as sediment influx, nutrients, or light availability within reef domains at a local or regional scale (Greb et al., 1996, modern Panama; Nose, 1995; Nose and Leinfelder, 1997; Leinfelder et al., 1996, Jurassic). Also, diversity within a reef may reflect biological stress, such as diseases, or simply change intrinsically through time (the pioneer-diversification-dominance concept *sensu* Walker and Alberstadt, 1975). On a longer time scale, maximum (cumulative) diversity of reef-builder taxa of all reefs in a given time interval changes by general biological evolution punctuated by extinction events.

Data on diversity patterns of Jurassic reefs are not generally available and differ mostly in respect to evaluation method and terminology. The reef database summarizes the available data in three categories (low, medium, high), which allows for better comparison but is biased by the very different quality of the original data. Moreover, Jurassic corals are insufficiently defined and need taxonomic revision, so that the present comparisons of species numbers are of reduced relevance. Although Jurassic genera also are not always substantiated and their actual number is a matter of debate, it is believed that comparing numbers of genera through time gives a reasonable picture of Jurassic coral phylogeny and generic diversity (Leinfelder, 1994b). Additionally, the genus level is considered to be the most stable level of the present-day classification of corals (Lathuilière, 1996).

The Jurassic period was a time of worldwide reef proliferation, which was presumably linked to a complete reconfiguration of the global oceanic circulation (see below). However, corals suffered severe extinction at the Triassic-Jurassic boundary and therefore were extremely rare in the beginning of the Early Jurassic. Elmi (1987, 1990) mentions a small coral reef of Hettangian age in France, but it is still awaiting closer inspection and description. Besides this enigmatic Hettangian example, earliest coral reef occurrences are from the Sinemurian and are all situated on exotic terranes later accreted to the western margin of North America (Stanley and McRoberts, 1993), which was interpreted by Stanley and Beauvais (1994) and Stanley (1996) as an expression of long-term isolation of corals surviving from the Triassic on exotic islands in the paleo-Pacific. From the Pliensbachian, and particularly Toarcian, onwards, coral reefs become more common, and it is since that time that available coral taxa were sufficient to form variable types of coral reefs. Remarkably, among the earliest coral reefs in the Early Jurassic, some resemble relics of Middle Triassic buildups; the reef fauna is composed partly of few surviving Late Triassic coral taxa, together with coralline sponges including sphinctozoans (Beauvais, 1984, 1985; Leinfelder, 1994b). However, corals diversified rapidly during the late Early Jurassic (approx. 60 coral genera) and particularly during the Middle Jurassic (92 coral genera) (R.G. Stanley, 1981; G.D. Stanley, 1988; Beauvais, 1984, 1989a; Leinfelder, 1994b). It was in the Late Jurassic that the probable all-time global maximum of coral diversity occurred, with 150 genera recorded in the European Tethys and 51 in the Panthalassa ocean (Beauvais, 1989a; Leinfelder, 1994b; Veron, 1995).

Whereas the general increase in abundance of coral reefs is due not only to evolutionary radiation of corals (Leinfelder, 1994b), the coral fauna diversified and the development of specialized taxa such as very morphovaryable species or brackish-water specialists allowed the conquering of previously hostile

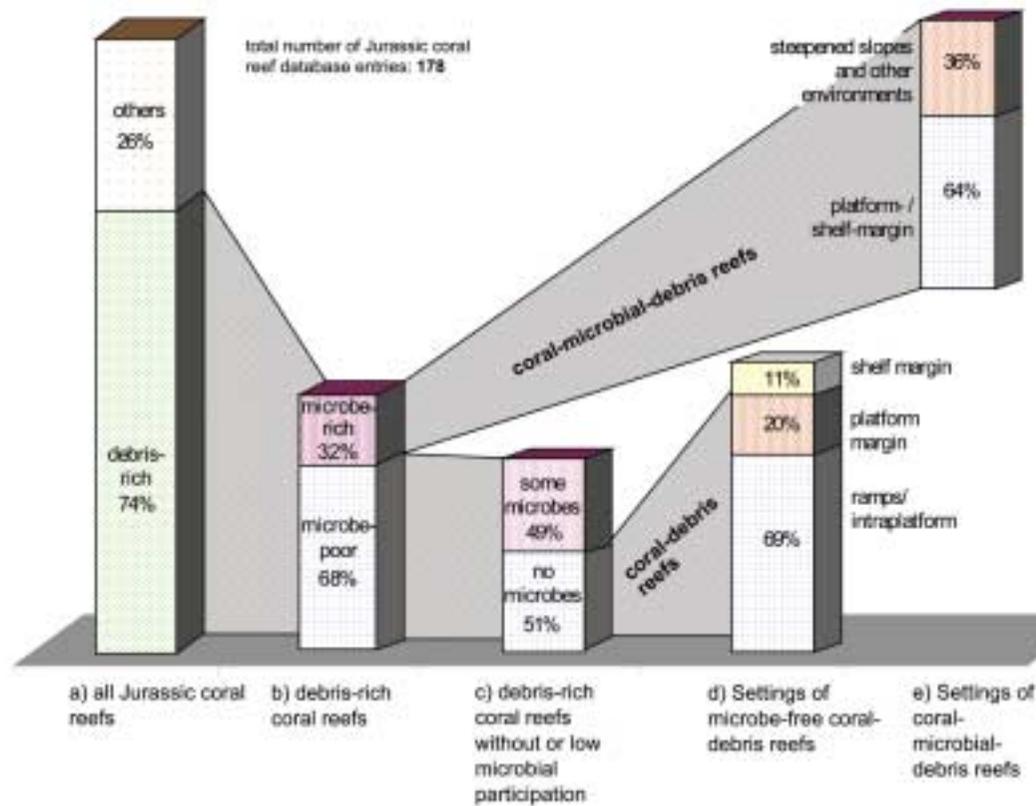


FIG. 10.—Proportions and environmental settings of Jurassic coral–debris reefs and coral–microbial–debris reefs, based on abundances of reef sites. Coral–microbial–debris reefs characterize steep shallow-water slope breaks, whereas microbolite-free coral–debris reefs are mostly found in the shallow part of flat ramps and epeiric platforms.

environments, which is a positive evolutionary feedback on the size of the “reef window”.

Siliceous sponge associations and siliceous sponge reefs are known from all three epochs of the Jurassic. On the northern Tethyan shelf they increase strongly in abundance during the Middle and Late Jurassic, whereas on the southern Tethyan shelf they were more widespread during Early Jurassic time. With the exception of the lychniskid sponges, which are known only since the later part of the Middle Jurassic, all other groups of these ultraconservative organisms existed prior to the Jurassic (Mehl, 1992). Although exact numbers of taxa are not available to date, the occurrence of Lower Jurassic siliceous sponge mounds demonstrates that the general possibility of formation of sponge reefs existed throughout the entire Jurassic period. A certain evolutionary increase of sponge taxa was therefore induced by increasing availability in sponge reef habitats rather than vice versa (Leinfelder, 1994b).

Abiogenic Control of Reef Patterns

Whereas the demands and abilities of reef organisms available in a given time slice exert the principal control on reef development, and span the margins of the “reef windows”, it is abiogenic control that actually determines whether, when, and where reef organisms find their chance to build up reefs or, in other words, where the “reef window” may actually open. These abiogenic control factors can be subdivided into (1) tectonic setting, (2) sea-level-related controls, and (3) climatic and oceanographic factors, all of which were not stable throughout the

Jurassic and many interactions among the three existed as well. The interplay of these three determined the general physico-chemical factors and dynamics with which reef organisms had to cope during the Jurassic.

Relation of Jurassic Reefs to Shelf Configuration.—

The general basin setting of reefs has a major influence on the potential for reef growth. Leinfelder (1993a, 1994a, 1994b) and Leinfelder et al. (1996) have presented a model in which not only tectonic activity (eventually resulting in changes of terrigenous influx) but particularly the configuration and steepness of the shelves are of paramount importance in determining the appearance and composition of Jurassic reefs. The concept is based on the fact that extrinsic terrigenous and carbonate sedimentation and resedimentation is not only a key parameter for the appearance and disappearance of reefs but—when within the tolerance field of reefs—is a sensitive modifier of reef composition and diversity (see above). The exhaustive new database on Jurassic reefs (Kiessling and Flügel, this volume) allows further substantiation and refinement of this model.

Shelf Configuration Controlling Shallow-Water High-Energy Coral Reefs.—Frequent or continuous resedimentation of particles causes strong abrasion and eventually is lethal for reefs even if not much sediment actually accumulates. Such abrasion by sand-size or larger reef debris in shallow-water high-energy reefs cannot be tolerated by most reef organisms. Modern reefs can, however, react to abrasive, wave-driven forces by changing their organis-

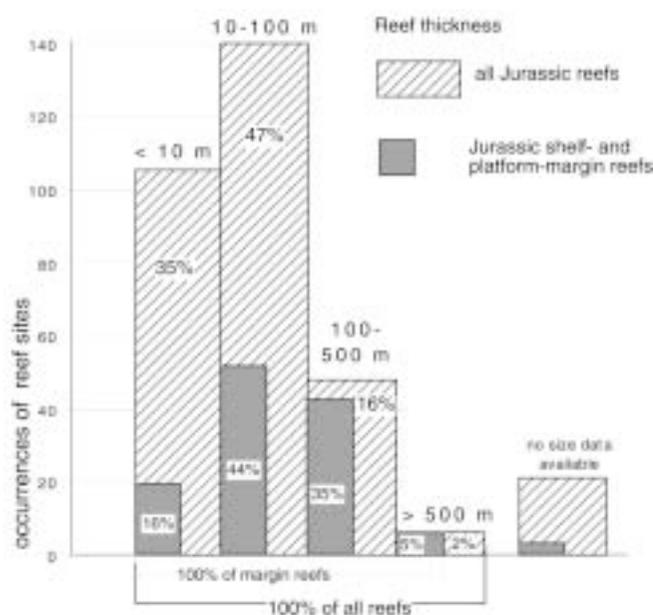


FIG. 11.—Size categories of Jurassic reefs. Note that the average size of reefs at shelf or platform margins is larger than the average of all reefs. Evaluation is based on PaeoReef database.

mic composition. Geister (1983, 1992) has shown for Caribbean reefs that encrusting soft corals and melobesioid coralline algae substitute for high-energy reef associations in abrasive settings. Both group of organisms, particularly the coralline algae, are capable of fixing loose, noxious material by encrustation even in an abrasive regime.

Nothing is known about encrusting soft algae in the Jurassic, and melobesioid red algae did not exist except for some predecessor forms, such as *Marinella lugeoni* from the Upper Jurassic. *Marinella* actually was adapted to abrasive marginal marine settings but did not play a major role in Jurassic reefs (Leinfelder and Werner, 1993). Solenoporacean red algae appeared in abrasive settings, such as debris-rich reefs, but they had no major capacities in fixing loose reef rubble. It was largely the widespread microbial crust producers that had to try to cope with this situation.

Unlike modern reefs, Jurassic reefs rich in both debris and "algal" carbonate encrusters (corallines in modern reefs, microbial crusts in Jurassic reefs) are relatively rare, even though microbial crusts were so common in Jurassic reefs. On the other hand, many coral-debris piles, often with signs of transportation, can be found, which often are interpreted as reefal debris halos of unknown reefs not at outcrop. It is more likely, however, that most of these piles represent the normal type of Jurassic high-energy reef relics, with coral fauna growing only for very short times before becoming abraded and being suffocated by their own debris. Episodes of resettlement and reworking must have changed rapidly, to result eventually in a coral-debris reef. There are a couple of transitional reefs with coral frameworks partly preserved *in situ* but mostly eroded, such as the Liesberg reef of Switzerland (unpublished data, Leinfelder, 2001) or many Upper Jurassic reefs in Portugal and Spain (Nose, 1995). This results from the impossibility of microbial encrusters to settle on, and stabilize, large amounts of reefal debris in high-energy waters, owing to their vulnerability to abrasion (Leinfelder, 1992; Leinfelder et al., 1996).

Similarly, the less common coral-microbial-debris reefs also show little sign of preserved coral framework and are very rich in debris, but in contrast to coral-debris reefs, they contain large amounts of microbial crusts. The model example is the Ota reef from the Lusitanian Domain (Leinfelder, 1992, 1994a). One of the ways to reduce abrasion on such reefs is to find a mechanism to export most of the debris produced within the reef to prevent continuous abrasive action in the shallow reef. Steep depositional or bypass margins (aggradational or tectonic) facilitate winnowing of the reefs by waves and export of most of the debris towards forereef or backreef areas. The Ota reef actually shows an enormous accumulation of reef debris behind the reef crest, and seismic analysis reveals the bypass character of the entire platform margin (Leinfelder and Wilson, 1989; Ellis et al., 1990; Leinfelder, 1994a). In such settings, microbes had the chance to efficiently stabilize the remaining debris within the reef, giving rise to coral-microbial-debris reefs, which we interpret as characteristic of settings at the margin or within the shallow-water parts of steepened slopes.

When using the reef database, 90 Jurassic (including Berriasian) coral reefs show large amounts of debris and reduced amounts of micrite; another 42 show medium amounts of debris and reduced amounts of micrite. Among these debris-rich reefs, about one third are also rich in microbial crusts (Table 1, Fig. 10) (which is about 24% of all Jurassic coral reefs). Such coral-microbial-debris reefs occur preferentially, but not exclusively, at tectonically controlled shelves within or at the margins of microplates of the southern Tethys realm as well as at rift-dominated settings in the North Atlantic. The Apulia-Adria microplate polygon exhibits many examples, such as the Oxfordian shelf-margin coral reefs at the edge of the Friuli Platform (Winterer and Bosellini, 1981; Sartorio et al., 1987; Geyer, 1993), the Kimmeridgian to Tithonian reefs of the Ernstbrunn and Plassen limestone from Austria (Bachmayer and Flügel, 1961; Fenninger, 1967), or Middle Jurassic to Tithonian shelf-edge reefs in Slovenia and Montenegro (Bosellini et al., 1981; Turnšek et al., 1981; Turnšek, 1968). From the North Atlantic realm, Oxfordian to Kimmeridgian examples are from Portugal (e.g., Tavira reefs, Leinfelder et al., 1993a; Ota reef, Leinfelder, 1992; Montejuento reefs, Ellis et al., 1990) and also at some occasions at the U.S. Atlantic Coast and Gulf Coast. Similar debris-microbolite-rich coral reefs have also been described from the Oxfordian of Uzbekistan and Turkmenistan (Fortunatova et al., 1986; Iljin, 1981), the Upper Jurassic reefs of Tibet and Thailand (Liao, 1982; Yue and Liao, 1986; Fontaine, 1986), and the Tithonian of Japan (Yabe and Sugiyama, 1935) amongst other examples. Many of these sites appear to have been at pronounced shelf or platform breaks (e.g., microplates in the southern Tethys, along the Upper Jurassic U.S. Atlantic-Gulf reef trend), and at shallow-water slope breaks related to salt pillows and rift tectonics in southern and central Portugal. Almost all of these reef sites (i.e., 39 of 42) are Late Jurassic, indicating the more widespread occurrence of steepened margins during that period, which we interpret to have been a result of intense rifting in the western part of the southern Tethys and in the North Atlantic-Gulf Coast realm. Just like the other examples the East European to Asian occurrences are likely to have formed along generally steepened slopes as well. However, debris-rich coral-microbolite reefs may also occur occasionally in ramp-type reef domains such as Spain, France, Germany, and England. Probably these are a product of aggradational pinnacle growth from deeper settings into the shallow water, as a consequence of which debris became incorporated into microbial-dominated edge and flank settings (see below).

Reef sizes also reflect general reef setting very well. Only about 18% of Jurassic reefs are thicker than 100 m, with about 35% being smaller than 10 m and 47% being between 10-100 m (Fig. 11).

According to the reef data base, about 38% of all reef sites are situated at shelf or platform margins. Of all coral reefs thicker than 100 m, however, only one out of 34 is not positioned at a platform or shelf margin. These thick shelf-edge or platform-edge reefs are concentrated mostly in the Lower Jurassic of Morocco, the Middle and Upper Jurassic of Madagascar, the Ukraine, Uzbekistan and the Caucasus, Montenegro, Bosnia and Slovenia, the Lusitanian Domain, and Israel. We are, however, aware of a possible bias in determination of reef thicknesses, which in survey studies often tends to represent platform rather than reef thicknesses.

On the other hand, micrite-poor, debris-rich coral reefs lacking microbial crusts are considered by us as diagnostic of less steep, depositional bypass margins and low-angle high-energy ramp settings, possibly together with lack of storm events to sweep reefs clean of excess debris. Actually, 69% of such coral-debris reef sites in the database are interpreted as situated in shallow ramp positions; the rest are related to platform margins and, to a minor extent, shelf margins. Such coral-debris reefs occur scattered throughout the entire Jurassic and the entire globe but are more common in Morocco (chiefly Early and Middle Jurassic), Saudi Arabia, France, Luxembourg, and Switzerland (Middle and Late Jurassic), hence showing only partial overlap with distribution of coral-microbial-debris reefs. Well studied Oxfordian reefs of this type related to positions at shallow ramps, inboard of, or at gentle slope breaks, exist in St. Ursanne, Switzerland (unpublished data) or in the French Lorraine Platforms (Insalaco et al., 1997; Latenser, 2000). Kimmeridgian reefs of this type are common in Iberia, such as reef bodies of the Amara Formation, some of which represent debris reefs with partially preserved reef framework (Nose, 1995).

The database also reveals many coral reefs that are considerably rich in both carbonate mud and debris, without or with some microbial participation. Such entries in the database may be partially biased by misinterpretation of indistinct microbial crusts as micrite as well as poor data sets showing bulk data for reef successions. Quite a number of these reefs, however, might have grown in protected, mud-rich settings, where debris was largely produced by bioeroders. The importance of biogenic debris production in modern reefs was emphasized by Geister (1983), Hallock (1988), and Highsmith (1980). Highsmith (1980) found a strong correlation between strongly bioeroded reefs and elevated nutrient supply. The reef database indicates that nearly 80% of all coral reefs show signs of bioerosion by macroborers, but current knowledge and data are not sufficient to allow determination of different rates of bioerosion.

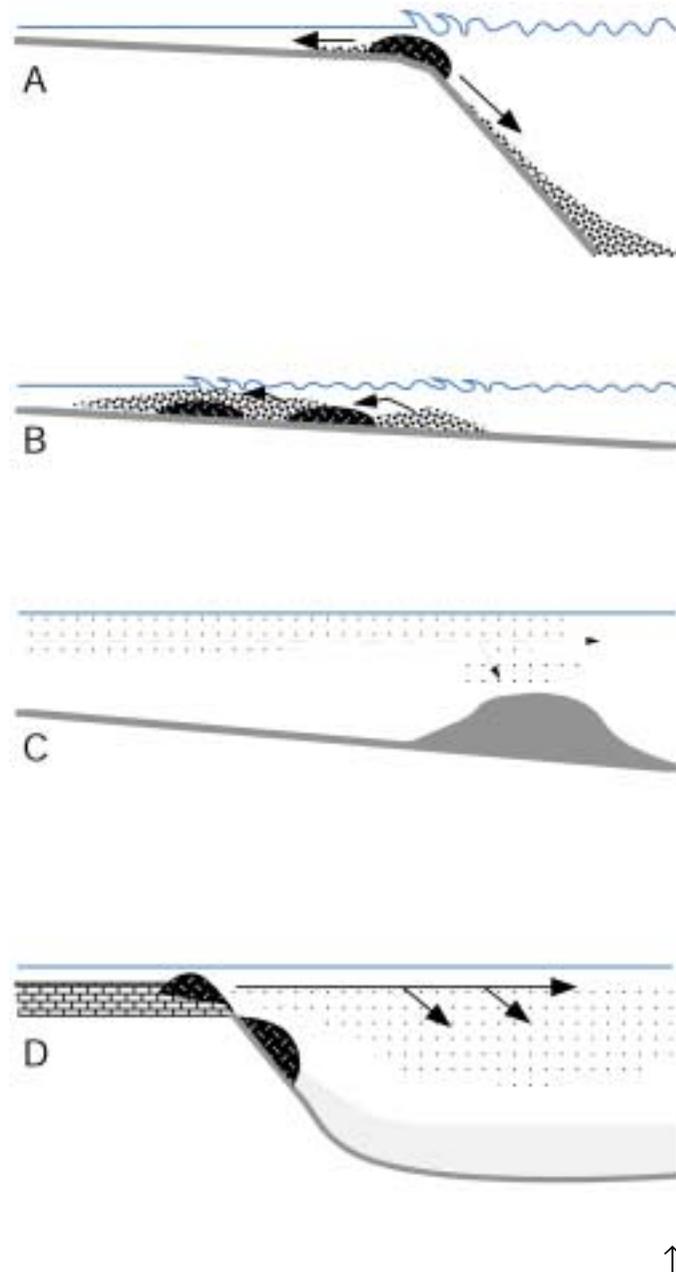


FIG. 12.—Control of reef growth and reef type by shelf and platform configuration. **A)** Coral-microbial-debris reefs characterize Upper Jurassic high-energy shelf and platform margin breaks with steepened slopes, allowing export of excess debris. Selected examples: Lusitanian Basin, southeastern U.S.A., Adria-Apulia plates, Uzbekistan. **B)** Coral-debris reefs are typical of shallow-water high-energy ramp settings or margin settings with very moderate breaks. Reefs are rapidly suffocated in debris. Very subordinate microbial participation. Selected examples: all across northern Tethys shelf, southeastern U.S.A. **C)** Siliceous sponge-microbial mounds grow only where shallow-water carbonate factories are remote. Muddy sedimentation, though very reduced and possibly intermittent, is nevertheless crucial (examples: Oxfordian and Kimmeridgian northern Tethys shelf). No allochthonous sedimentation results in sediment-starved sponge-biostromal faunal condensations (examples: southeastern Spain), elevated sedimentation in muddy biostromes (example: southern Germany). Note that occurrence of sponge reefs is additionally governed by sea-level fluctuations. **D)** Depending on bathymetric position, coral-microbial reefs, coral-siliceous sponge-microbial reefs, or pure microbomite reefs characterize slope settings. High microbial participation results from bypassing of sediments around reef structures. Selected examples: southern Portugal, Spain, Switzerland, southeastern U.S.A. Despite suitable bathymetry, sponge mounds and reefal biostromes do not develop under increased rates of allochthonous muddy sedimentation owing to proximity of shallow-water carbonate factories (example: Oxfordian of Lusitanian Basin). Note that reefs might also appear in settings of generally elevated sedimentation when rapid transgression reduces influx of terrigenous material or mud export from carbonate platforms, allowing for short-term opening of the “reef window” (cf. Fig. 15). Highstand shedding may also be shut down by subaerial exposure of carbonate factories (Leinfelder, 1993a).

Shelf Configurations Favorable for Siliceous Sponge Reefs.—Large siliceous sponge mud mounds are restricted mostly to lower-mid to outer, often homoclinal, ramp settings distant from shallow-water carbonate factories, because this position provides the favorable, reduced but noticeable amount of allochthonous muddy material necessary for their growth. Without such influx of muddy material only sponge biostromes develop, an example of which are the Oxfordian siliceous sponge biostromes of eastern Spain, which covered vast areas (Krautter, 1997). Sponge biostromes may also develop under elevated influx of carbonate mud, but in contrast to the sediment-starved individual-rich biostromes these are mud-rich and contain lower sponge numbers than low-sedimentation biostromes as well as different siliceous sponge morphotypes. Many examples exist in the Upper Jurassic of southern Germany (e.g., Kimmeridgian Treuchtlingen biostromes) or Switzerland (e.g., Oxfordian Birnenstorf beds) (Leinfelder et al., 1996; Krautter, 1997). If carbonate factories were too near, because of steep shelf slopes, neither biostromes nor biohermal mounds could develop (Fig. 12). An obvious example stems from the deep-water facies of the Oxfordian Montejunto beds in central Portugal, which are rich in siliceous sponge spicules but represent high sedimentation rates

of allochthonous mud and debris originating from a nearby shallow-water platform (Ellis et al., 1990; Leinfelder, 1994a).

Low-angle to nearly level-bottom ramps may grade into rugged morphologies owing to the development of sponge mounds. This created local steep slopes and bathymetric differences, giving rise to the differentiation of reef types to flanking reefs and capping reefs. During the Oxfordian, and particularly the Kimmeridgian, this occurred frequently in the pericontinental seas of the northern Tethys, particularly on the broad deepened shelf of southern Germany.

The database reveals 36 entries for siliceous sponge reef sites, 4 of which are from the Lower Jurassic, 6 from the Middle Jurassic, 18 from the Oxfordian, 7 from the Kimmeridgian, and 1 from the Tithonian–Berriasian. Most are considered mounds, but 10 entries refer to biostromal facies. Nearly all are attributed to deeper parts of epeiric seas or moderately deep ramp settings.

Early Jurassic siliceous sponge reefs are Sinemurian to Toarcian in age and occur in Morocco, the Lusitanian Basin, and Italy. Middle Jurassic sponge reefs are almost exclusively of Bajocian to Bathonian age and are largely concentrated in Spain, with additional occurrences in Hungary, France, and India. The distribution of Oxfordian sponge reef facies was described in detail

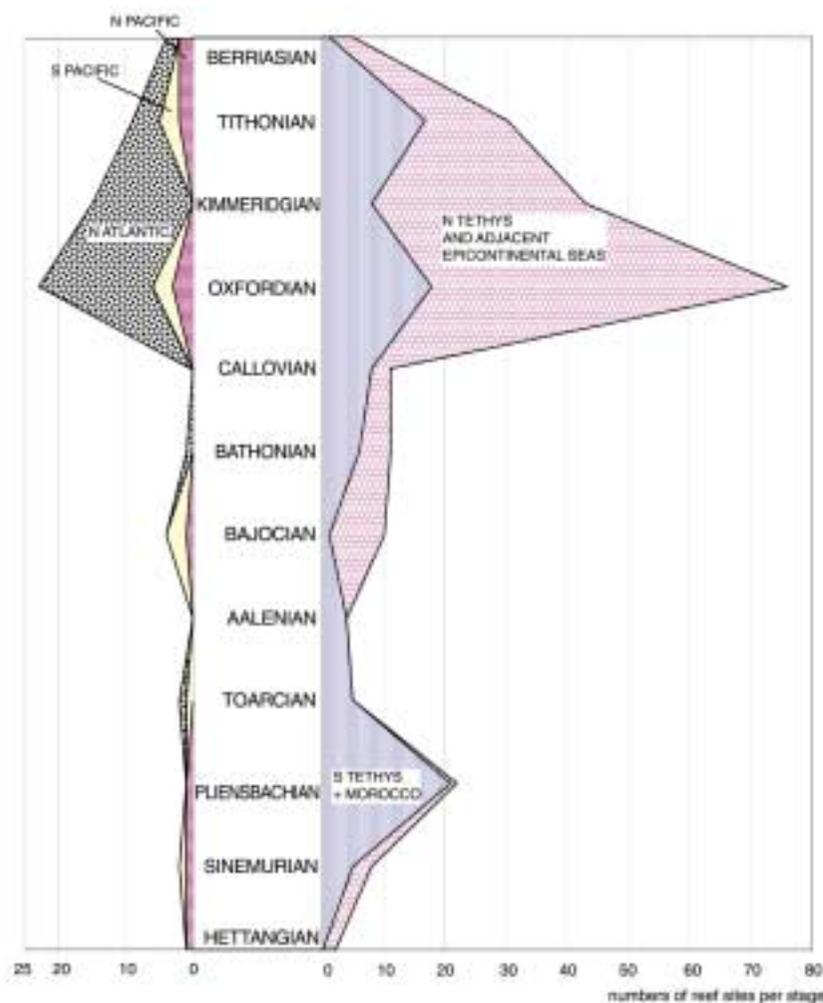


FIG. 13.—Abundances of reef sites per stage, differentiated for the Atlantic, Pacific, and Tethys realms. Morocco has a transition position between the southern Tethys and the North Atlantic realm but was added here to the southern Tethys. See text for further explanation.

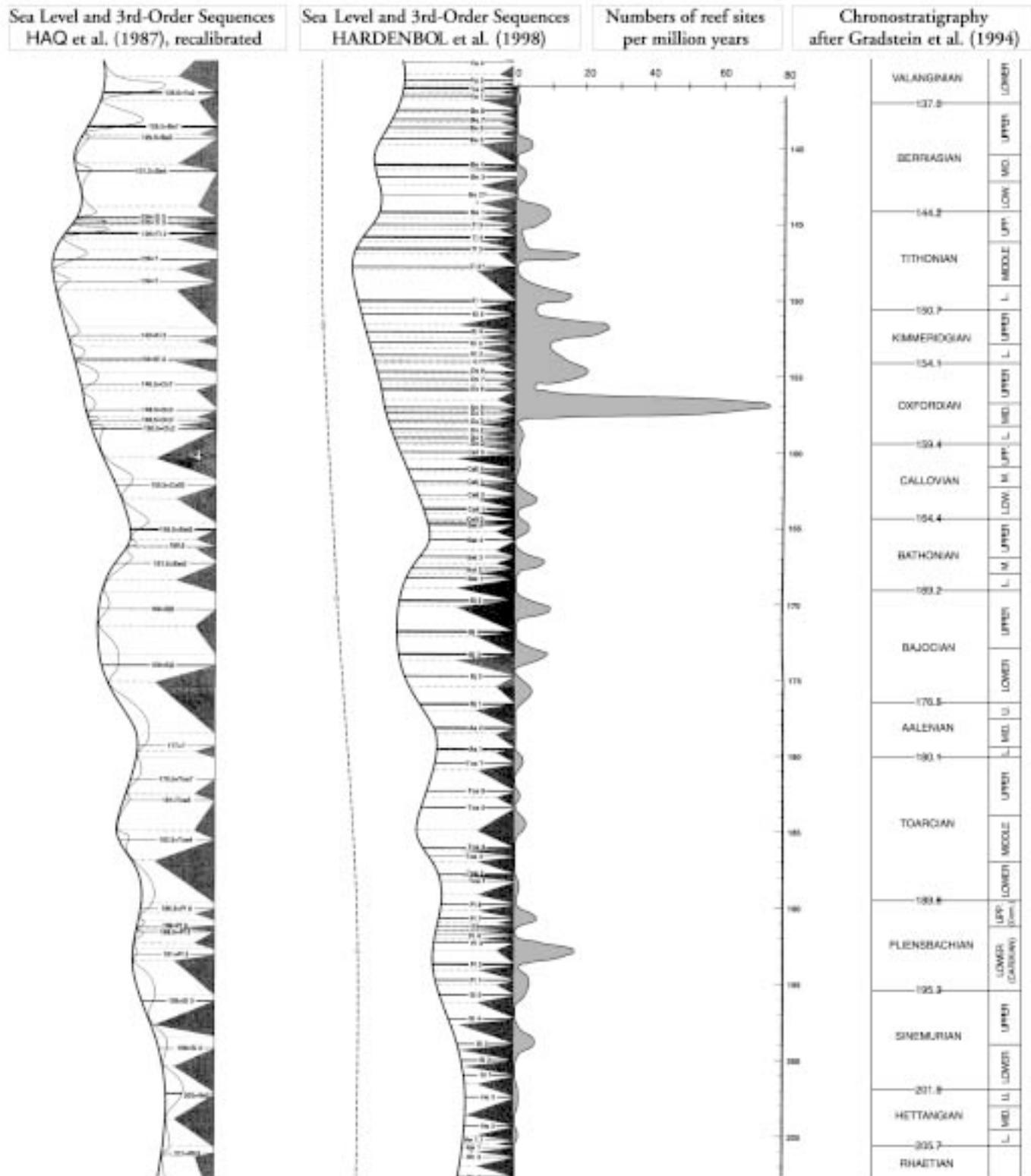


FIG. 14.—Occurrence of reef site number versus time, and correlation with sea-level change. Jurassic reefs do not mirror the long-term sea-level rise but mostly match well with third-order transgressive episodes. Reef ages are based on the reef database. Sea-level columns: solid lines = sequence boundaries, dashed lines = maximum flooding surfaces, dotted lines = top lowstand. Note that the Haq et al. (1987) curve is recalibrated to Gradstein et al. (1995); original age determinations are however indicated in column. Sea-level columns reprinted with kind permission of SEPM.

above, with the majority of Oxfordian sponge reefs occurring along an enormous belt at the northern Tethys margin extending from southern Portugal through eastern Spain, France, Switzerland, southern Germany, Poland, Romania, and with a major interruption, until the Caucasus, evidencing a vast shelf with productive carbonate factories being remote enough to permit growth of sponge reefs. Late Jurassic siliceous sponge reefs in the southern hemisphere are very rare, being reported only from Argentina and Kachchh. This distribution is evidence of the lack of deeper epeiric seas and widely flooded shelves in the eastern part of the northern Tethys realm, at the southern Tethys margin, and in the Pacific realm, where steep margins prevailed. But even on the European northern Tethys margin the vast carbonate-dominated shelf vanished totally during the Kimmeridgian, being substituted by shallower, often terrigenously influenced, coral-dominated seas. The only exception was southern Germany, where siliceous sponge facies kept on developing.

Reef Settings on Slopes.—Even given optimum conditions of depth and temperature for the growth of deeper-shelf sponge mud mounds, such mounds would not have grown if a productive shallow-water carbonate factory exporting carbonate fines and silt had been nearby. This means that given steepened slope, we do not expect a coral belt being accompanied by an adjacent sponge-reef belt. Owing to partial bypass situations, however, steepened slopes may have been a preferred site for many microlite-rich reefs of moderately to considerably deep waters such as coral-siliceous sponge-microlite reefs or siliceous-sponge-bearing microlite reefs. We therefore expect slope settings to frequently result in parallel adjacent belts of shallow-water coral-microbial-debris reefs accompanied by a belt of coral-sponge-microlite or sponge-microlite reefs, both of which may laterally amalgamate. All these reef types are known

from the U.S. Atlantic Gulf Coast–eastern Canada trend (Baria et al., 1982; Eliuk, 1978, 1989; Montgomery et al., 1999a; Montgomery et al., 1999b) or from southern and central Portugal (Tavira, Leinfelder et al., 1993b; Serra Isabel: Werner et al., 1994). Siliceous sponge mounds building up to shallow waters may be topped by coral-debris reefs, rimmed by coral-microbial-debris reefs and flanked by coral-sponge microlites. This appears to be the rule for the pinnacle-type buildups of the Cotton Valley Reef Play in East Texas (Montgomery et al., 1999a; Montgomery et al., 1999b), but similar situations also existed locally in southern Germany (Leinfelder et al., 1996).

Microlite-dominated reefs, most of which contain siliceous sponges, were common in the Late Jurassic North Atlantic realm (11 out of 24 reef database entries from the southeastern U.S.A., eastern Canada, and Lusitanian domains), but they also occurred in other places such as Sicily, Oman, and Yemen, thus showing hardly any overlap with true sponge mound and biostrome facies. Together with coral-siliceous sponge-microbial reefs, also occurring particularly in the North Atlantic realm, they are considered as diagnostic for the deeper parts of steepened slopes.

Figs. 5 and 6 highlight the strong control of shelf tectonics on reef types: the Late Jurassic example shows that during the Oxfordian coral reefs occurred likewise across the northern and southern Tethys reef domains in large numbers, whereas the steepened slopes of the North Atlantic realms triggered microbially dominated, mostly mixed coral-siliceous sponge reefs. The distribution of siliceous sponge facies reveals the difference between the tectonic styles: the stable, ramp-type but deepened northern Tethys shelf of Europe, mostly with a lateral gap between Tethys-facing sponge reefs and more inland coral reefs. Steepened shelf margins along microplates excluded sponge reefs farther east, except for the local Caucasus occurrence, as well as on the entire southern margin of the Tethys shelf. This is also reflected in the type of coral reefs on

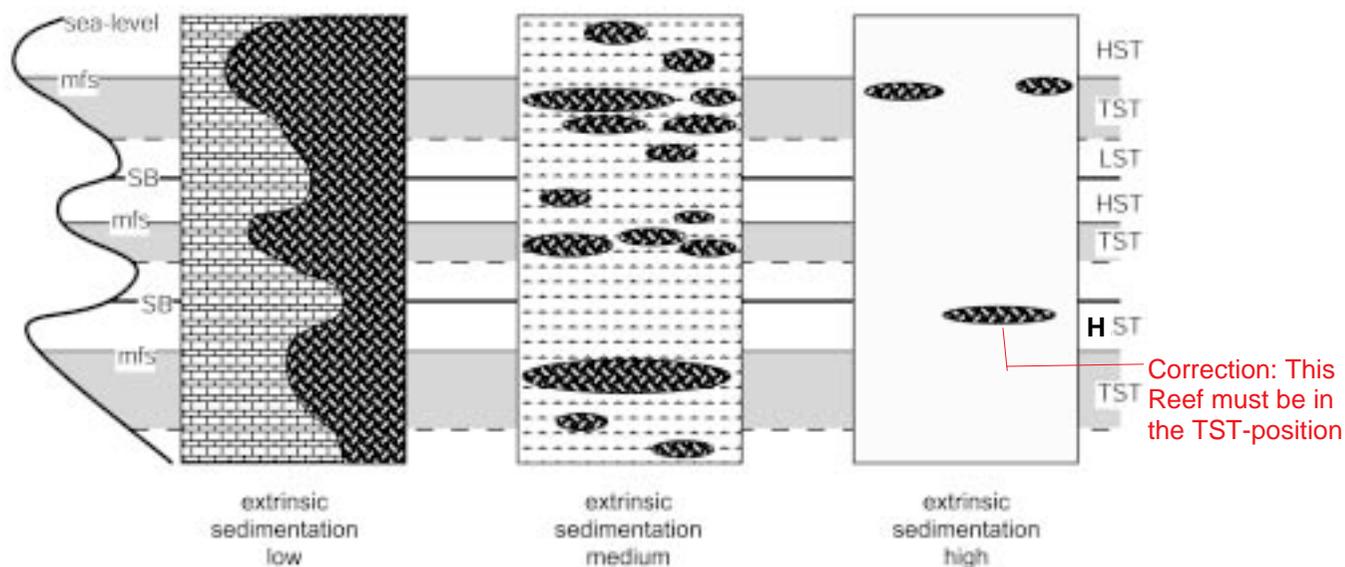


FIG. 15.—Reef occurrence in relation to sea-level change and general sedimentation regime. **A)** In a regime of low allochthonous sedimentation, reef growth is possible throughout all stages of sea-level change but lateral expansion of reefs largely mirrors sea-level change (e.g., Upper Jurassic of southern Germany). **B)** In a regime of moderate allochthonous sedimentation, reef development is mostly related to main sea-level rise (TST), although low-diversity-adapted reefs may occur during highstand (HST) and, if developed, lowstand (LST) episodes (e.g., Kimmeridgian of central Lusitanian Basin, southern Portugal, southeastern Spain). **C)** In a regime of generally high allochthonous sedimentation, the only chance for possible reef growth is close to the maximum flooding surface (e.g., Kimmeridgian of northern and western Lusitanian Basin, Tithonian of central Lusitanian Basin). All models are related to ramp settings; sea-level oscillations may be of third-, fourth-, or fifth-order.

the maps (Figs. 5C, 6C): high-debris, mostly microbolite-rich reefs dominate by far at the southern Tethys margin, the eastern part of the northern Tethys, and the North Atlantic realm, whereas high-energy, debris-rich and microbolite-poor inner-ramp reefs are accompanied, in deeper waters, by moderate-debris and low-debris reefs in the European part of the northern Tethys. Even diversity is strongly related to shelf style, with well-washed and microbially stabilized shelf-margin coral-debris reefs mostly yielding high diversities, and inner-platform and inner-homoclinal-ramp reefs causing restrictions in diversities.

Sea-Level-Related Occurrence Patterns.—

Sea level is another important control on the evolution and distribution pattern of Jurassic reefs, at both large and small scales. First-order sea-level rises set the general conditions for reef development, by enlarging available shelf areas and restricting terrigenous influx to coastal areas. Second- to third-order sea-level rise provided time windows with predisposition for reef growth, whereas it was mostly fourth-order and higher-frequency events that switched reef growth on and off or modified growth and compositional patterns of longer-lasting reef episodes.

General Sea-Level History.—According to Haq et al. (1987), Hallam (1988), and Hardenbol et al. (1998), global sea level rose, with oscillations, throughout major parts of the Jurassic, i.e., until the end of the Kimmeridgian. On the European part of the northern Tethys shelf this is well reflected up to the base of the Kimmeridgian in the increase of reef sites and reef domains through time and by the widespread occurrence of both shallow-water and deeper-water shelf reefs during the Oxfordian, coinciding with the increasing reduction of terrigenous influx to the shelf, part of which may be a climatic effect (see below). Fig. 13 shows the increase of reef sites towards the Late Jurassic on the northern Tethys shelf, whereas there is no such trend on the southern Tethys shelf. The Jurassic peaks of reef distribution partially mirror the general outline of the eustatic sea-level curve, demonstrating dominance of reefs at major episodes of accelerated sea-level rise and high sea level, such as during the Pliensbachian, Bajocian–Bathonian, and Oxfordian to Early Tithonian (Fig. 14; cf. Figs. 7, 8).

Although the general pattern of sea-level rises correlates with peaks of reef development, there is no good correlation between general accommodation created by sea level and numbers of reef sites and reef domains. Global sea-level charts show that sea level kept on rising throughout the Jurassic. However, there is no corresponding increase in numbers of reef sites between the Early Jurassic and the Middle Jurassic (Fig. 7), but an enormous jump in number of reef sites at the beginning of the Late Jurassic. Sea level continued to rise from the Oxfordian through the Kimmeridgian into the early Tithonian, which even on the stable northern Tethys shelf of Europe does not correlate with the same increase in reef sites and reef domains (Figs. 7, 8, 14). Rather, reef settings shallowed, leading to the disappearance of sponge reefs except for the south German domain, where sponge reefs kept on thriving. Also, despite the continuing sea-level rise, many reef domains suffered strong terrigenous influx, parts of which could have been an indirect influence of sea-level rise towards a more humid climate (see below). Consequently, disappearance of major areas of deeper shelf reefs despite rising sea level may be a compensation effect. Enormous carbonate production during the Oxfordian and parts of the Kimmeridgian together with accumulation of Kimmeridgian siliciclastics gave rise to catch-up shoaling successions which overcompensated accumulation po-

tential created by sea-level rise. Besides climatic effects, the main reason for increased siliciclastic influx during the Kimmeridgian is thought to be accentuated rift tectonics in the North Atlantic rift zone, with maximum effects in the Lusitanian Basin but also in other areas, such as Spain, southwestern France, northern Germany, and England. Similarly, transpressional movements and crustal segmentation in the western Tethys and southern North Atlantic overprinted the rapid sea-level rise of the Callovian to Early Oxfordian. This caused increased influx of terrigenous clastics as well as tectonic uplift in central and southwestern Portugal (cf. Ziegler, 1988; Leinfelder, 1994a), resulting in very low numbers of reefs during this time interval.

Third-Order and Fourth-Order Sea-Level Rise.—Leinfelder (1993a), Leinfelder et al. (1993a), Leinfelder et al. (1993b), Leinfelder (1994a), Leinfelder (1994b), and Nose and Leinfelder (1997) have evaluated the onset and cessation of reef growth as well as reef type and diversity patterns for the widespread Jurassic ramp-situated reefs of the European northern Tethys shelf in terms of third-, fourth-, and fifth-order sea-level change (Fig. 15). The strong dependence on sediment starvation for high-diversity reefs to develop, and the importance of variable extrinsic sedimentation as a modifier for faunal composition, normally relates episodes of reef growth to ecological “windows” opening within third- to fifth-order sea-level rise. If reduction in extrinsic sedimentation and resedimentation within the reefs could have been achieved by other controls, such as steep shelf margins, sea-level change may have played a negligible role in controlling onset and cessation of reefs, and accounted only for internal modifications of platform architecture or episodes of subaerial exposure. In ramp settings, however, during stable and falling sea level, reefs were mostly restricted to constantly wave-washed zones, giving rise to the dominance of high-energy reefs. Most of the shelf had elevated sedimentation rates, excluding reefs, except for some low-diversity reefs adapted to siltation stress. During rising sea level, sediment influx was reduced and growth of bathymetrically differentiated reefs was widespread. Partial oxygen depletion in deeper settings may have given rise to pure microbial reefs. The equable climate of the Late Jurassic may have resulted in pull-up of dysaerobic waters, thus giving rise to episodes with pure microbolite growth in fairly shallow waters (Leinfelder, 1993a; Leinfelder et al., 1996). These models have successfully been applied to sequence stratigraphic analysis in the Upper Jurassic of Portugal, Spain, and Germany (Leinfelder, 1993a, 1993b, 1994a; Leinfelder and Wilson, 1998; Nose, 1995). Nose and Leinfelder (1997) and Leinfelder (2001) further refined these models by highlighting that actual reef growth occurred mostly during fourth-order or lower-order sea-level rise within the framework of third-order sea-level rise.

As an example, the Kimmeridgian of the European northern Tethys shelf between southern Germany and southern Portugal and the adjacent Lusitanian Basin illustrates third-order sea-level control. The Kimmeridgian deposits of this region represent large-scale shallowing-upward successions. The successions exhibit frequent intercalation of reefs (Iberia) but differ strongly in frequency, composition, and duration of reef growth as well as in their general facies development (e.g., Leinfelder, 1993a, 1994a). Biostratigraphic resolution is good to excellent in the deeper-water parts of the succession, as in Germany and parts of Switzerland, but is very poor in the shallow-water facies of France, Switzerland, Spain, and Portugal. Marker beds occur locally but do not extend across the shelf. Additional time-line correlation and sequence stratigraphic interpretation can be performed, however, using reef patterns, because occurrence, extent, compo-

sition, and diversity of reefs can be used as a monitor for allochthonous sedimentation. This allows a best-fit correlation of the resulting pattern, which shows that reef growth was governed largely by regional or eustatic sea-level fluctuations (Leinfelder, 1993a; Nose, 1995; Leinfelder and Wilson, 1998). Such correlatable levels of enhanced reef growth can be partially dated by ammonites, allowing their comparison with the global sea-level chart. We focus on some peculiarities of the resulting pattern. There were two major episodes of reef growth during the Kimmeridgian of southwestern Europe, one with a peak at the transition from the *hypselocyclus* chron to the *divisum* chron, and the other with a peak during the *eudoxus* chron (Leinfelder, 1993a; Leinfelder 2001). During this time interval very different reefs grew, from brackish-water oyster reefs through marginal marine sediment-stressed monospecific coral thickets, lagoonal coralline sponge and coral patch-reef clusters or biostromes, large shallow-water coral reefs, deeper-water siliceous sponge biostromes and mounds, to pure microbolite mounds. In southern Germany, because of a remote position from the productive shelf, sponge mounds grew through major parts of the Kimmeridgian, but they show a maximum distribution in respect to underlying and overlying reefs that is correlatable with the episodes mentioned (Fig. 15). These episodes can be correlated with third-order sea-level rises, although actual reef growth occurred mostly during fourth-order or fifth-order transgressive pulses within the third-order framework (see below).

Actually, most Kimmeridgian reefs of southwestern Europe grew either during the transition from the Early to Late Kimmeridgian (*hypselocyclus* / *divisum* chrons) or within the *mutabilis* and *eudoxus* chrons of the Late Kimmeridgian, both of which correlate well with the third-order transgressive intervals of the revised Haq curve (Hardenbol et al., 1998) at 152.5 and 151.5 Ma, respectively. Reefs of the final Kimmeridgian and the Tithonian also correlate with the sea-level curve.

The reef database reveals that not only in Iberia major episodes of reef building frequently coincided with episodes of third-order sea-level rise. Fig. 14 shows that even on a global scale there is a noticeable to strong correlation between reef site frequencies and sea-level change for the Early and Late Pliensbachian, the Bajocian, and the Bathonian, as well as for most Late Jurassic reefs. Fig. 14 also reveals, however, that although sea-level rise is of major importance for improving the environmental settings towards potential reef growth there is no direct correlation between reef numbers and magnitude of sea-level rise, even on a third-order scale. Remarkably, many third-order sea-level rises were not accompanied by reef growth, particularly during the Early and Late Jurassic. The important reef domain of Morocco is a good example of this. Moroccan reefs also grew during episodes of sea-level rise, but on the other hand, many episodes of rising sea level remained totally devoid of reefs, and the general trend of reef expansion is almost opposite to the large-scale sea-level history, with most reef sites mentioned from the Early Jurassic and relatively scarce reef growth during the Middle and even Late Jurassic.

In settings with generally more reduced background sedimentation, such as southern Germany, growth of reef complexes could last longer than third-order episodes, but again, maximum lateral expansion of reefs coincided with rising sea level. Again, the maximum extent of south German siliceous sponge reefs is in the *eudoxus* chron. In contrast, in areas with elevated allochthonous sedimentation, reefs were concentrated, or even restricted, to episodes of rapidly rising sea level, which retained terrigenous sediments in coastal estuarine and swamp areas (cf. Fig. 15; see also Leinfelder, 1993b; Nose and Leinfelder, 1997).

The models of Fig. 15 show the interplay of the general sedimentation regime with sea-level change in ramp settings. Shelf structure is another strong modifier of sediment influx, as was shown in the text above. A suitable area to test the importance of sea-level control versus structural control is the Lusitanian domain of the Atlantic realm. In this basin, both tectonically steepened blocks and gentle slope settings occurred penecontemporaneously and were controlled both by sea-level change and tectonics (Leinfelder and Wilson, 1998).

Evidence for High-Frequency Sea-Level Oscillations in Jurassic Reefs.—Correlatable peritidal Purbeckian cycles are evidence of orbital cycles in the Milankovitch range (Strasser, 1988; Joachimski, 1991), although amplitudes were very low owing to probable lack of polar icecaps (see below). Many other low-amplitude cycles of Jurassic carbonate platforms are not persistent and hence are probably of autocyclic origin (Leinfelder, 1994a). Correlation of subaerial exposure surfaces and other sedimentary features of the Ota and Amaral carbonate platforms (Lusitanian domain) and the nearly coeval Kimmeridgian shallow-water carbonate platform of eastern Spain suggests the development of fourth-order and even fifth-order rhythms (Leinfelder, 1994a; Nose, 1995), although time resolution of this complex pattern is not yet possible.

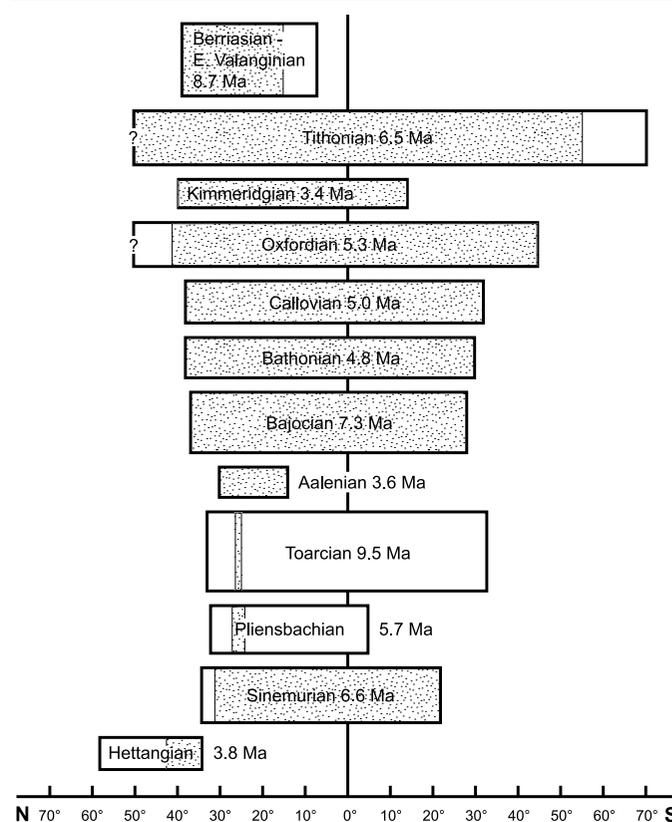


FIG. 16.—Maximum paleolatitudinal ranges of Jurassic reefs considering the position of more than 300 reef localities in the maps used in this paper (Golonka, this volume). The stippled section of each bar represents the range of coral-dominated reefs. Height of bars reflects differences in the duration of time intervals. Paleolatitude values for reefs where the stage is unknown (Early / Middle / Late Jurassic undifferentiated) are not included here but lie within the range of the values for the corresponding stages. See text for further explanation.

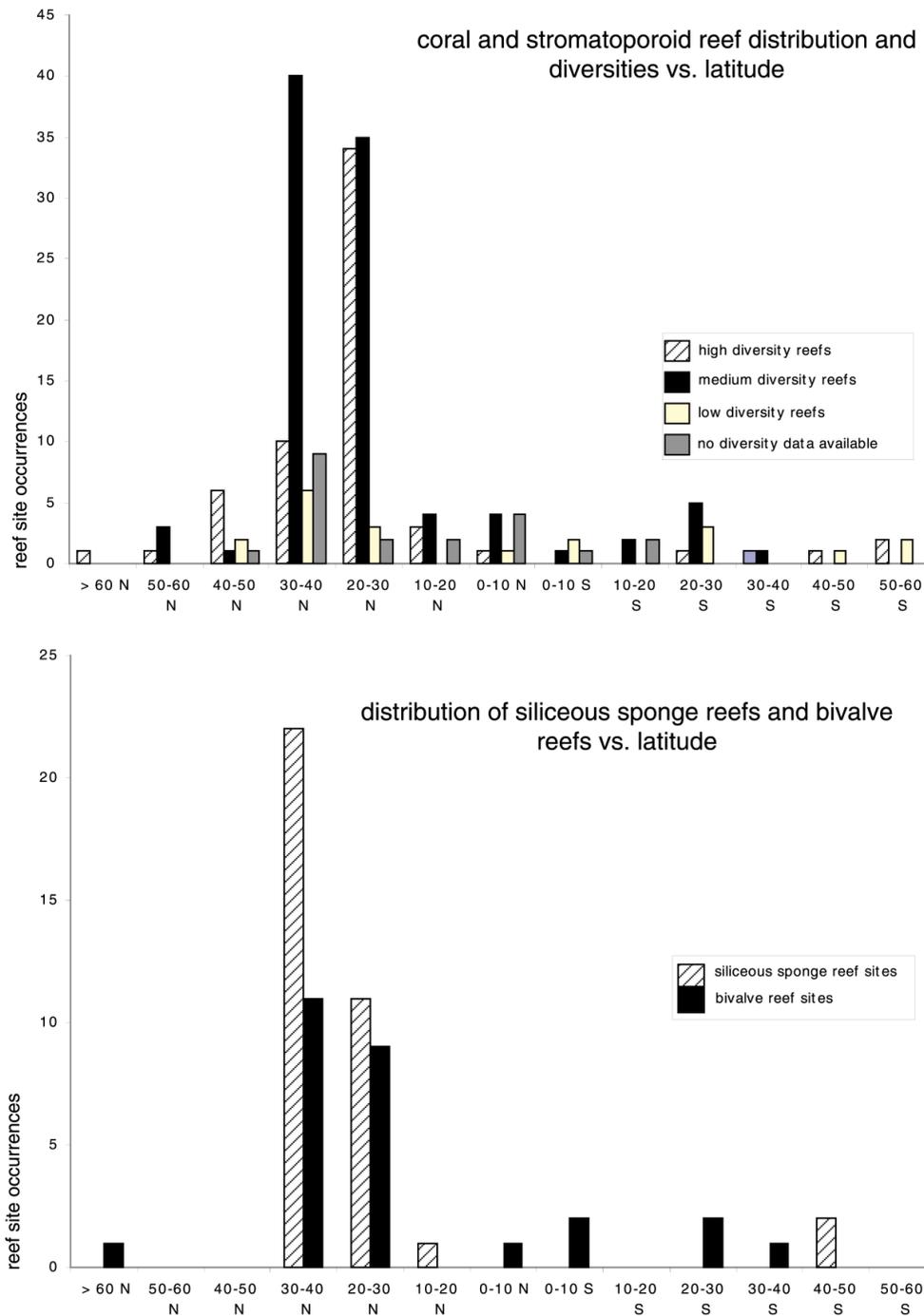


FIG. 17.—Paleolatitudinal distribution of Jurassic reefs. Jurassic coral and sponge reefs span an enormous range of latitudes. High-diversity coral and stromatoporoid reefs also existed in high latitudes, whereas low latitudes are characterized by low abundance and reduced proportions of high-diversity reefs. Bivalve reefs, most of which are Early Jurassic, also spanned a broad range of latitudes. Siliceous sponge reefs and bivalve reefs exhibit low to medium faunal diversities. All reef types had their maximum distribution around 20–40° N, i.e., along the broad shelf seas of the northern Tethys. Distribution might be biased by poor quality of many diversity data but is thought to reflect important trends. See text for further explanation.

Annual growth rates of Late Jurassic corals and microbolites provide good evidence for very rapid growth of individual Late Jurassic reefs, being in the range of thousands to ten thousands, and rarely hundreds of thousands, of years (Schmid, 1996). This shows that reef growth events occurred during times of third-

order sea-level rise but were often associated with events, i.e., probably sea-level rises, of higher order. Short-term, partly repetitive stacked successions of eutrophic or dysaerobic pure microbolite reefs to mesotrophic sponge or coral reefs (Leinfelder et al., 1993a; Leinfelder et al., 1993b; Leinfelder, 1994b) indicate

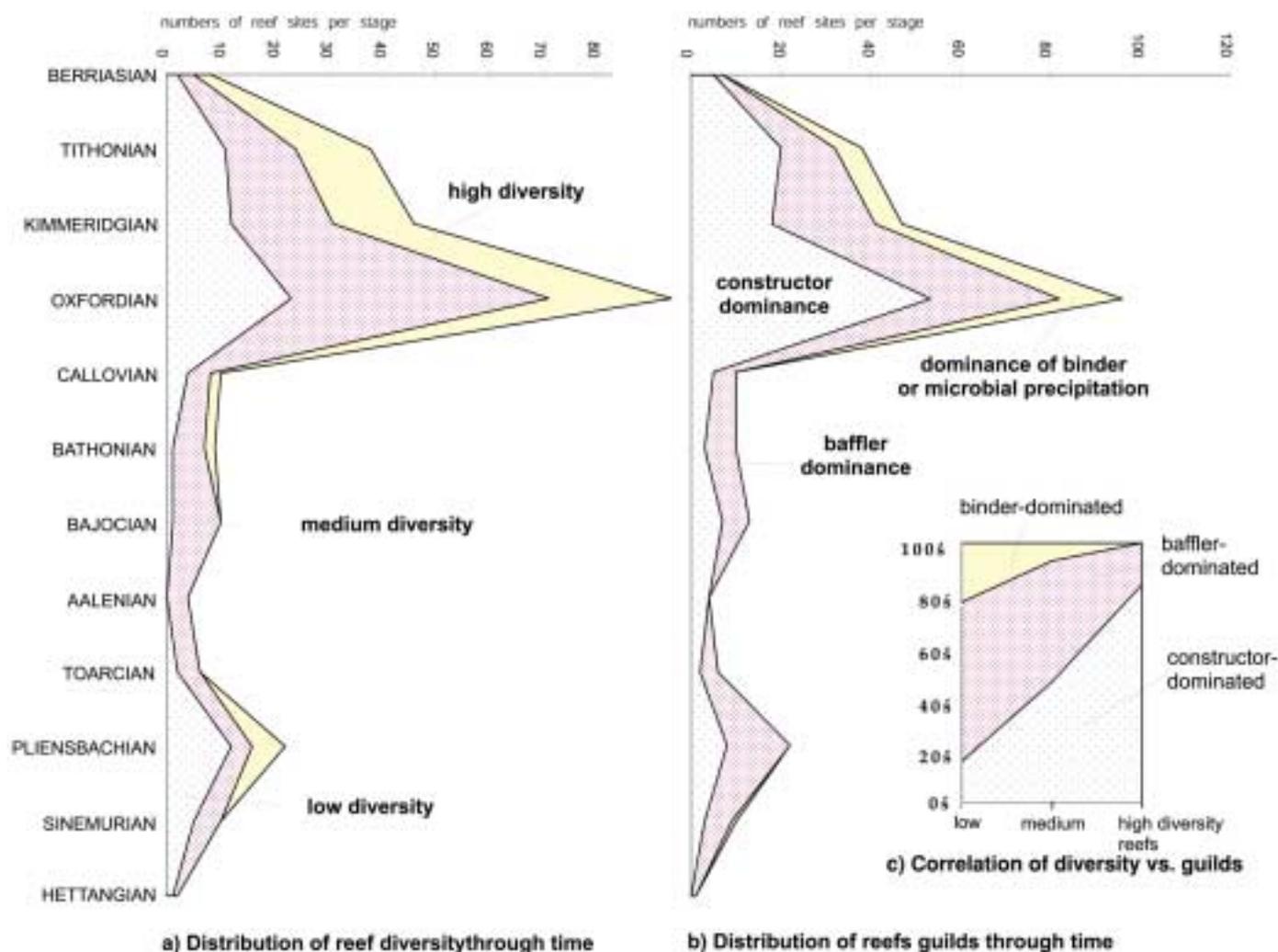


FIG. 18.—**A)** Diversity of Jurassic reefs is partially time-dependent, with the highest proportion of low-diversity reefs during the Early Jurassic, a dominance of medium-diversity reefs during the Middle Jurassic, and a balanced proportion of low- to high-diversity reefs during the Late Jurassic. **B)** This trend is paralleled by an increasing dominance of constructors towards the Late Jurassic. **C)** Low-diversity reefs mostly show a dominance of bafflers, whereas high-diversity reefs have the highest proportions of constructor-dominated reefs. Note that constructor-dominated reefs normally also contain a large amount of binding organisms, thus the correlation does not show a restriction of binders to low-diversity reefs but rather a higher proportion of binder-dominated reefs for low-diversity reefs than for high-diversity reefs.

that environmental conditions could have changed rapidly, possibly at a fifth-order or higher frequency.

Pure microbolite reefs are interpreted by us as dysoxic because of their association with glauconite, pyrite framboids, and horizons with *Chondrites* and the dysaerobic bivalve *Aulacomyella* (Leinfelder et al., 1993a; Leinfelder et al., 1993b). They nevertheless contain scattered, small, oxygen-dependent fauna such as siliceous sponges or, if shallower, reef corals. This is indicative of pulses of improved oxygenation, which probably were related to high-frequency environmental cycles. Whether or not oceanographic oscillations were always correlated with high-frequency sea-level changes or rather represent random oscillations of environmental factors remains a matter of debate. However, the Kimmeridgian example of southwestern Europe indicates oceanographic changes accompanying sea-level change. In this area, most pure microbolite reefs, or reefs with a repetitive stacking pattern of coral or sponge reefs with pure microbolite, are re-

stricted to the *hypselyclum-divisum* chron. Such reefs occurred in southern and central Portugal, eastern Spain, and southern France. Another peculiar reef type, siliceous sponge reefs with abundant individuals of rhynchonellid brachiopods (the *Lacumosella* mounds), occurred in southern Germany and was restricted to this level as well. We interpret these pure, fully marine microbolites as evidence of partial oxygen depletion, whereas stacked structures mirror oscillations of oxygen depletion and oxygen availability. Oxygen depletion might have been related to increased nutrient influx, although this cannot be proven. Portuguese pure microbolite reefs or stacked microbolite-coral reefs (e.g., within the so-called Isabel level) were accompanied by the dysaerobic bivalve *Aulacomyella*, authigenic glauconite, framboidal pyrite, and secondary gypsum, evidencing partial oxygen depletion (Werner et al., 1994). Southern France coral bushes encased in huge microbolite masses do not show direct signs of oxygen depletion, but frequent large oysters accompany-

ing microbolite growth indicate elevated nutrient rates (Leinfelder, 2001; Leinfelder et al., 1993b; Schmid, 1996). This might also apply to the *Lacunossella* mounds of southern Germany, which are accompanied by a bed of dysaerobic benthic bivalves (G. Schweigert, personal communication, 1999).

The Late Jurassic *Tubiphytes*, an encrusting, probably oxygen-dependent foraminifer associated with endosymbiotic algae (Schmid, 1996) may be common in otherwise pure microbolites. Because foraminifers grow over periods of days and weeks, shifts from *Tubiphytes* to non-*Tubiphytes* dominance might possibly be indicative of annual cycles (Leinfelder et al., 1996).

Climate and Oceanography Controlling Jurassic Reef Growth.—

General Aspects.—The example of modern reef distribution shows that reef growth is certainly dependent on suitable shelf configuration and, possibly, transgressive seas, providing shallow-water environments and sheltering from terrigenous or resedimented carbonate fines (e.g., Geister, 1983; Kühlmann, 1984, 1988; Rogers, 1990; Leinfelder, 1997), but climate and oceanic currents play an important role in reef distributions (e.g., Veron, 1995). Modern reefs are confined largely to water temperatures not dropping below 18–20°C, and they intimately mirror oligotrophic situations created by the ocean current system. They particularly avoid upwelling zones along western sides of continents, even if water temperatures would still be sufficient, but they have their maximum distribution in distant offshore positions (e.g., Great Barrier Reef), along oceanic islands, and atop seamounts. Reefs in coastal positions, such as the frequent Red Sea reefs in particular, are a feature of arid areas, where lack of riverine influx causes oligotrophic situations. No coastal reefs exist in areas of major terrigenous influx such as off the Amazon delta. Another lesson from the modern setting is that extant warm-water reefs cannot tolerate seasonal peaks of hot water, particularly if peaks continue over weeks or months, an example of which are the bleaching events of the last two decades (Wilkinson, 1998).

Global distribution of Jurassic reefs shows many exceptions to the constraints on modern reef distribution, many of which cannot be explained solely by the generally higher sea level of the Jurassic or different shelf styles between, e.g., the northern and southern Tethys and the North Atlantic and Pacific realms. Of particular interest in terms of climatic and oceanographic control of Jurassic reef patterns are latitudinal distribution of reef occurrences, spatial and temporal diversity patterns, and reef control by patterns of nutrients, oxygenation, and rainfall. Additionally, sea-water chemistry may have played an important role in calcification and dominance patterns of reef-building organisms. Hardie (1996) and Stanley and Hardie (1998) stated that variations in Mg/Ca ratios are strongly responsible for the oscillating episodes of aragonite and calcite seas through the Phanerozoic Eon (cf. Sandberg, 1983). Moreover, Mg/Ca ratios and Ca concentrations are thought to exert control not only on the mineralogy of inorganic carbonate precipitates but also on patterns of calcification in many marine organisms (Wood, 1987; Harper et al., 1997; Stanley and Hardie, 1998). For example, the shift of aragonite seas to calcite seas in the Late Jurassic is considered to have promoted the appearance of reef-building calcitic demosponges (stromatoporoids and chaetetids) in marginal shelf settings (Stanley and Hardie, 1998). The geological distribution of microbolites might also be controlled by physicochemical factors like the saturation state of sea water driven by changes in pCO₂, supersaturation, or Mg/Ca ratios as well as global temperatures (Wood 1999). According to Webb (1996), microbolites were more widespread in ancient reefs, especially before the

Cretaceous. This was probably due to a high supersaturation state from the Cambrian to the Cretaceous (Knoll et al. 1993), which would also explain the widespread distribution of microbolites in the Jurassic. The marked decline in abundance of microbolites from the Cretaceous onwards may be the result of the relatively reduced saturation state of sea water, which can be related to the rise of calcareous plankton in the Cretaceous.

Reef Patterns in Relation to Climate and Ocean Circulation.—This section attempts to demonstrate that Jurassic reef patterns can be also partially explained by climate and ocean systems. In addition, the patterns help to refine climate and ocean circulation interpretation and allow us to rule out some climatic models.

One of the most outstanding features of Jurassic reefs is their very broad latitudinal distribution. This is particularly true of Late Jurassic reefs (Fig. 2). Reefs from the Late Jurassic spanned latitudes from 75° N to 70° S. Although the 70° S occurrence is a climatically irrelevant cold-seep reef, coral and stromatoporoid reefs occurred from 75° N (Tithonian of Japan, see Fig. 4) to 55° S (Tithonian of Patagonia) (Figs. 4, 16, 17). The maximum lateral distribution of coral and stromatoporoid reefs during the Oxfordian was 74° N (Japan) to 45° S (Neuquén Basin, Argentina), whereas during the Kimmeridgian they were much more laterally restricted (from Poland, 40° N; to Oman, 7° S; Fig. 17). Although the paleolatitude of Japanese reefs might be uncertain to a considerable extent (Kiessling, personal communication, Fig. 4), the Neuquén and Patagonian reefs developed in back-arc or continental-margin basins, making their correct position quite obvious (Ramos, 1978; Legarreta, 1991). The Sakhalin coral reef occurrence, positioned on a transfer plate, also is of debatable position (plotted in reef database with only 35° N). However, many reefs of central and northern Europe, such as reefs from southern England, Ukraine, Poland, and Uzbekistan, plot higher than 37° N. The peak of Jurassic coral reef distribution is within 30 to 40° N, although there is a second maximum at 20–30° N (Fig. 17). Astonishingly few reefs are related to low latitudes, although sufficient shelf seas, e.g., on the Arabian Peninsula or on the Yucatan–Mexican–Venezuelan shelf, would have been available (cf. Fig. 4). Although a bias in recording reefs cannot be ruled out, the general trend of this pattern of coral reef distribution is obvious and does not at all match the modern latitudinal distribution of reefs.

There are sufficient criteria for the warm-water character even of the high-latitude reefs, although for most of them, detailed ecological analysis has not been performed to date. Neuquén and Patagonian reefs occur with dasycladacean algae and oolites, and partially are of high diversity, with coral taxa being known also from lower latitudes (Legarreta, 1991; Morsch, 1989; Ramos, 1978). Beauvais (1973) and Leinfelder (1994b) have taken this as diagnostic for elevated surface water temperatures at high latitudes. Beauvais (1977, 1989a) mentioned additional sites with supposedly hermatypic corals (e.g., southern Greenland, Scotland, U.S. West Coast), but these occurrences are not reefs in the sense used in this paper. Leinfelder (1994b) pointed to a distinct misfit with general circulation models, particularly with the Moore numerical general circulation model (GCM), which suggests water temperatures less than 10°C off the Neuquén basin and partial cover of Patagonia waters by sea ice (Moore et al., 1992a; Moore et al., 1992b; Ross et al., 1992). The numerical GCM model of Valdes and Sellwood (1992) postulates water temperatures down to 8°C in the Neuquén and Patagonia area, which also appears implausible considering the reef varieties there. Kiessling et al. (1999) have argued that the Neuquén and Patagonia basins might have been well protected by an elevated arc system, allowing for a differentiation of water temperatures relative to the open ocean. The peak of all coral

reefs well above 30°C latitude, however, shows that sea-water temperature and thus climate was much more equable than today, at least in marine and coastal areas.

There are no extreme high-latitude sites for Middle Jurassic reefs (Figs. 3, 17), but coral reefs still show a somewhat wider distribution than today, ranging from 37° N (England) to 32° S (Madagascar). This difference from the Late Jurassic situation is considered to be caused by a less equable climate and by the lack of suitable carbonate-dominated habitats, because shelves were not as widely flooded as during the Late Jurassic.

Early Jurassic coral reefs grew mostly within the range of 30° N to 30° S (Fig. 17), thus mirroring the distribution of modern reefs, whereas the widespread bivalve banks of this epoch expanded from 58° N (western Canada) to 38° S (Chile).

Insalaco (1996b) and Insalaco et al. (1997) have attempted to evaluate differences in growth rates and diversities of Oxfordian corals along a paleolatitudinal gradient to highlight climatic differences. Fig. 17 shows, however, that in nearly all latitudes reefs of various diversities co-occurred, emphasizing the decisive role of local and regional environmental settings for the determination of diversities (Nose, 1995; Leinfelder et al., 1996). However, Late Jurassic south Tethyan reefs are much rarer than north Tethyan reefs, are mostly small, and generally show only low to medium diversities (Fig. 17). This partially reflects the lack of favorable shelf settings, whereas the maximum distribution of reefs and the largest ratio of high- and medium-diversity to low-diversity reefs coincides largely with the availability of a broad shelf along the northern Tethys. Heavy tropical to subtropical rainfall at the northern margin of Gondwana (Parrish et al., 1982; Valdes and Sellwood, 1992) might have caused accelerated influx of terrigenous mud, explaining the scarcity of reefs, e.g., in northern India and northern Australia. In addition, the poor development of low-latitude reefs could be due to overheated waters, as in the "Supertethys scenario" of Moore et al. (1992a) and Moore et al. (1992b). Restricted nutrient availability (see below) and nonclimatic effects like ramp systems too wide to export reefal debris may additionally account for the scarcity of southern low-latitude reefs.

Modern reefs are generally adapted to nutrient-poor pelagic settings with low primary productivity. Excess of nutrients rapidly causes death of reefs, which is a major problem in conserving modern reefs (Hallock and Schlager, 1986). Individual reefs differ, however, in their nutrient situation. Highsmith (1980) and Hallock (1988) suggested that nutrient and related productivity patterns are directly reflected in the degree of bioerosion, which would be a challenging task to reproduce for Jurassic reefs. To date, global quantitative or at least semiquantitative data on Jurassic reefs unfortunately are not available, and the reef database indicates only that about 60% of all Jurassic reefs contain macroborers. Their distribution shows no distinct pattern, however, and data on rates of bioerosion are lacking. Local or regional investigations show that rate of bioerosion in Jurassic reefs varied enormously. Bertling (1997a), focusing on Oxfordian reefs from northern Germany, emphasized that increased bioerosion occurs in reefs suffering siliciclastic influx, which is in accordance with reports of intense bioerosion in many Upper Jurassic reefs of Iberia (Oschmann, 1989; Leinfelder, 1994a; Nose, 1995 and Schmid, 1996), France (Laternser, 2000) and England (Fürsich et al., 1994a; Insalaco, 1999). Intense bioerosion by boring sponges took place in somewhat deeper reefs rich in crusts from the Kimmeridgian of southeastern U.S.A. (Montgomery et al., 1999b; personal observations). Schmid (1996) also noted that microbial crusts from European Upper Jurassic reefs were frequently attacked by lithophagid bivalves. Middle Jurassic coral reefs from France and India may also be bored intensely (Lathuilière, 1982; Pandey and Fürsich, 1993).

The intimate relationship between rate of bioerosion and nutrients in modern reefs is due to the dependence of most boring organisms on availability of plankton and on the availability of soft algal turfs for epibenthic bioeroders such as echinoids. This in turn reflects higher nutrient availability (Highsmith, 1980; Hallock and Schlager, 1986; Hallock, 1988). It is partially the bioeroders themselves that prevent direct demise of the coral reef by overgrowth of soft algal turfs, showing that coral reefs in settings with slightly elevated nutrient values are dependent on these bioeroders. If this concept is correct, not only boring bivalves and sponges but also increased occurrences of filtering organisms such as serpulids and pteriacean bivalves, as well as mass occurrences of spines of regular echinoids, should be additional indicators of slightly elevated nutrient availability within Jurassic reefs (cf. Highsmith, 1980). Many of the Iberian reefs contain these features, and particularly high-latitude reefs of the Tithonian have considerable amounts of bivalves (Ramos, 1978; Scasso *vide* Flügel, personal communication).

If deposition of fine siliciclastics within reefs can be proven to have been coeval, it supplies another argument for slightly increased nutrient availability. On the basis of partially higher faunal diversities in terrigenously contaminated reefs, as well as on the ratio of high-density to low-density banding in Jurassic corals, Nose and Leinfelder (1997) and Leinfelder (2001) have argued that many Jurassic corals might actually have benefited from slightly increased nutrient rates. This shows that Jurassic scleractinians had started but not yet perfected their evolutionary pathway towards superoligotrophic settings of most modern reef corals (Leinfelder and Nose, 1999).

The numerical upwelling model for the Kimmeridgian (Price et al., 1995) yields an astonishing overlap with major reef domains of the Late Jurassic. According to this model, reefs west and north of South America (e.g., Patagonia, Mexico, Colombia), the southeastern U.S.A., the Lusitanian Basin at the Atlantic side of Morocco, the Oman–Madagascar–Kachchh area, the eastern part of the north Tethys, and Japan might have been affected by seasonal upwelling. Kimmeridgian black shales in the western part of Europe might be indicative that despite sluggish circulation, there was also increased availability of nutrients in parts of the European north Tethys shelf. Shelf configuration and postulated currents (Figs. 5, 6) might suggest a partial though very reduced and possibly seasonal upwelling driven by weak westerly winds, as suggested by Leinfelder (1993a, 1994b).

Microbial crusts, which normally show intense bioerosion, are particularly common along the U.S. Gulf Coast and in Iberia. Whereas their development depends on a variety of factors, particularly reduction of extrinsic sedimentation either by steepened slope settings or by transgressive episodes, their frequency in this area might also be partially due to increased nutrient availability, particularly when considering the extremely intense bioerosion by the boring sponge *Aka* in the Texas reefs (see above). Interestingly, Late Jurassic reefs from the Adria–Apulia triangle are attributable neither to any of the postulated weak upwelling zones nor to sluggish ocean circulation as postulated by the model by Price et al. (1995), but judging from the available data, almost all of them show high diversity. Data on faunal diversity seem, however, to reflect a broader participation of reef builders other than corals. Reefs represent a distinct concentration of stromatoporoid-dominated reefs and coral reefs with a high proportion of stromatoporoids and chaetetids. A possible explanation might be that these organisms were already better adapted to very oligotrophic settings than the corals themselves.

At the present state, this first picture of a global correlation of Jurassic reef growth and ocean currents can be only tentative and indistinct until further quantitative data are available.

At a more regional scale, however, interesting results on dependence of Jurassic reef development on the oceanic circulation system can be drawn in some greater detail already.

The sea-level-related punctuation of the Kimmeridgian succession of southwestern Europe and Germany by coral, sponge, and microbolite reefs was discussed in the sections above. Pure microbolites and stacked reefs with alternations of microbolite reefs and reefs with benthic organisms were interpreted as reflecting oceanographic changes during sea-level rise. All pure microbolites alternate, or are intercalated, with benthos-rich reef facies, or at least show horizons of benthic reefal fauna, which allows for bathymetric interpretation of these reefs (Leinfelder et al., 1994; Leinfelder et al., 1996). From this the minimum depth of dysaerobic or eutrophic events during the sea-level rise of the *hypselocyclus-divisum* chron can be evaluated, ranging from deeper than 90 m in southern Germany to 60 m in southern Portugal and 60 m in central Portugal but shallowing to 30–40 m in southern Spain and southwestern France (Leinfelder, 2001). The Spanish and French occurrences show only signs of strong eutrophication, indicating that oxygen depletion might have occurred somewhat lower. This example shows that, apart from bathymetric interpretation of reef-bearing levels, paleomapping of boundary layers, such as the oxycline, might also be possible by reef analysis.

APPLICATION OF JURASSIC REEF STUDIES TO HYDROCARBON EXPLORATION— A CURRENT EXAMPLE

Because structure and composition of Jurassic reefs intimately reflect physicochemical parameters and their dynamic change, Jurassic reefs represent valuable tools for basin analysis and, thus, hydrocarbon exploration, monitoring shelf configuration, tectonic activity, bathymetry, sea-level changes, and climatic and oceanographic patterns. In addition, Jurassic reef and carbonate platform systems belong to the most prolific and promising reservoir rocks of the world (e.g., the classical Arabian Upper Jurassic–Lower Cretaceous reservoir rocks: Sun et al., 1996; the Canadian–U.S. Gulf Coast reef trend: Presley and Read 1984; Montgomery, 1996; Hogg, 2000; or promising plays in central and northeastern Asia: Pätz and Kulke, 1994). One of the best land-exposed plays within Jurassic reefs and platforms is the Lusitanian Basin, which is thought to have lost most of its hydrocarbons by leaching and microbial decay owing to Tertiary tectonic inversion (Wilson et al. 1989). It nevertheless serves as a perfect case study for the tectonic, sequence stratigraphic, and ecological control of Jurassic reefal oil habitats (Leinfelder 1994b). The following example should illustrate such applications in a current hydrocarbon play.

Reef Studies Aiding Cotton Valley Reef Exploration (Upper Jurassic, East Texas, New Mexico)

For the past several years there has been intense, and partially quite successful, exploration activity in the East Texas basin, after discovering that 3D-seismic pinnacle structures might actually represent reef or reef complexes mostly of Kimmeridgian age (Cotton Valley Pinnacle Reef Play: Montgomery, 1996; Montgomery et al., 1999a; Montgomery et al., 1999b). Reefs are situated in at least two trends on carbonate ramps or tectonically more structured shelves along rift basins.

New results on Jurassic reefs from other parts of the world can be successfully applied to the reef play. No refined data can be published, but on the basis of the available literature, recently reviewed and updated by Montgomery et al. (1999a) and Montgomery et al. (1999b), open reports, and one of the writer's own inspection, reef types appear to be very similar to European

examples, including various types of coral reefs, mixed coral–sponge reefs, microbolite-dominated structures, and, to a lesser extent, siliceous sponge mounds. Porosity may be both primary (particularly in debris-rich high-energy types) and secondary (e.g., in sponge reef types), but porosity development appears to be related largely to primary facies development (Montgomery et al., 1999a; Montgomery et al., 1999b). High porosity appears to be also in some places due to reef-type-related intense activity of boring organisms, which can completely wipe out original structures (unpublished data). The partially very thick pinnacle structures as well as available well data suggest that reef growth occurred in different time intervals, so that reef pinnacles represent stacked reef structures developing discontinuously and exhibiting bathymetric jumps, rather than continuously growing keep-up or catch-up reefs. Buildups of the outboard trend such as the Vanderbeek buildup were situated off an indistinct shelf break. Vanderbeek starts with a shallow-water, debris-rich initial coral buildup deepening into a microbial-crust-rich coral–sponge buildup to possibly shallow again before finally becoming drowned, which implies growth during different episodes of sea-level rise and stillstand (Montgomery et al., 1999a). Outboard reefs hence show partial similarities with vertically zoned, partially drowning Oxfordian and Kimmeridgian reefs of the Portuguese Lusitanian Basin, such as the Barreiro buildup (Ellis et al., 1990) or the Monte Gordo reef (Leinfelder, 1994a), although the Portuguese reef structures are much smaller. Inboard buildups probably started growing behind the outback buildups, possibly during a pronounced backstepping event related to the drowning of the outboard buildups (Montgomery et al., 1999a; Montgomery et al., 1999b). A published example of an inboard buildup is the Frost buildup. Frost, Riley, and others may show several cycles of coral–microbial reefs intercalated with reef debris and debris-rich coral reefs, again suggesting several subsequent episodes of sea-level change including subaerial exposure events (Montgomery et al., 1999b). Upper-ramp reefs encased in debris, and partially with vertical differentiation, are also widespread in the Lusitanian Basin (e.g., reefs of the Amaral formation; Nose, 1995) and in eastern Spain (e.g., Tormon reefs, Yabaloyas reefs; Baumgärtner and Reyle, 1995; Leinfelder et al., 1993b; Nose, 1995). Position of the East Texas inboard reefs is not always arbitrary, however, inasmuch as quite some structures appear to be situated at the edges of faulted uplifts and tilted blocks, partially related to development of salt pillows (Montgomery et al., 1999b). This is again similar to other reef settings from the Lusitanian basin, such as the Ota and the Montejunto buildups, both of which exhibit strong lateral facies differentiation. A more detailed bathymetric and sequence stratigraphic analysis of some of East Texas stacked reef structures should allow the development of a better sequence stratigraphic framework and allow updip and downdip predictive interpretation of the facies and associated porosity development of other pinnacles known only from seismics. Side track interpretation should also not be neglected because it can be expected from the Lusitanian examples that Texas inboard reefs situated along structural highs and at the margins of salt pillows may exhibit distinct lateral facies differentiation.

SYNTHESIS AND CONCLUSIONS: JURASSIC REEFS THROUGH TIME AND SPACE

The Interplay of Factors Controlling Reef Growth at a Regional and Global Scale

The evolution of reef patterns during the Jurassic reflects the modulation and positive feedback of various controlling mechanisms, which encompass (1) evolution and radiations of corals

and other reef organisms, accompanied by (2) new adaptational strategies of corals; (3) continental reorganization owing to the increasing breakup of Pangea, resulting in major reorganization of current systems, and (4) sea-level rise. These had important feedbacks on climatic changes, which itself is another crucial factor controlling reef growth.

Evolution and Diversification of Taxa.—

After scleractinian corals almost became extinct at the end of the Triassic, coral taxa had to evolve and radiate anew. The capacity for building coral reefs was achieved already during the Hettangian and Sinemurian but still by taxa surviving the end-Triassic faunal collapse. It was not before the Late Sinemurian that reef growth became more common. True Jurassic coral associations did not exist before the Pliensbachian, and more widespread reef growth did not take place before the Sinemurian. Numbers of Oxfordian and Kimmeridgian genera amount to about 130, with major new groups of corals evolving. Siliceous sponges had reef-building potential throughout the entire Jurassic. Among the bivalves, the lithotid evolution very successfully created an extended belt of biostromes in lower latitudes during the middle part of the Early Jurassic, but the group became extinct shortly afterwards already. In contrast, oysters showed a continuously growing potential to produce reefs in the Middle and Late Jurassic, although generally restricted to marginal, salinity-controlled environments. Encrusting organisms also diversified during the Late Jurassic, with new forms such as the Jurassic–Cretaceous *Tubiphytes morronensis*, *Koskinobullina*, or the newly formed association of the *Lithocodium–Troglotella* consortium. Coralline red algae were of no importance. Their first ancestors developed during the Late Jurassic, but unlike today they played no major role in reef formation. As in Triassic times, solenoporacean red algae acted as additional but rarely dominating reef builders. The same can be stated for stromatoporoids, chaetetids, and calcisponges, which diversified in the Late Jurassic.

New Adaptational Strategies.—

Scleractinian corals started conquering nutrient-poor settings owing to the development of the photosymbiotic relationship with zooxanthellae. Growth rates and stable carbon isotopes show, however, that such adaptation was far from being perfect even in the Late Jurassic. As a consequence, coral reefs were frequently situated in settings influenced by a mild terrigenous influx or in supposed upwelling zones. Growth within terrigenous material triggered partial adaptation towards turbidity and siltation stress, such as mud-sticking corals. One coral association even conquered brackish-water settings during the Late Jurassic. Microbolite development benefited from slightly elevated nutrient concentrations and, possibly, enhanced alkalinity, and helped corals form true frameworks. Stromatoporoid reefs or mixed coral–stromatoporoid reefs might have been better adapted to oligotrophic settings than pure coral reefs. Siliceous sponges probably showed no new adaptational strategies, but could occur in a great variety of nutrient regimes. Owing to such adaptational strategies there was a wide environmental range of reef settings, particularly during the Late Jurassic, resulting in very broad dimensions of the “reef window” and the rapid spreading of reefs all around the globe.

Abiotic Regional and Global Factors.—

Jurassic reef growth occurred on very stable ramp-type, passive continental margins and adjacent epicontinental seas (e.g., European northern Tethys), at steepened and tectonically frac-

tured passive continental margins (e.g., parts of southern Tethys margin), within rift basins (e.g., North Atlantic, Lusitanian Basin, Kachchh Basin) and at active plate margins (e.g., Chile, Peru, Argentina). However, there was a pronounced structural reorganization in the course of the Jurassic. Rifting led to subsequent drowning of shallow-water platforms and related loss of reefal shallow-water settings in the southwestern Tethys. After an initial rift stage characterized by deposition of evaporites and dolomites, the Lusitanian Atlantic–Caribbean realm underwent a subsequent gulf-stage development. Some Tethyan carbonate platforms with steep bypass margins remained uplifted. A structural “revolution” was the crustal segmentation and deep connection of the Tethys–Atlantic seaway at the transition from the Middle to the Late Jurassic, resulting in the creation of many new reef environments by transpressional movements (southern Tethys) and a second rift episode (Lusitanian and U.S. Atlantic domains). Crustal segmentation was followed by increased sea-floor spreading, raising sea level further, thus creating new sites for reef development, particularly on the north Tethys shelf. This established a global circumequatorial seaway facilitating larval distribution, reorganized upwelling zones, and equalized the climate, which in turn allowed coral and stromatoporoid reefs to expand into very high paleolatitudes. The buffering of climatic contrasts slowed down oceanic circulations in many parts, giving rise to occasional but widespread oxygen depletion. This still might have allowed reef growth, though only in the form of pure microbolite reefs. In this scenario, reef growth was additionally governed by third-order sea-level rise, which increased the potential for reef growth by further reducing extrinsic sedimentation. However, it was often only during fourth-order or fifth-order sea-level rise that “reef windows” actually opened.

The Early Jurassic Reef Pattern: Starting Anew, Experimenting with Bivalves, Concentrating in Morocco

The general scarcity of Early Jurassic coral reefs was caused mainly by evolutionary restrictions (Stanley, 1988, 1996; Flügel, this volume) as well as by the lack of available habitats (Leinfelder, 1994a). The few, worldwide scattered Hettangian and (Early) Sinemurian coral reefs are dominated by survivors of the Triassic faunas generally adapted to the siliciclastic sedimentation regime of the earliest Jurassic. With Morocco as the central domain, the main radiation of the typical Jurassic coral fauna apparently occurred in the Late Sinemurian and the Pliensbachian (cf. Beauvais, 1986). The concentration of Lower Jurassic reefs, especially in Pliensbachian time, on the Moroccan and the western Tethys region was induced by rift tectonics, causing the development of extended isolated platform areas and adjacent deep marine troughs (e.g., High Atlas trough), which separated platforms from neighboring cratons and reduced sediment input into the platform areas. On the other hand, the extensive rift-related salt deposits of the earliest Jurassic in the North Atlantic Lusitanian Basin (Ziegler, 1988) indicate a strong aridity in adjacent areas and also a reduced sediment input. Sponge–microbial mud mounds and coral reefs could therefore develop continuously in the Moroccan domain, whereas in other siliciclastically stressed domains the growth of rare reefs was limited to short highstand phases of the sea level (e.g., microbial mud mounds of Portugal; Dromart, 1991). Difficult to interpret in terms of climate and temperature is the distribution of *Lithotis* (s.l.) reefs. They are common and span a relatively wide latitudinal range (34° N to 33° S) but are generally restricted to the southern Tethys margin. This bivalve group was apparently able to colonize different ecological, partly highly stressed habitats on inner-platform areas (Dresnay, 1977; Geyer, 1977) and at the platform edge (Scheibner and Reijmer, 1999) and apparently partly competed with corals. However, this experiment ended in the Toarcian with the disappearance of *Lithotis*

reefs. In addition, the occurrence of *Lithiotis* in the eastern Pacific (Oregon) during the Pliensbachian is a good hint for the opening of the Hispanic corridor already at this time (Nauss and Smith, 1988). Other evidence for the existence of this seaway comes from benthic ostracods (Boomer and Ballent, 1996). However, this seaway could apparently not be used by corals to extend reef growth into the western hemisphere, except for some minor migrations (Stanley and Beauvais, 1994).

*The Middle Jurassic Reef Pattern:
Preparing the Way for the "Reef Age"*

At the beginning of the Middle Jurassic, reefs were driven back to possibly one single reef domain in Morocco (Dresnay, 1971; Park, 1983), although reefal coral limestones of possible Aalenian age are additionally reported from Tadjikistan (Baratov, 1976). Subsequently, scleractinians rapidly extended, mainly on the northern Tethyan shelf (Fig. 3). As in the Early Jurassic, coral-bearing deposits were still rare around the Pacific and scleractinian reef sites developed mainly in the shallow shelf areas of the Tethys (e.g., Europe, Saudi Arabia, Madagascar). Most probably, connecting seaways existed between western Canada, South America, Europe, and the southern Tethys, whereas communications across Panthalassa between southeast Asia and America still seem very unlikely in Middle Jurassic times (Beauvais, 1989a). In the Callovian, reef frequency declined a little but remained on a moderate level. Siliceous sponge-dominated reefs, occurring in deeper platform settings, gained no wide distribution, and mixed coral-siliceous sponge reefs are not found except in one domain (southern France; Lathuilière, 1982).

In general, Middle Jurassic reef sites and reef domains were not much more common than Early Jurassic occurrences (Figs. 7, 8), extending from 32° S to 38° N without conquering the high-latitude zone. This distribution reflects, to some degree, the reduced availability of suitable carbonate-dominated shelf habitats owing to the still lower sea level relative to the Late Jurassic. It also partially reflects tectonic drowning of south Tethys shallow-water platforms such as the Trento platform of the Adria-Apulia triangle, which still existed during the Early Jurassic (Leinfelder, 1994b; see Ziegler, 1988). Unlike for parts of the Early Jurassic, taxa availability was high enough to construct considerably complex coral reefs (Leinfelder, 1994b), which occurred whenever suitable habitats were available (e.g., eastern France, Lusitanian Basin; see above). Corals already had the ability to grow in restricted settings (e.g., Kachchh, India; see above), although this feature became more pronounced during the Late Jurassic. A major difference from the Late Jurassic was, however, the lack of a circum-equatorial seaway (the "Hispanic" corridor), which, except for its Early Jurassic predecessor, opened only at the transition from the Middle to the Late Jurassic.

The Late Jurassic "Reef Age": Reef Expansion and Diversification Owing to Major Reorganization of the Globe

The Late Jurassic "Reef Age" was initiated by the creation of the global east-west current system, which must have aided considerably in the global distribution of coral larvae and mixing of genetic codes, stimulating further radiative evolution (cf. Veron, 1995).

The new oceanic corridor, together with the rapid sea-level rise of the Callovian-Oxfordian, must also have greatly reduced mid-latitude climatic contrasts, which might have been a hindrance for further development of Middle Jurassic reefs.

The vast expansion of Oxfordian coral reefs was possible owing to a large number of available reef taxa and by improved adaptation to a broad range of environments, such as

terrigenously influenced settings, environments with different primary productivity and nutrient characteristics, or even hyposaline environments. A great variety of structural and environmental reef settings was caused by renewed rifting and halokinetic uplift in the North Atlantic-Lusitanian and west Tethys realm, by widening the Tethys ocean, by ongoing sea-level rise enlarging epicontinental seas, and by occasional regional oxygen depletion. Very different reef types, including coral reefs, stromatoporoid reefs, siliceous sponge mounds, pure microbial mounds, oyster reefs, or mixtures of them consequently found suitable places to develop.

The distinct reduction of coral reef occurrences from the Oxfordian into the Kimmeridgian and the coeval disappearance of most siliceous sponge mound settings is in partial contrast with sea level still rising. The increased influx of siliciclastic material onto the northern Tethys shelf is the main culprit; it often overcompensated accommodation space and impoverished reefal settings. Increased terrigenous influx was, however, related not only to rift activity but particularly to a further balancing of the Jurassic climate as a result of the high sea level, probably resulting in increased rainfall and related terrigenous runoff. During the Oxfordian about 50% of all reef sites were situated in deeper waters, nearly all of which were on the northern Tethys shelf and in the Atlantic realm. In contrast, only about 25% of Kimmeridgian reefs are assigned to deeper-water reef sites in the reef database, all of which were concentrated in southern Germany except for three occurrences in Portugal and Spain.

Loss of habitats triggered further reduction of reef sites during the Early Tithonian, which also resulted from overcompensation of sea-level rise by sedimentation and, possibly, reduced subsidence. Development of coral and sponge reefs persisted locally in southern Germany, occurred on the short term during some flooding episodes in the Atlantic Lusitanian realm as well as scatteredly in some other settings, including high-latitude occurrences. Early and Mid-Tithonian reef formation, however, had a peak development on the Adria-Apulia polygon. From the Mid-Tithonian onwards, falling global sea level dramatically accelerated the withdrawal of reefs in most areas.

*The Latest Tithonian-Berriasian Time:
Decline of the "Reef Age"*

Reduction of reefal settings in the Late Tithonian and Berriasian coincided with extreme shallowing and subaerial exposure owing to a general sea-level fall. Mostly impoverished reefs grew whenever third-order sea-level rise opened the "reef window" for a short while. This was again contrasted by the development on the Adria-Apulia platform.

*Jurassic Reefs from the Adria-Apulia Polygon as
Ancestors of Modern Reefs?—A New Hypothesis*

Summarizing Jurassic reef patterns through time, Jurassic reefs started very scatteredly in the Hettangian to develop a first major reef domain (Morocco) during the Sinemurian-Pliensbachian. This was followed by an episode of punctuated conquering of new reef domains in the course of the Middle Jurassic. Major crustal reorganization and associated climatic and oceanographic changes led to a worldwide bloom of coral, siliceous sponge, and microbial reefs during the Oxfordian. Reef domains then disappeared in a mosaic fashion to find their final major refuge on the Adria-Apulia polygon, which was close to the first major reef domain of the Jurassic, i.e., Morocco. Throughout the Late Jurassic, the shallow-water Adria-Apulia reefs differed from other shallow-water reefs by the dominance, or strong participation, of stromatoporoids and chaetetids. On the basis of

this peculiar character of reef biota, together with its isolated occurrence within the Tethys sea, and indicators from oceanographic modeling pointing to oligotrophy in this area, we propose the new hypothesis that these reefs had already developed adaptations to strictly oligotrophic settings similar to modern coral reefs. Jurassic reef development thus probably encompassed two evolutionary strategies: (1) the adaptation to terrigenous settings and fluctuating or slightly increased nutrient concentration, allowing for the wide expansion of Late Jurassic reefs in a great variety of environmental settings, and (2) the adaptation to superoligotrophic tropical intra-ocean settings. The first strategy was largely wiped out by the demise of such marginal settings owing to the Late Jurassic–Berriasian sea-level drop as well as by strongly fluctuating coastal and epicontinental environments and competition with rudist bivalves during the mid- and Late Cretaceous. However, the second strategy, having developed on a cluster of remote seamounts and carbonate platforms within the Tethys, might have provided the nucleus for further colonization of superoligotrophic seas and thus represents the ancient heritage of our modern reefs.

ACKNOWLEDGMENTS

We are particularly indebted to Erik Flügel and Wolfgang Kiessling for stimulating this challenging evaluation, and for their manyfold support and patience. Jörn Geister, Bern, and Markus Bertling, Münster, critically reviewed the manuscript. This paper benefited greatly from an eight-year collaboration with many German and foreign colleagues under the umbrella of the priority program "Biogenic Sedimentation—Evolution of Reefs" from the German Research Foundation (DFG). Financial support by the DFG is gratefully acknowledged (projects Le 580-4/1-6, Le 580-10/1).

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