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A Coral-microbialite Patch Reef from the Late Jurassic (*florigemma*-Bank, Oxfordian) of NW Germany (Süntel Mountains)

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KEYWORDS: CORAL MICROBIALITE PATCHREEF – *THAMNASTERIA DENDROIDEA* – ECOLOGICAL SUCCESSION – NW-GERMANY – JURASSIC (OXFORDIAN)

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SUMMARY

An *in situ* Oxfordian patch reef from the Süntel hills (*florigemma*-Bank, Korallenoolith, NW-Germany) is described. It is composed of an autochthonous reef core overlain by a 'parautochthonous' biostrome. The exposed reefal area amounts to about 20 m in lateral and up to 4 m in vertical direction. Nearly all major marine reefal fossil associations from the Tethyal realm are present.

In the reef core two facies can be distinguished: (1) *Thamnasteria dendroidea* thicket facies and (2) thrombolite facies.

The first facies is composed of a thin branched autochthonous coral thicket mainly constructed of *Th. dendroidea* colonies with only a minor portion of *Stylosmilia*. Frequently, the *Th. dendroidea* branches laterally coalesce bridge-like forming a delicate initial framework which was subsequently reinforced by thick microbial coatings, that make up approximately 80% of

the rock volume. This facies is an excellent example for microbialite binding in reefal architecture. Additionally, several generations of micromorphic and partly cryptic encrusting organisms settled on the *Th. dendroidea* branches and microbialite crusts. They successively overgrow each other and fill the space between the coral branches in the thicket forming a characteristic community replacement sequence.

Initial colonization of the *Thamnasteria dendroidea* took place on an oncoidic/bioclastic hardground. During this early phase of reefal development, microbialites also played an important role in stabilizing and binding the reef body.

The thrombolite facies (2) occupying nearly the same volume of the reef body as facies type (1) consists of a thrombolitic microbialitic limestone which fills the interstice between the coral colonies. It shows a considerably lower faunal diversity than the *Th. dendroidea* facies. Numerous cavities are interspersed in the thrombolite and are almost completely filled with dolomitized allomicrite. In contrast, microbialite and allomicrite adjacent to the reef core rarely reveal any dolomitized areas.

Above the reef core, mostly toppled *Solenopora jurassica* thalli occur together with a few massive *Isastrea* colonies forming a parautochthonous biostrome. They are inhabited by a low diverse assemblage of encrusting organisms. Microbialites are only rarely present in this biostromal unit.

The patch reef is developed within a lagoonal limemud facies both separated by a sharp interface. In contrast, continuous facies transition exists between the *Solenopora* biostrome and adjacent deposits which are characterized by micritic to pelmicritic limestone sometimes with lenses of oncoids. Debris derived from the patch reef is only sporadically intercalated in the reef surrounding lagoonal sediments. Gastropods, bivalves, and dasycladalean algae dominate the lagoonal biota. Up-section following the *Solenopora* biostrome nerinean gastropods become the most abundant species amounting to a '*Nerinea*-bed'. This horizon moderately elevates above the patch reef indicating, that it arose above the surrounding sea floor forming a relief.

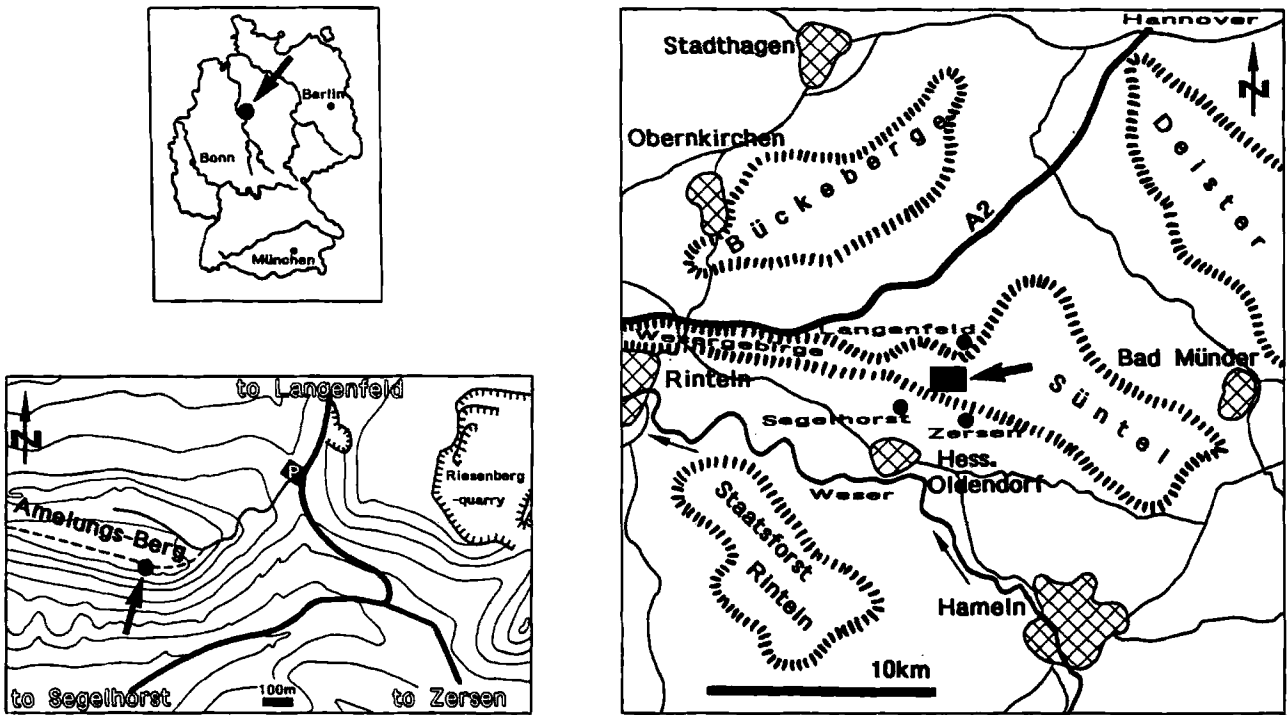


Fig. 1. Geographic position of the examined patch reef.

The patch reef established on a secondary hardground probably released by a minor transgression and a non-depositional regime. It grew up on a well-illuminated sea floor only a few meters below sea level. Only a low background sedimentation rate and modest water circulation are assumed during reefal growth. These features characterize an open marine lagoon.

A subsequent shallowing upwards trend caused emergence of the early lithified *florigemma*-Bank sediments. In the following erosional phase the reef core, *Solenopora* biostrome and 'Nerinea-bed' were sharply cut. Paleokarst phenomena (karst solution of the rocks, selective leaching of the aragonitic corals) truncate the surface of the *florigemma*-Bank. Released by a transgressive sea level, the paleokarst surface is densely inhabited by marine boring and encrusting organisms (oysters, serpulids). Karst cavities are filled with an oncoid-bearing bioclastic limestone with a large portion of siliciclastics. The *florigemma*-Bank is overlain by the reddish bioclastic sandstone of the 'Zwischenflözregion'.

1 INTRODUCTION AND PREVIOUS WORK

According to LEINFELDER (1993) and LEINFELDER et al. (1994), three different facies groups can be distinguished: (1) coral reef facies, (2) siliceous sponge reef facies and (3) microbial reef facies. Prominent examples of well-developed transitional facies types between the above terminal types are distributed nearly worldwide: e.g. sponge-microbialite buildups (BRUNTON & DIXON 1994, HERRMANN 1996, KRAUTTER 1997, MATYSZKIEWICZ & KRAJEWSKI 1996), or coral-microbialite reefs (INSALACO et al. 1997).

Compared to the well-studied SW-European Late Jurassic Tethyal reefs, those from high palaeolatitudes are insufficiently known (LEINFELDER et al. 1994:51). This is especially true for the Late Jurassic reefal facies of NW Germany, from which only little detailed paleontological data have been published. BERTLING (1989, 1993a) described corals and coral-associated taxa and discussed their guild structure. He attempted to define the environment in which the corals and Late Jurassic patch reefs or biostromes respectively grew (cf. NOSE 1995). REITNER (1994) and DELECAT (1996) studied a Lower Kimmeridgian oyster (*Nanogyra nana*) patch reef especially focussing on the reef-associated and binding microbialites. Mainly dealing with a redescription of an thecideidid brachiopod, SCHÜLKE (1997) gave a short characterization of a *Microsolenia* *Isastrea*-biostrome. Its megafaunal content was described by ZAWISCHA & SCHORMANN (1994).

This study focuses on an autochthonous coral-microbialite patch reef almost monospecifically composed of an *Thamnas-teria dendroidea* thicket. With the exception of HELM (1997), who provided the database also for this study, no similar reef type has been reported from the Late Jurassic of NW-Germany.

Additionally, this study aimed to describe a 'community replacement sequence' in the *Th. dendroidea* thicket during its growth. BRACHERT (1992), INSALACO (1996a), LEINFELDER et al. (1994), and SCHMID (1996) studied ecological replacement sequences in Late Jurassic reefs. FÜR- SICH & WERNER (1991) figured a comparable sequence but without discussing its implications. The sequence described here may help to identify counterparts in the Tethyal realm.

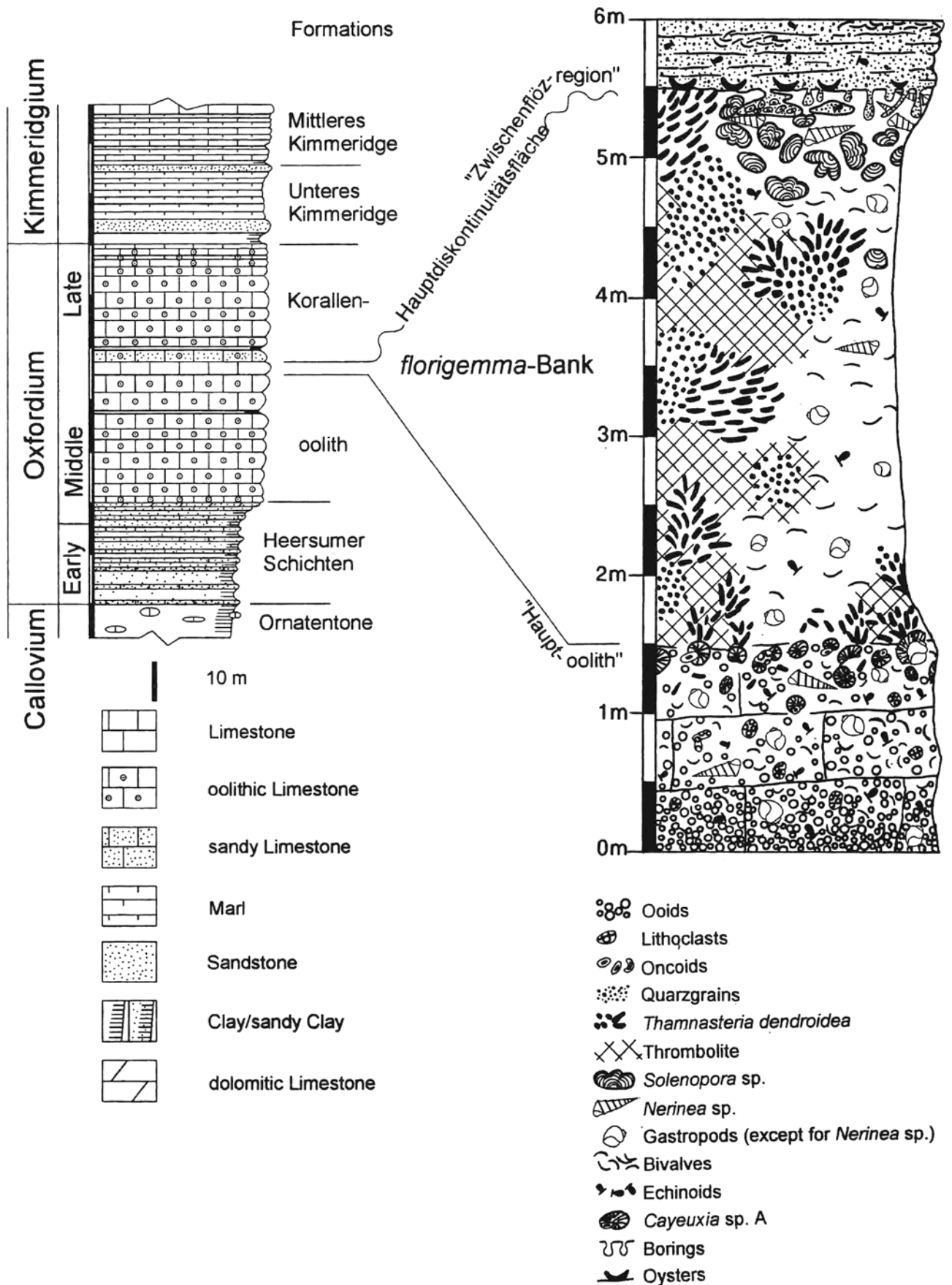


Fig. 2. Standardized vertical section of uppermost Callovian to Middle Kimmeridgian strata from the Süntel area (left; altered from SCHÜLKE 1992) and vertical section of exposed rocks from the outcrop studied (right).

2 GEOLOGICAL SETTING

Locality: The section examined is situated in the National Park 'Naturschutzgebiet Hohenstein' (Süntel) about 35 km WSW Hannover, NW Germany (Fig. 1), near the road between Langenfeld and Zersen. The strata crop out on the southern slope of the Amelungsberg (r 3518525/h 5785075).

Geological setting: The sedimentary sequence studied here is part of the Korallenoolith Formation, ?Middle to Late Oxfordian in age. The Korallenoolith Formation is mainly composed of oolitic limestones, followed by siliciclastics, iron-oolites and micritic limestones which are predominantly deposited in marine environments (MÖNNIG & BERTLING 1995, SCHULZE 1975). The reefal facies is restricted to a few horizons (BERTLING 1993b: Fig. 3; SCHÜLKE et al. 1998) in the Korallenoolith formation which is about 48 m thick in the Süntel area (KLÜPFEL 1931).

Late Jurassic was a time of tectonic instability in the study area released by crustal bulging of the 'North Sea Rift Dome' (ZIEGLER 1990). This instability resulted in extensive synsedimentary faulting in the Lower Saxony Basin: high subsidence in some areas, crustal uplifts in others (e.g. Süntel) (BETZ et al. 1987). Considering the NW-German Korallenoolith, this resulted in short distance lateral facies changes or omission surfaces, and stratigraphic lacunas mainly in uplift position (GRAMANN et al. 1997, MÖNNIG & BERTLING 1995, STINDER 1991).

The patch reef reported here is situated in the *florigemma*-Bank, a marker horizon which allows a lithostratigraphic subdivision of the Korallenoolith sequence (e.g. HOYER 1965). The *florigemma*-Bank consists of micritic limestone a few decimeter to several meters thick. It can be traced continuously over a distance of some tens of kms from the Wesergebirge (abandoned quarry "Wülper Egge", STINDER 1991) in the W to the Deister in the E (HOYER 1965). The erosional disconformity at the top of the *florigemma*-Bank (Hauptdiskontinuität) represents the Early to Middle Korallenoolith boundary in the WeserMountains (STINDER 1991).

New investigations in the Süntel uplift area indicate, that the *florigemma*-Bank is generally characterized by small patch reefs, constructed of almost monospecific thickets of *Th. dendroidea* with dense microbialitic coatings (SCHÜLKE et al. 1998).

The scarcity of ammonites in the Korallenoolith sediments (GRAMANN et al. 1997) and rare occurrences of microfauna (STINDER 1991) prevent a biostratigraphic subdivision of the Korallenoolith sequence. From the *florigemma*-Bank only a few ammonites are reported. According to KAISER (1979) the *florigemma*-Bank of the Hohenstein area (locality "Grüner Altar") has to be placed in the ammonite zone of *Perisphinctes cautisnigrae* which indicates lower Upper Oxfordian age. However, STINDER (1991) disagreed with this stratigraphical placement. In our opinion, the biostratigraphical data are by far too insufficient to subdivide the Korallenoolith sequence in the Wesergebirge

exactly, since they mainly base on the occurrence of 'facies-restricted' index fossils (Ostracoda, foraminifera). The exact biostratigraphical position of the *florigemma*-Bank remains unknown.

Correlation with sealevel curve: Relative sealevel changes of Late Jurassic in the Lower Saxony Basin are released by mainly two controlling factors. The global sealevel curve shows a shallowing upwards trend (e.g. HALLAM 1988) during most of the Late Jurassic. This development is recorded in a sedimentary sequence within the outcrop area ranging from outershell fine-grained siliciclastics in the uppermost Middle Jurassic, followed by fine- to coarse-grained siliciclastics and carbonates ('Heersumer Schichten', comp. Fig. 2) in Early Oxfordian, and oolites, iron-oolites, lagoonal carbonates, and micrites in Middle and Late Oxfordian (Korallenoolith) deposited on a carbonate platform.

The general trend is partly overprinted by extensive blockfaulting with synsedimentary horst and graben development (e.g. GRAMANN et al. 1997, HOYER 1965, SCHÜLKE 1993). Crustal uplift in the Süntel area is indicated by several omission horizons, e.g. the 'Hauptemersionsfläche' at the top of the *florigemma*-Bank' (HELM in press, SCHÜLKE 1992, 1993). Block-faulting in this part of the Lower Saxony Basin releases a highly differentiated facies distribution which can not be followed over 5 to 15 km in each direction. Even the most prominent 'Hauptemersionsfläche' can not be observed over more than a few tens of kms.

Following a maximum lowstand at the base ('Unteres Kimmeridge' Lower Kimmeridgian) represented by a 5 m thick sedimentary sequence of tidal or possibly beach sediments ('Unterer Grenzsandstein', cf. SCHÜLKE 1993), the Kimmeridgian is developed transgressively again.

3 SEDIMENTARY SUCCESSION OF THE OUTCROP

The studied outcrops are a small vertical cliff (HELM, in press) and a small isolated rock needle about 8 m south of it (Fig. 3). The beds gently dip (3-5°) in northward direction. The patch reef is exposed in the vertical cliff. The reefal architecture can be observed in weathered surfaces perpendicular to bedding.

The sedimentary sequence ranges from the top of the 'Hauptoolith member' to the base of the 'Zwischenflöz-region' (Fig. 2). The base of sequence, (about 6 m thick) is exposed in the isolated rock needle. The uppermost part of the Hauptoolith is developed as massive fossiliferous (gastropods, bivalves, brachiopods, echinoids) oolite. Towards its top the ooids become rarer and the matrix more abundant. It is overlain by the 4 m-thick *florigemma*-Bank containing the patch reef. The *florigemma*-Bank of the Korallenoolith is represented by a massive fossiliferous micritic limestone with an increased organic (bituminous) content (KAISER 1979). The base of the *florigemma*-Bank is exposed at the peak of the crag (Fig. 3). Outcropping beds at the vertical cliff allow a maximal lateral observation of about 20.5 m (Fig. 3).

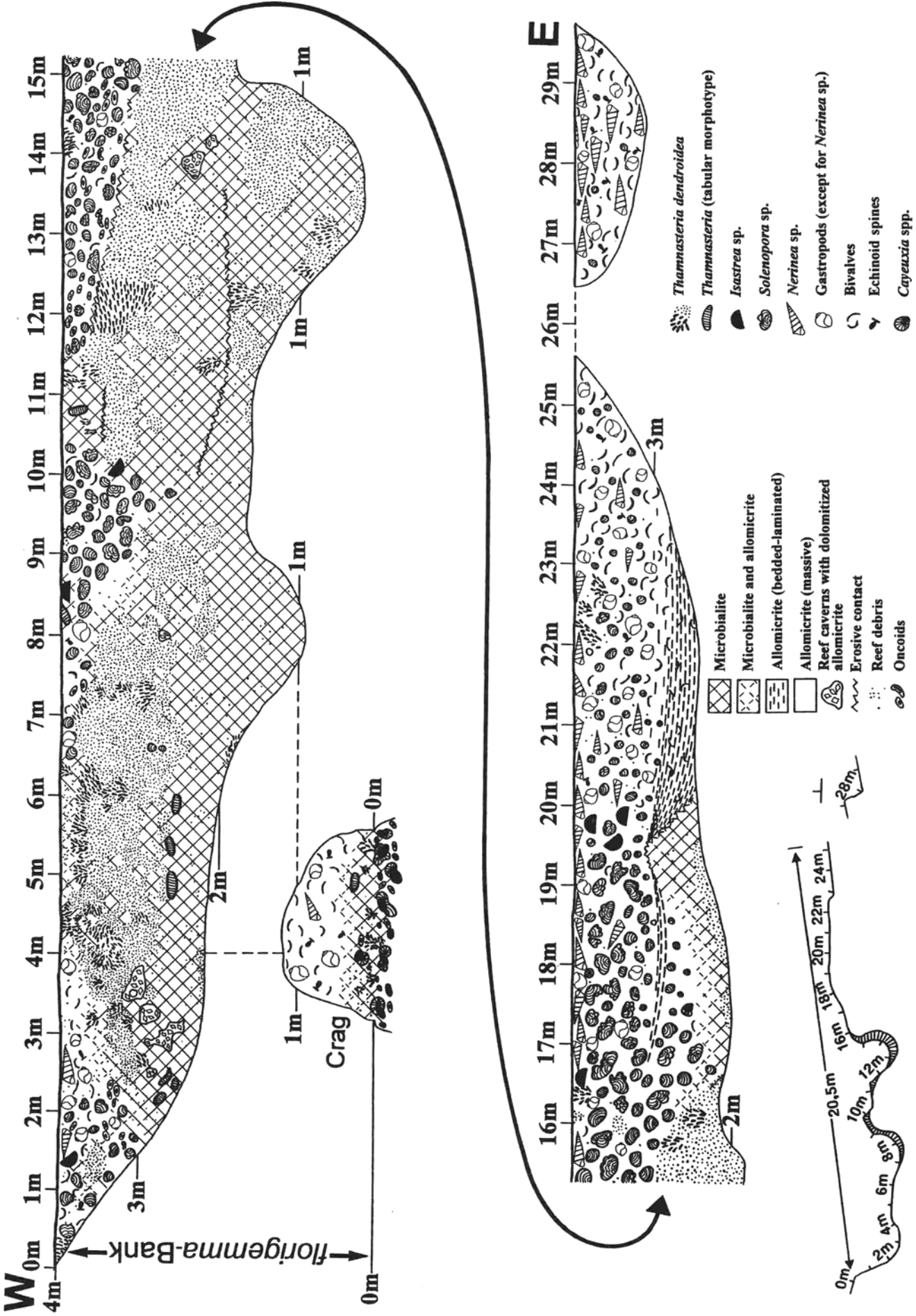


Fig. 3. Simplified sketch of exposed patch reef and facies distribution.



Fig. 4. Map of a *Thamnasteria dendroidea* thicket on a weather worn surface. Dark spots represent cut coral branches. The mapped surface is positioned between 3.5 and 6 m lateral extension in Fig. 3. Scale of bar is 10 cm.

The top of the *florigemma*-Bank is developed as an erosional unconformity resulting from subaerial exposure, the so-called 'Hauptdiskontinuität' (HELM, in press). Paleokarst features such as karst pockets and leached coral branches penetrate the topmost part of the *florigemma*-Bank. Following the re-establishment of marine conditions, oysters and serpulids encrusted the karst relief and were subsequently bio-eroded. Following a sharp contact, ferriferous and calcareous sandstone overlies the unconformity filling the karst caverns. Up-section, lenses rich in bioclasts (bivalves) are intercalated in the sandstone. Overlying beds belong to the *Zwischenflözregion*; its exposed thickness does not exceed 0.5 m.

4 METHODS

The patch reef which is exposed on weather-worn surfaces was studied in the outcrop and by microfacies analysis. During field work, well discernible *Th. dendroidea* branches (Fig. 4) and *Solenopora* thalli (Fig. 5) were outlined with permanent markers on about 80 plastic

sheets (German DIN A4 size, cf. WEIDLICH et al. 1993). They were arranged in order to gain information about overall reef fabric, colony size and distribution, intra-colony patterns, population density, orientation of *Th. dendroidea* branches and *Solenopora*-thalli (cf. KÖNIGSHOF et al. 1991). All the plastic sheets cover a rock surface of approximately 4.5 m² (Fig. 4). About 60 oriented samples were cut and polished mainly to identify the presence of reefal framework, encrusting biota, borings and the distribution of microbialites around *Thamnasteria dendroidea* branches. Samples containing interesting fossils and structures were used for 15 thin sections.

It was nearly impossible to extract macrofossils from the rock surrounding the patch reef. Rare specimens were identified to generic or specific level. Best preserved samples with corals (cf. Chap. 6.7) have been dissolved in hydrochloric acid. Coral moulds (Pl. 14/1-7) and the insoluble residue (Pl. 14/8, 19/3) have been examined. The material is housed under catalogue number 1998 I 1 ff. in the collection of the Institut für Geologie und Paläontologie at the Universität Hannover.

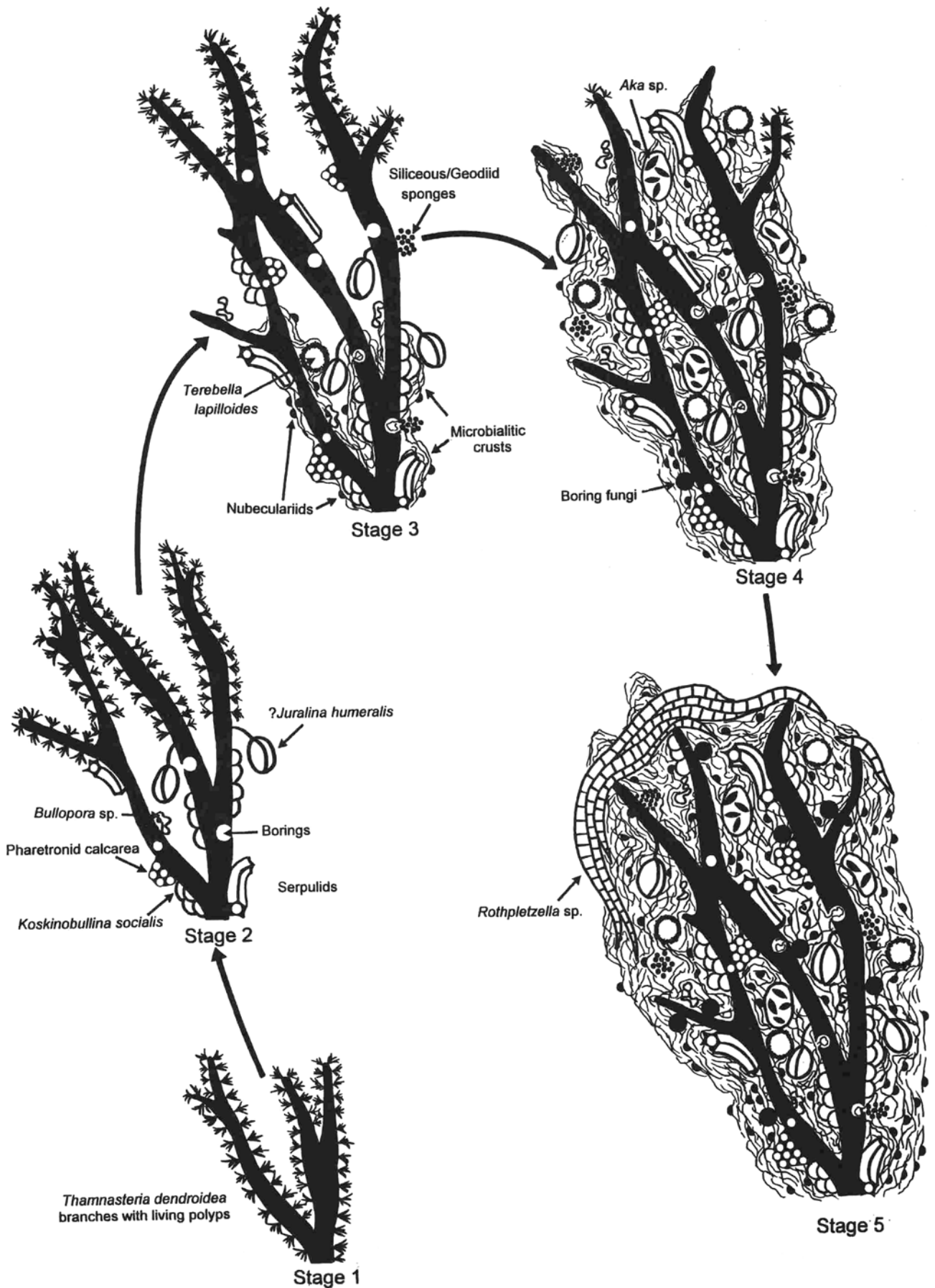


Fig. 5. Schematic sketch of community replacement sequence (Chap.6.3).

5 HAUPTOOLITH: PRE-REEF DEPOSITS

The uppermost part of the Hauptoolith (1.5 m) exhibits a microfacies sequence, that comprises packstones to grainstones or oosparite in the lower part grading upwards into wackestone or biomicrite.

In the lowermost part of the Hauptoolith, ooids are the most common rock-building components. Their size varies around 0.2-2 mm in diameter. Compound ooids are subordinate to frequent. Intraformational oolitic limestone fragments are rare (Pl. 19/4). Detrital quartz occurs scattered in the matrix or rarely serves as nuclei of ooids.

The rich macrofauna includes bioclasts up to 1 cm in size of gastropods (e.g. *Nerinea* sp.), bivalves, rhynchonellid brachiopods and echinoid spines. The latter are in places syntaxially overgrown. In the upper part, *Th. dendroidea* clasts have been identified most of them larger than 1 cm. The diverse microfauna of the Hauptoolith member is frequently recorded as nuclei of ooids. Predominately coarse agglutinated lituolid foraminifers (*Ammobaculites*) occur similar to those figured by HÜSSNER (1985), LEINFELDER (1994) and WENDT-JUBER (1990). Their walls consist of peloidal grains without internal structure, and fragments of *Acicularia*. Even large ooids and tests of smaller foraminifers (mainly miliolids) were used for wall construction. Grains originate from the adjacent sediments.

An environmental control of grain choice and size used for agglutination is assumed (cf. BUCUR et al. 1996, HÜSSNER 1985). Foraminifers are in early ontogenetic stages closely coiled, later uncoiled, rectilinear and reach sizes of up to 6 mm length. Chambers are filled with micrite or sparitic cement. Smaller-sized lituolid or loftusiid foraminifera agglutinating finer-grained components (e.g. *Pseudocyclamina*) are also present.

Additionally, hyaline foraminifers (e.g. *Lenticulina*, *Nodosaria*, *Trocholina*) and Miliolids form a considerable part of the microfauna. Only one specimen of *Textularia* was observed. Bryozoans are rare in this part of the section. Broken thalli of dasycladalean algae (*Acicularia*) are frequent.

Bioclastics are frequently coated. The crusts vary from typical coated grains to micritic microbial rims enveloping the bioclasts. Both, terminal and transitional types are abundant. In addition, microbial envelopes on *Th. dendroidea*

clasts sometimes bear encrusting nubeculariid foraminifers. Cores of bioclasts are often recrystallized.

A few bioclasts and micritic crusts are bored by *Troglotella incrustans* WERNLI & FOOKES as described by HERRMANN (1996), FOOKES (1995), NOSE (1995) and WERNER (1986) from the Late Jurassic Tethyal realm. The encrusting ontogenetic stage of this enigmatic foraminifer (SCHMID 1996, SCHMID & LEINFELDER 1996) has never been observed.

The top of the Hauptoolith is characterized by an increased occurrence of *Cayeuxia* sp. A (Pl. 19/4). This porostromate algae encrusts bioclasts and other components (e.g. ooids) frequently by wrapping them partly to completely with a thick crust (Pl. 18/1) or growing in fan-like 'bushes'. The biggest specimen found is 1 cm in diameter. The inner diameter of the filaments varies between 0.045 mm to 0.085 mm. Tubes are closely juxtaposed to each other in a parallel to fan-like patterns. The angle of divergence of single tubes can reach up to 25°.

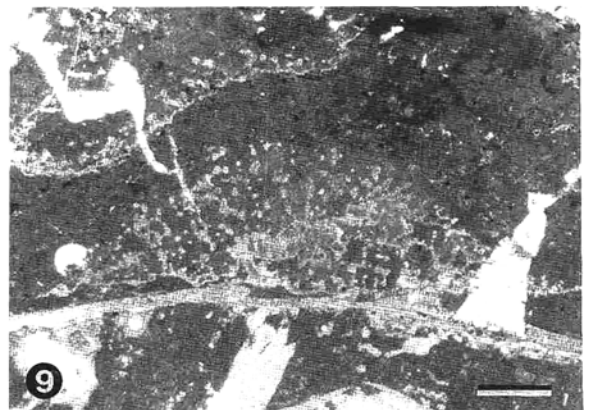
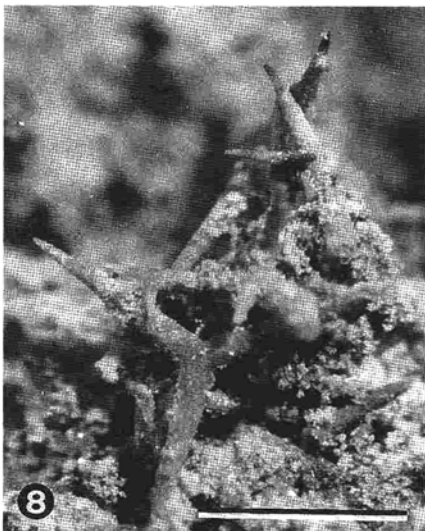
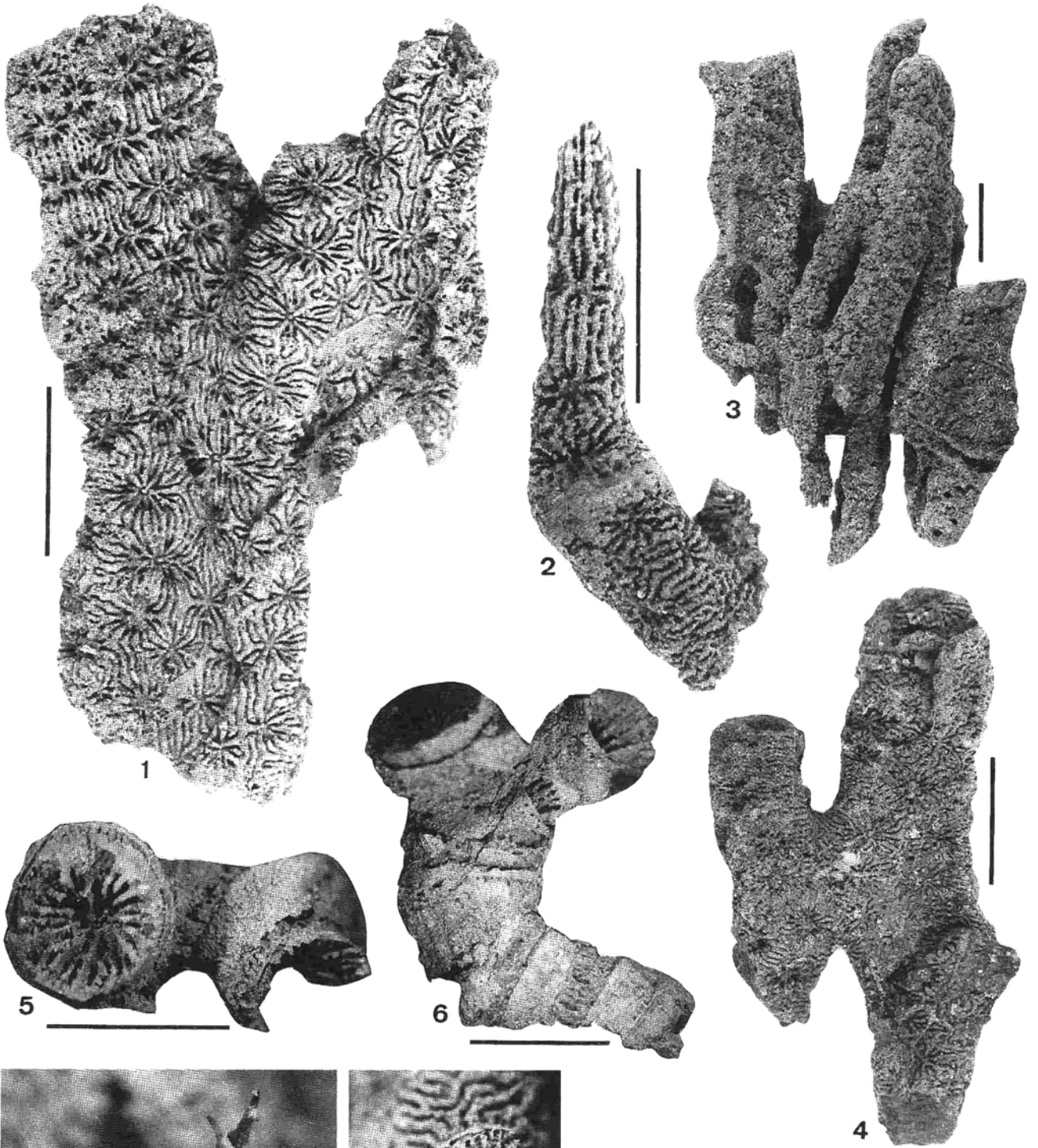
In the basal part of the exposed Hauptoolith, sparitic to microsparitic matrix and grain-supported components dominate, the latter showing stylolithitic contacts. Up-section the component content decreases and micritic, weakly dolomitized matrix forms the main part of the rock (cf. Pl. 19/4). Dolomite rhomboids are distributed irregularly to patchy.

Interpretation: Closely packed ooids in sparitic cement at the base of the succession are assumed to have been deposited in an environment with relative high water energy in a shallow water setting. The dominating micritic matrix and the poorly sorted components up-section indicate reduced water circulation (e.g. SCHULZE 1975) and a tendency towards less turbulent conditions.

With the exception of the abundant *Cayeuxia* sp. A in the topmost part of the Hauptoolith, all components are allochthonous. According to FEZER (1988), FOOKES (1995), NOSE (1995), SCHMID (1996), and SCHMID & JONISCHKEIT (1995), the growth of *Cayeuxia* took place in a (protected) lagoonal environment where it frequently coats bioclasts and other components (e.g. oncoids). The presence of *Troglotella incrustans* (SCHMID 1996; SCHMID & LEINFELDER 1996) and *Acicularia* (e.g. BAUMGÄRTNER & REYLE 1995, HERRMANN 1996, LEINFELDER et al. 1994) indicate a shallow environment with low to moderate water energy.

Plate 14 An Upper Jurassic coral-microbialite reef from the Süntel area, Lower Saxony. Reef core (*Thamnasteria dendroidea* thicket facies). Fossils of figure 1-8 delivered as coral or sponge castings. Scale of bar of Figs. 1-6 is 5 mm, scale of bar of Figs. 7-9 is 1 mm.

- Fig. 1. *Th. dendroidea* branch with flattened outline.
- Fig. 2. Uppermost part of a *Th. dendroidea* branch. Note the branch tapering to a tip.
- Fig. 3. Detail of *Th. dendroidea* thicket with nearly parallelly aligned and sometimes coalesced branches.
- Fig. 4. Coalescence of *Th. dendroidea* branches.
- Fig. 5. Two calices of *Stylosmilia* sp..
- Fig. 6. Side view of phaceloid *Stylosmilia* colony (Fig.5)
- Fig. 7. Juvenile ?*Stylosmilia* (arrow) in calicinal view fixed on *Th. dendroidea* branch.
- Fig. 8. Not identified siliceous sponge, etched sample of spicules with split tips.
- Fig. 9. Pharetronid *Calcarea* sp. B encrusting on bioclast.



6 FLORIGEMMA-BANK: PATCH REEF AND ADJACENT DEPOSITS

6.1 Facies distribution in the outcrop (Fig. 3, Tab. 1)

Vertical cliff: The patch reef consists of an autochthonous reef core and an overlying 'parautochthonous biostrome' as defined by KERSHAW (1994). The lateral extension of the reef core amounts to about 20 m with a maximum height of approximately 4 m. The reef core is cut after 3 m by an erosional disconformity (HELM in press).

The coral biohermal unit is subdivided into two separate facies types: (1) Coral thicket composed of branched morphotypes (Chap. 6.3) and (2) thrombolite (Chap. 6.4). Both types occupy approximately equivalent parts of the reef core volume in the middle to western part of the outcrop. They are overlain by the *Solenopora* biostrome facies (Chap. 6.5). In the eastern part of the cliff the surrounding non-reefal facies (Chap. 6.6) is developed.

Outcrop Crag: Here only the lower part of the *florigemma*-Bank is exposed showing small immature *Th. dendroidea* colonies which reveal extensive bioerosion. Microbialites expand from the coral colonies, coalesce, and fill up the space in between forming a brittle structure. About 30 cm above the Hauptoolith/*florigemma*-Bank boundary, a facies transition into lagoonal deposits can be observed.

6.2 Initial reef growth

As frequently stated (e.g. MULLINS et al. 1981, WERNER 1986), corals need hard substrates for their development. Size, surface, and stability strongly influence the success of their initial colonization (GEISTER 1983, NOSE 1995, SCHUHMACHER 1974, WERNER 1986). Although a contact between *Th. dendroidea* and its hardground base - in particular components coated by *Cayeuxia* sp. A - has never been observed, these components combined with a reduced sedimentation rate at the top of Hauptoolith initiated the development of patch reefs. Similar settings of

corals and reefs on secondary hardground layers, e.g. oncoids (FLÜGEL 1981, LEINFELDER et al. 1994, NOSE 1995, WILSON 1979) as well as the similarity of underlying deposits and the initial reef growth support this interpretation.

Due to continuous growth of the branched colonies, they rise above the non-stabilized substrate and become 'top heavy'. If their growth is not accompanied by (clastic) sediment input filling up the space between branches of colonies and adjacent to the colonies (cf. COATES & KAUFMAN 1973, RONIEWICZ & RONIEWICZ 1971), susceptibility to toppling increases (WERNER 1986). In the section studied, *Th. dendroidea* colonies are protected from toppling by the binding capability of microbialites. They coat the coral branches and protrude up- and sideways. Microbialite coatings of adjacent coral colonies coalesce and fill the interstices. Their syndimentary lithification creates a rigid fabric and encourages further patch reef development (LEINFELDER 1992, BAUMGÄRTNER & REYLE 1995, LEINFELDER et al. 1993a, MATYSKIWICZ & KRAJEWSKI 1996, NOSE 1995).

According to LEINFELDER et al. (1993), the development of microbialites reflects a non-depositional environment or a reduced background sedimentation rate. At Riesenber quarry, not far from the section investigated (Fig. 1), the Hauptoolith/*florigemma*-Bank boundary exhibits hardground characteristics (SCHÜLKE 1993) supporting this assumption.

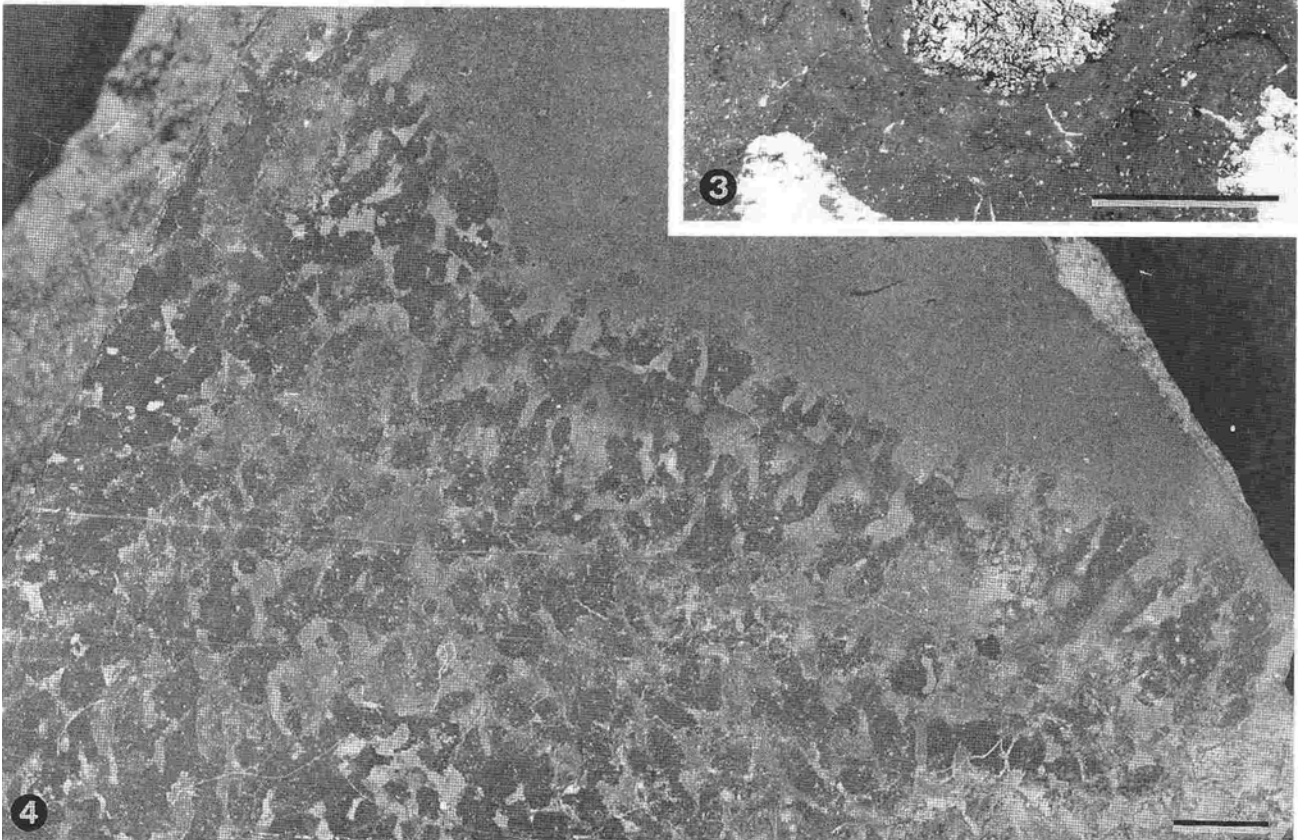
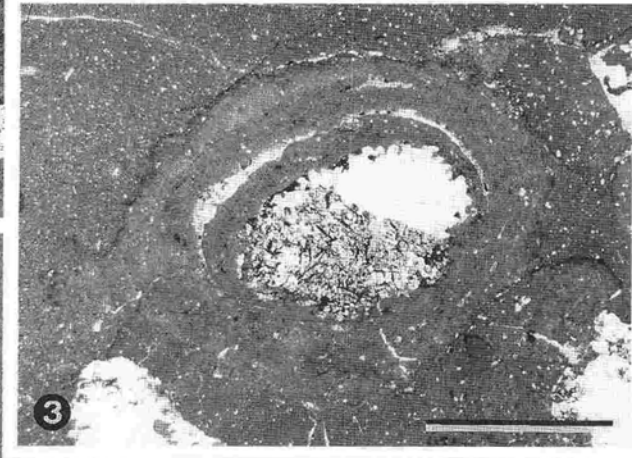
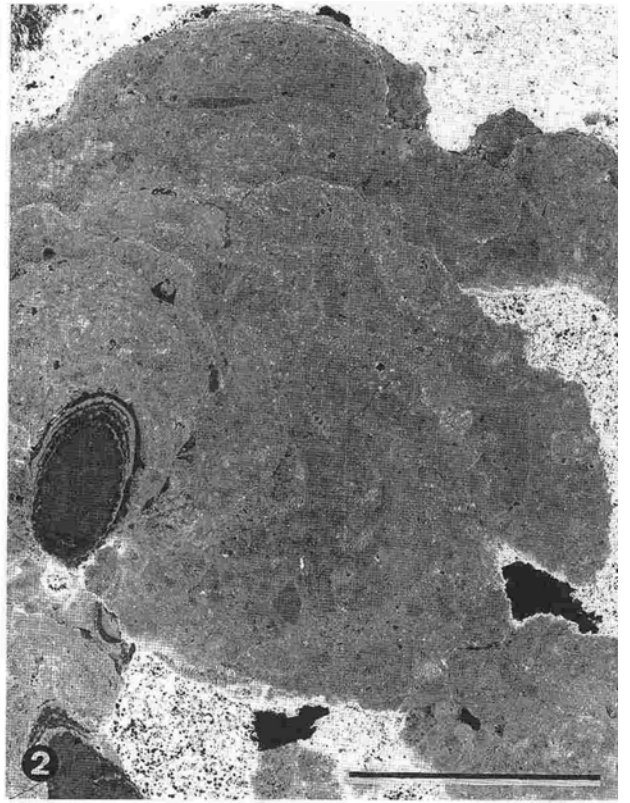
6.3 *Thamnasteria dendroidea* thicket facies

The coral fauna is dominated by thin-branched ramose *Th. dendroidea* colonies (Pl. 14/1-4) in growth position which are the predominant constructors. Branches of *Th. dendroidea* coalesce with each other (Pl. 14/4) creating a delicate, but rigid three-dimensional grid-like framework.

In the bioherm, coherent *Th. dendroidea* thickets form distributed patchy structures up to 1 m in width. The largest mapped outcrop surface with a *Th. dendroidea* thicket is up to 5 m wide, the third dimension can only be estimated. *Th.* colonies exhibit no distinct growth direction. Identification of separate colonies is difficult to

Plate 15 An Upper Jurassic coral-microbialite reef from the Süntel area, Lower Saxony. Reef core (microbialite). Scale of bar is 5mm.

- Fig. 1. Thrombolite in columnar growth form with domal upward growth consisting of layered thrombolite. Thrombolite displays borings (B) or is fragmented (white arrow). Serpulids (black arrows) encrust the columns or serve as nuclei of thrombolite. Growth cavities are filled with dolomitized allomicrite (light coloured spots). Sparry cement occupies the remaining space (black spots). Negative print of thin section.
- Fig. 2. Two *Stylosmilia* branches (center left and bottom left) affected by microbial crusts. Layered thrombolite coats the branches subconcentrically and with variable cortex thickness. Stages of microbialite crusts are outlined by serpulid tubes (S) and isolated chambers of a uniserial *Nodosaria* tests (arrows). Dolomitized allomicrite (light coloured areas) fills the framework pores. Negative print of thin section.
- Fig. 3. Thin section showing *Thamnasteria dendroidea* branches wrapped by generations of concentric microbial crusts. Thin layers of ?bryozoans/?*Rothpletzella* trace former growth stages. Arrows point to solution seams commonly found at the boundary between microbialite and allomicrite.
- Fig. 4. Thrombolite in dendroid growth form cut parallel to the growth direction. Allomicrite fills cavities and is overlain by bafflestone-fabric of thrombolite. Polished slab. Arrow pointing upward.



almost impossible (Fig. 4). Rarely, clusters of closely spaced autochthonous *Th. dendroidea* branches grow apart from the reef core (Fig. 3).

Inside the thicket, adjacent branches reveal the same growth direction. Especially in marginal positions colonies display a fan-like growth. Common are tips of branches turned sideward and growing horizontally over a distance of up to 70 cm. Branches seldom grow diagonally downward.

Phaceloid *Stylosmilia* colonies form an accessory component of the coral thicket (Pl. 14/5-6). A few isolated colonies unknown whether toppled or in life position seem to border the *Th. dendroidea* thicket.

The *Thamnasteria dendroidea* thicket facies includes a high percentage of framestones consisting mainly of encrusting organisms in growth position. Microbialite coatings form approximately 80% of the rock volume. A high-diverse reef community - the majority of taxa are encrusting forms which require hard substrate - colonize the framework (Tab. 1). Both encrusting and endolithic organisms colonize, stabilize and partly also destroy the *Th. dendroidea* thicket successively. We recognized the following community replacement sequence and distinguished 5 stages of reefal evolution (Fig. 6).

6.3.1 Community replacement sequence

Stage 1: Beginning with this stage, *Th. dendroidea* grows up creating an initial delicate framework. Rameose branches are occupied by calices closely connected, that formed an envelope of soft tissue. No or only moderate destructive bioerosional processes occur. Encrusting taxa, other dwellers, and coating microbialites are largely lacking.

Th. dendroidea varies in growth form between the common thin-branched morph (diameter of branches about 4 mm) and the rare thick-branched morph (up to 3 cm in diameter). Mostly, coral branches are elliptical to flattened in outline. Plate-like undulating morphotypes are present.

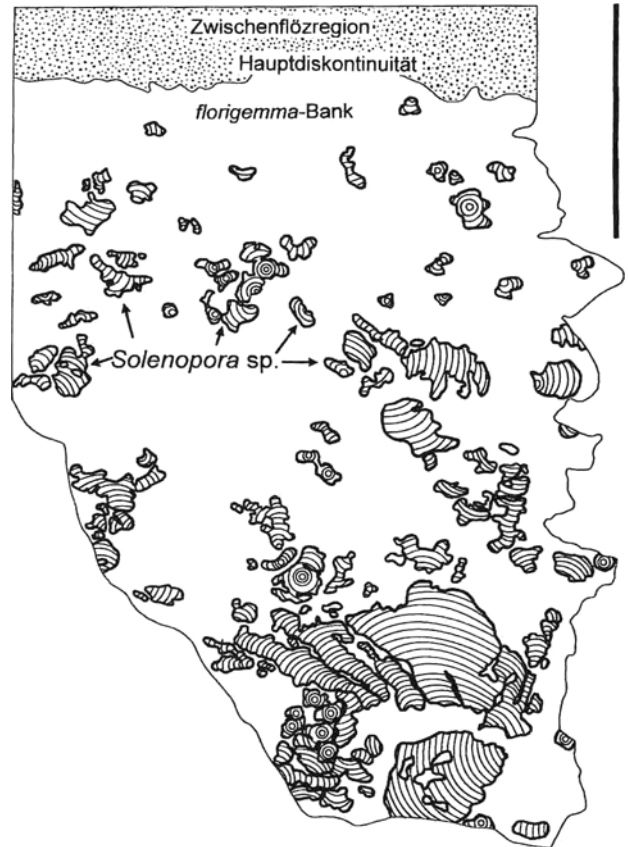
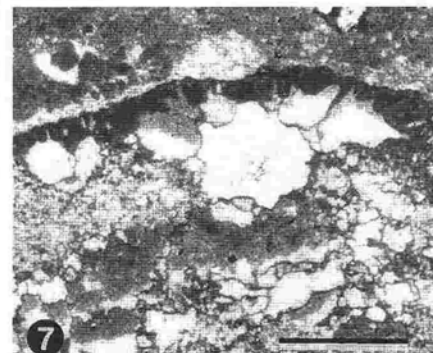
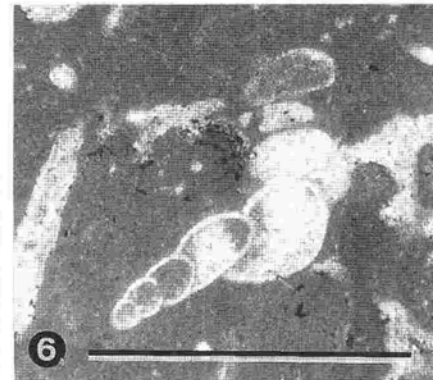
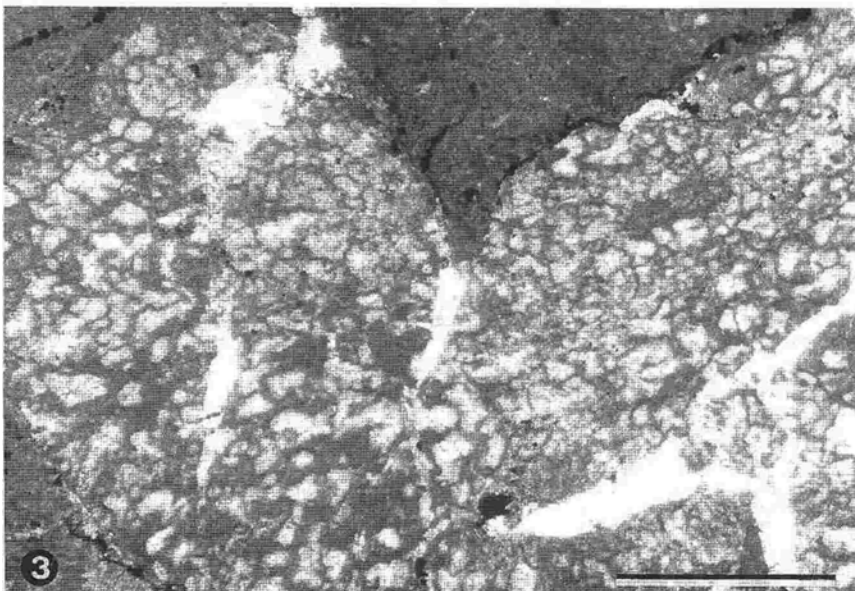
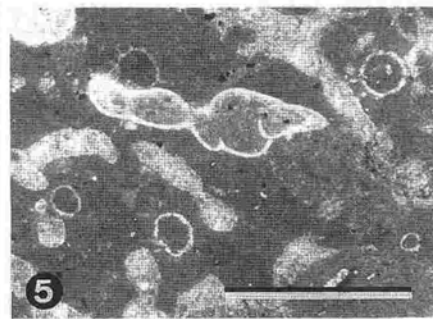
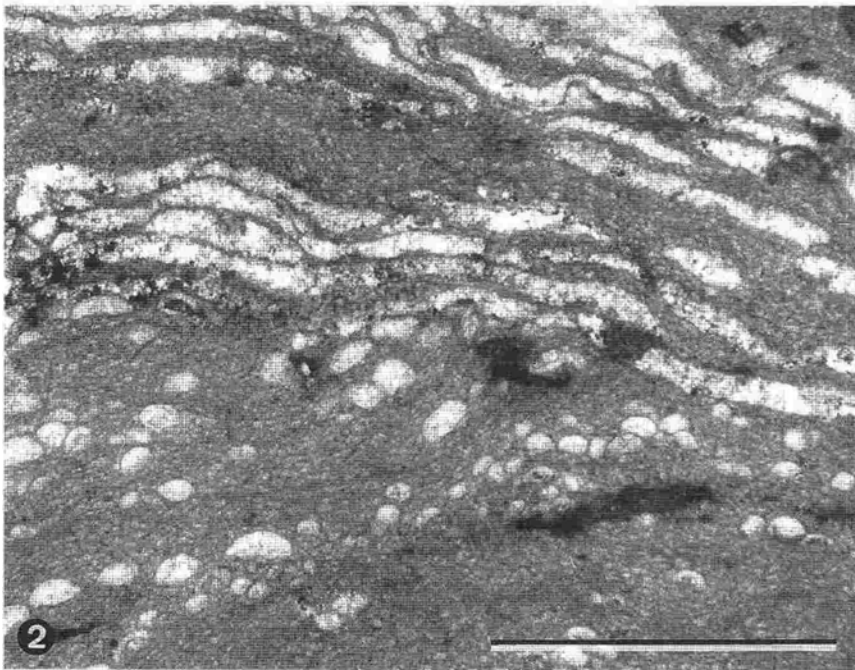
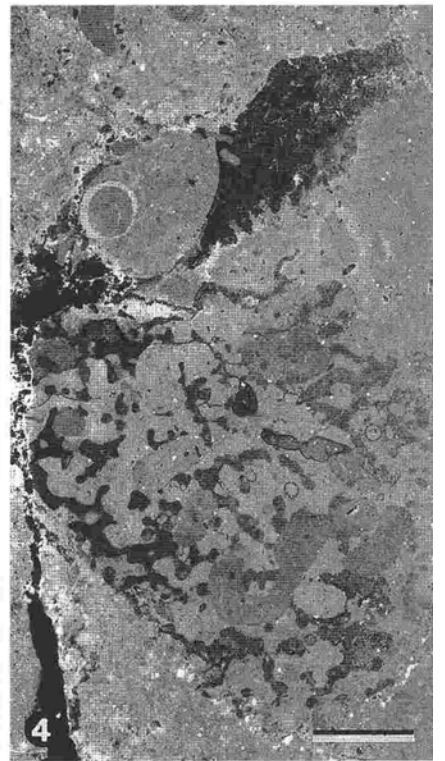
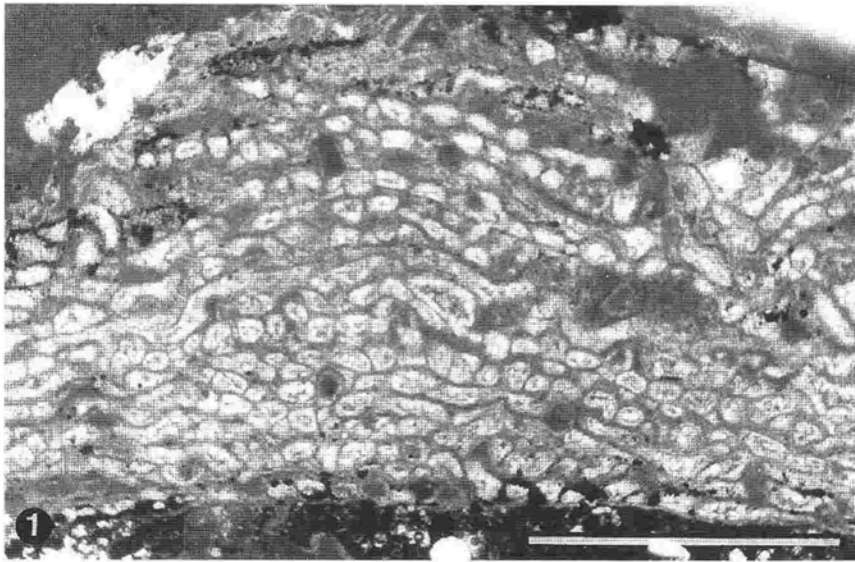


Fig. 6. Mapped area within *Solenopora* biostrome facies (top of the *florigemma*-Bank). Scale of bar is 10 cm.

Symmetrical thickening of branches interpreted as annual growth rings (cf. GEISTER & LATHUILIÈRE 1991) has not been observed. Each branch ends with a terminal tip (Pl. 14/2). Adjacent branches are arranged more or less parallel and exhibit identical growth direction (Pl. 14/3-4). Distance between branch centers in growth position varies around a few mm. Branches are locally cemented to each other (Pl. 14/4) or coalesce with neighboring branches forming a

Plate 16 An Upper Jurassic coral-microbialite reef from the Süntel area, Lower Saxony. Photographs of thin sections. Scale of bar of all is 1mm.

- Fig. 1. Detail of *Rothpletzella* layer growing from bottom to the top.
 Fig. 2. 'Krustenproblematikum' (sensu SCHMID 1996) with isolated and aggregated chambers of *Koskinobullina socialis*. Note transitions between small *Koskinobullina socialis* chambers (tangential section?) and 'Krustenproblematikum'. Center to above: Numerous cracks with clear calcite (void filling cement) are intercalated (comp. WENDT 1993).
 Fig. 3. Detail of *Bacinella irregularis* nodule.
 Fig. 4. Bored *Thamnasteria dendroidea* branch (T) overgrown by pharetronid calcarea sp. A. The sponge is inhabited by hyalin foraminifers (dark circles) fixed to the meshwork. Arrow points to specimen in longitudinal section (detail is also figured in Pl. 16/5) Frequent borings (discernible by darker coloured micritic filling) penetrate the skeleton of sponge and incorporated microbialites documenting early lithification. Remaining space around branches with fixed sponges is occupied by leiolite.
 Fig. 5. Detail of Pl. 5/4 showing enigmatic foraminifer in longitudinal (above to the centre) and cross section (white circles).
 Fig. 6. Pharetronid Calcarea sp. A-dwelling foraminifer species (cf. Pl. 16/6) in longitudinal section.
 Fig. 7. Rim of *Bacinella irregularis* nodule with *Lithocodium aggregatum*.



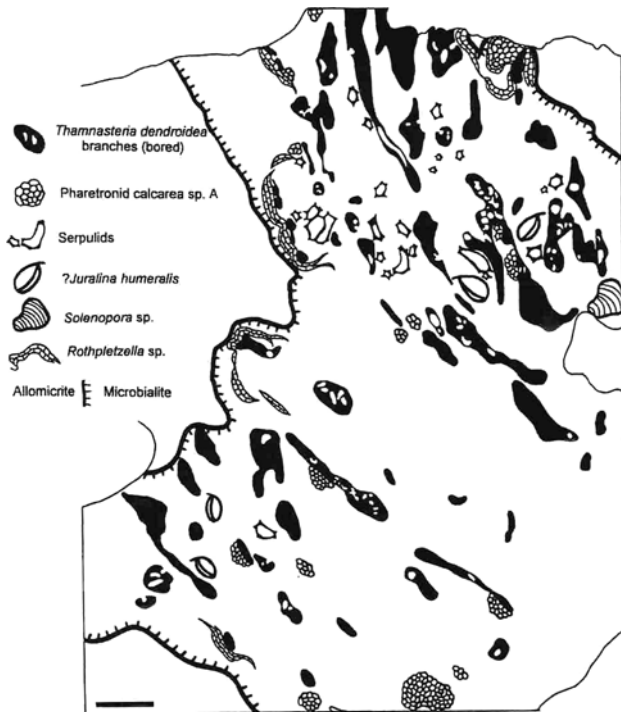


Fig. 7. Detail of *Thamnasteria dendroidea* thicket facies (drawing of a peel orientated perpendicular to bedding). *Thamnasteria dendroidea* form the reefal framework which is bored and successively colonized by pharetronid calcarea, serpulids, terebratulids, microbialite. Note *Rothpletzella* outlining thicket surface. Scale of bar is 1 cm.

three-dimensional 'grid'. These sideways coalesced branches strengthened the *Th. dendroidea* thicket in the initial growth phase without microbialite coatings.

Discussion: Concerning the growth form and rate of *Th. dendroidea* we follow INSALACO (1996b) who placed the ramose *Thamnasteria dendroidea* and the massive *Thamnasteria concinna* in synonymy. A different species identification previously carried out in the literature is based on the presence of only one of the morphotypes. However, GEISTER & LATHUILLIÈRE (1991) observed a morphological transition within one and the same colony. The following morphotypes are known: slender-branched colo-

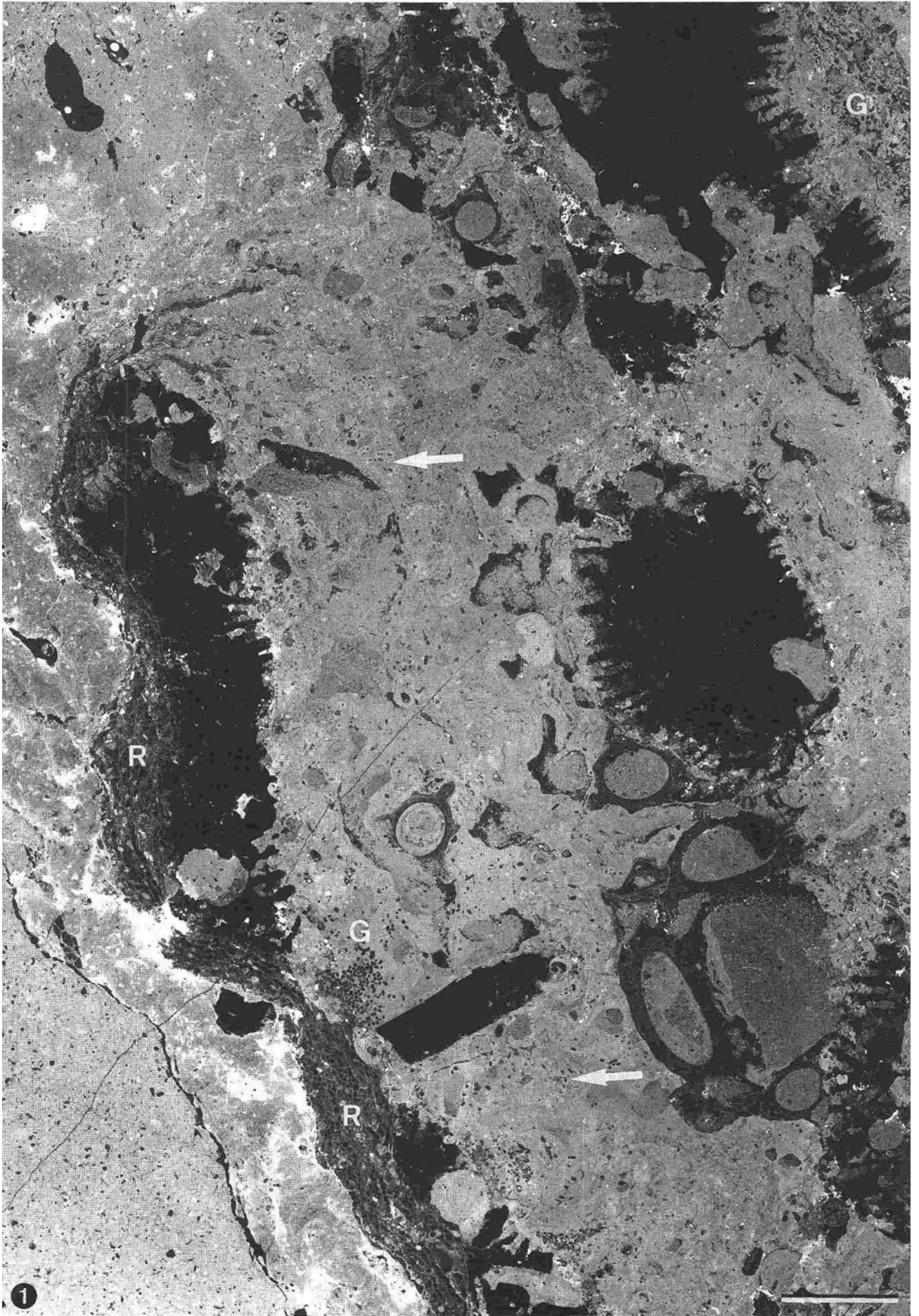
nies with commonly fused branches (HELM 1997), robust branching colonies with annual growth rings (GEISTER & LATHUILLIÈRE 1991), colonies with multicolumnar growth forms (HELM & ELBRACHT 1998, RONIEWICZ 1984), head-shaped colonies (e.g. BERTLING 1993b), tabular colonies (e.g. BERTLING 1993b) and (vertically) platy or foliated colonies (e.g. BERTLING 1993b). Differentiation of colonial growth form within a species is presumed to enable settlement in a wide variety of different environments (e.g. BERTLING 1993b). INSALACO (1996b) assumed that very shallow and quiet water conditions favoured the development of branched morphotypes as realized in the section studied (see also Chap. 6.8).

Growth rate of *Th. dendroidea* has to be discussed in connection with its morphotype and environment (INSALACO 1996b). The existence of growth rings in their samples suggests an annual growth of ca. 13 mm (GEISTER & LATHUILLIÈRE 1991, cf. INSALACO 1996b). In contrast, pronounced taper off branches described here with only restricted 'hot spot' (INSALACO 1996b) points tend to have extremely fast growing rates (up to a few cm in a year?). As a whole, development of our *Th. dendroidea* thicket is considered to have been very rapid. With regard to growth rates in recent ramose coral species (cf. JACKSON & HUGHES 1985, LEINFELDER et al. 1996), a growth rate of several cm a year is not unusual. For example, fast growing *Acropora cervicornis* exhibit an annual growth rate of 12cm/yr (TUNNICLIFFE 1981). During growth of *Th. dendroidea*, the diameter of branches increased. At some spots soft tissue of adjacent branches was fused, subsequently precipitated skeletal material coalesced during growth forming a delicate framework. Equivalent local 'bridges' connecting branches of ramose corals is frequent in recent reefs dominated by *Acropora* species (HUGHES & JACKSON 1980, NEIGEL & AVISE 1983). Only RIDING et al. (1991) observed this feature in fossil corals.

The prevailing sideward directed tips of branches indicate active growth. It can be an adaption to influx of water circulation mainly from a sideward direction (SHINN 1963, RONIEWICZ & RONIEWICZ 1971, SCHÄFER 1979, CHAMBERLAIN & GRAUS 1975).

Plate 17 An Upper Jurassic coral-microbialite reef from the Süntel area, Lower Saxony. Detail of Fig. 7 showing marginal area of *Thamnasteria dendroidea* thicket with well-developed community replacement sequence. Negative print of thin section. Scale of bar is 2mm.

Thamnasteria dendroidea branches (developed in stage 1) (black areas with serrated edge) display moderate boring (stage 2). Branches are surrounded by irregular microbial crusts (stages 3-4). Serpulids are fixed on the branches (stage 2) or encrust microbialite in the following stage (stage 3). Preservation of geodiid sponge spicules (G) indicates specimens in life position (microbialites prevent the disarticulation of sponge spicules) growing directly on *Thamnasteria dendroidea* branches in stage 2. Numerous isolated spicules occur also scattered in microbial crusts. In the latter, nubeculariid foraminifers are also presented in great quantities (stages 3-4) sometimes forming small aggregates (white arrows). The final stage 5 in the community replacement sequence involves the development of *Rothpletzella* (R). It builds layers encrusting the overhanging parts of the *Thamnasteria dendroidea* thicket. Eventually, pillar-like microbialite extends from *Rothpletzella* oblique upwards to upper left (arrows indicate the growth direction). In cavities inside the thicket, allomicrite or - rarely - sparite cement occurs. The big arrow indicates microbialite/dolomitized allomicrite boundary, overprinted by the formation of solution seams.



Stage 2: The connecting soft tissue of *Th. dendroidea* branches disappears first at the older lower parts of the branches. Subsequently, the remaining hard tissue is subject to moderate to extensive initial biological destruction by endoliths (Fig. 7). Their activity includes pear-shaped borings of bivalves (*Gastrochaenolites*) which reach up to 1 cm in diameter, and cylindrical borings up to 2 mm in diameter (*Trypanites*). Smaller sized borings are probably formed by sponges (*Entobia*) and *?Spirichnus spiralis*.

After partial death of soft tissue, the branches also served as habitats for encrusters and microbialites which are however only rare in this stage.

Serpulids attached to the branches frequently occur distributed randomly. They directly inhabit the branches as well as microbial crusts in the following stage 3 (Pl. 17/1, 18/5). Serpulids with sculptured outer surface of the tube have almost exclusively been observed, but allowed no specific identification.

A diverse encrusting taxon represented in the reef is the taxon Porifera which is dominated by pharetronid *Calcarea*. Six different micromorphic sponge taxa have been distinguished in thin sections.

Pharetronid *Calcarea* sp. A (Pl. 16/4) very similar to the sponge figured by GAILLARD (1983) appears to be the most ubiquitous species (Fig. 7). It is composed of a rigid meshwork with knobby outer shape up to 1 cm in diameter. This sponge is characterized as (possibly mutualistic) dwelling place of a foraminifer species locally attached to the meshwork (Pl. 16/4) and exclusively found inside this sponge. The occurrence of a foraminifer within a calcareous sponge contradicts the statement of SCHMALZRIEDT (1991) who denied their existence in this place. The test of the foraminifer is uniserial and consists of irregular globular chambers (Pl. 16/4-5). This hyaline foraminifer resembles *Bullopore* to a high degree, but may be a different species because it has no drop-shaped outline.

The pharetronid *Calcarea* sp. B (Pl. 14/9) in rare places directly settles on coral branches during this stage mostly

found attached to large bivalve shells in the sediment adjacent to the coral thicket (cf. stage 5). In contrast to pharetronid *Calcarea* sp. A, this sponge reveals a compressed hemispherical encrusting shape. Its meshwork exhibits a fan-like structure.

The third sponge taxon observed contributing to this stage is the knobby growing *?Neuropora* (coralline Demospongea, REITNER 1992) which occurs enriched in clusters (cf. PALMER & FÜRSICH 1981), but is much less abundant than the sponges described above.

Siliceous sponges are common members of the fauna directly dwelling on coral hard tissues. The Geodiida are most abundant. Their dispersed circular, elliptic and bean-like spicules are mostly found incorporated in microbial crusts which develop during later stages of the community replacement sequence. Rarely, they occur in a clustered mode interpreted as life position. In deposits adjacent to the reef the remains of these sponges are also abundant (Pl. 19/5).

Additionally, a siliceous sponge with *?triauxic* or *tetraxic* spicules (Pl. 18/5) has been identified. Traits for taxonomic determination are insufficient, though in a single case etched samples revealed residue of spicules with split tips (Pl. 14/8).

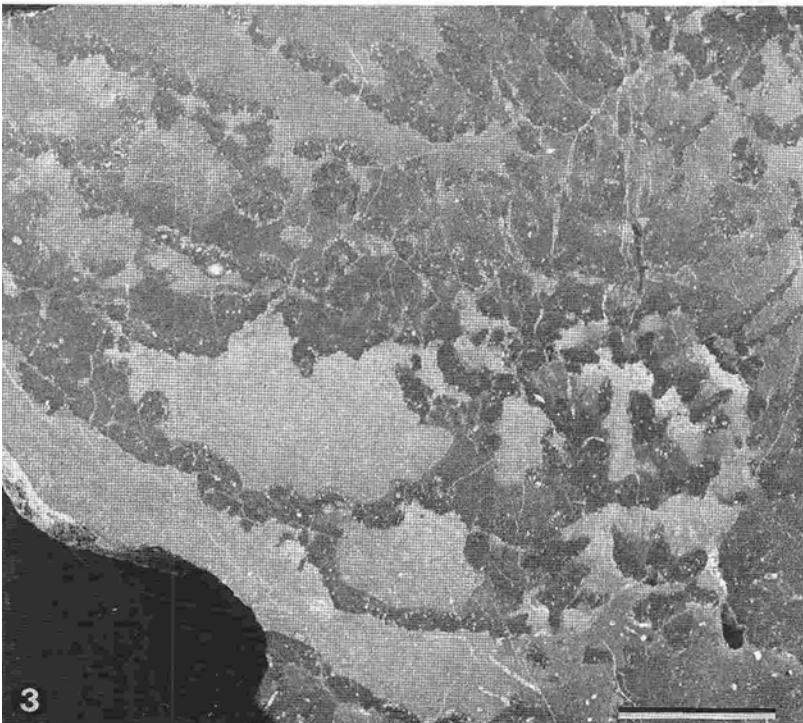
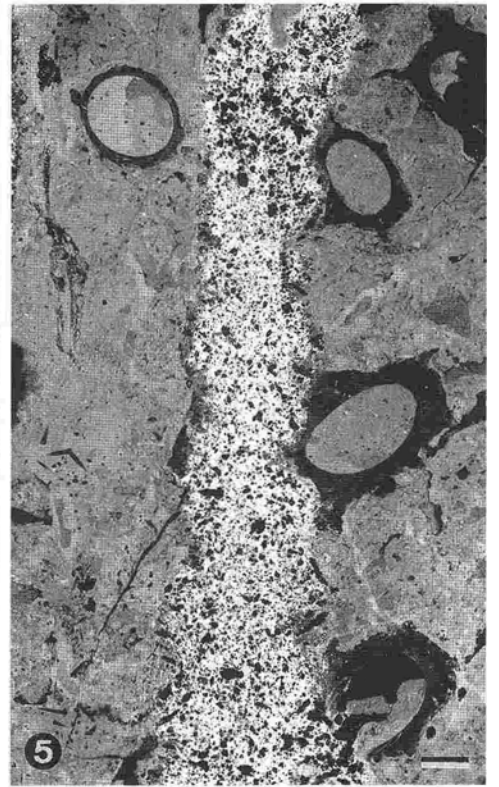
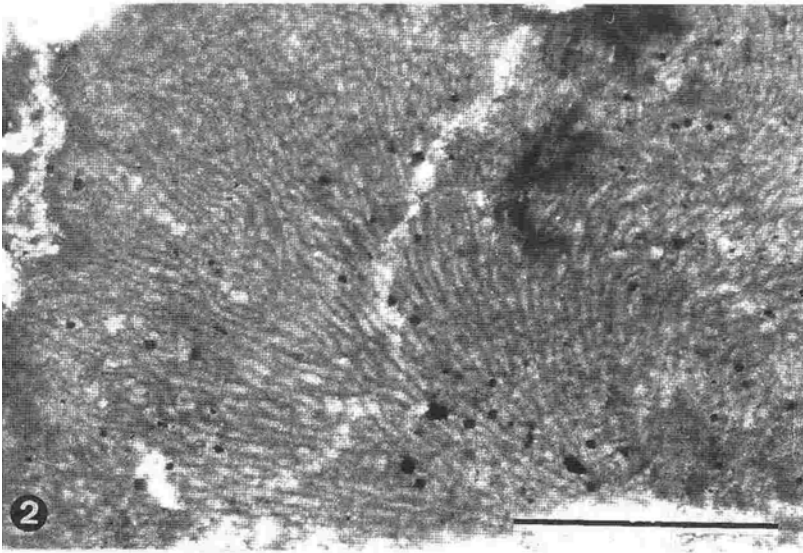
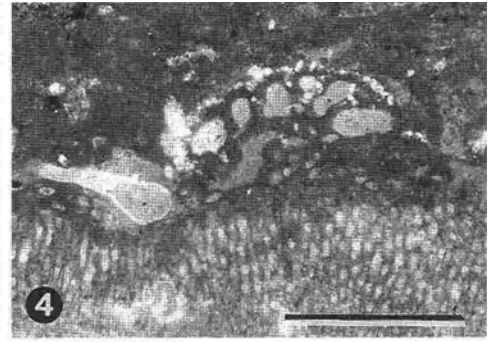
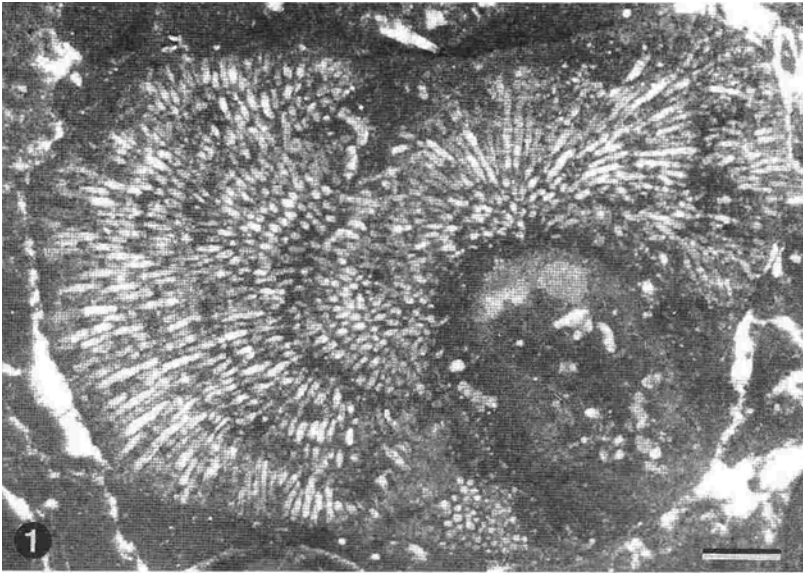
A reef dwelling micromorphic brachiopod fauna (Fig. 7) settles in between *Th. dendroidea* branches. It consists of numerous terebratulid brachiopods identified as *?Juralina humeralis*. Specimens are exclusively preserved with articulated shells, and reach up to 7 mm in length.

Micro-encrusting *Koskinobullina socialis* is rare and randomly distributed. It directly inhabits the branches building thin sheets. Also, *Bullopore ?rostrata* is rarely observed in this stage.

A minor element restricted to this stage is a micro-problematicum (Pl. 18/6). It is fixed directly on the coral hard tissue consisting of small undulating ribbons up to a few mm in lateral extension. Ribbons are aligned in lines parallel to the water surface (*?phototactic* growth). They

Plate 18 An Upper Jurassic coral-microbialite reef from the Süntel area, Lower Saxony. Scale of bar of Figs. 1-2, 4-6 is 1 mm and of Fig. 3 is 1 cm

- Fig. 1. Components encrusted by *Cayeuxia* sp. A are prominent constituents at the top of the 'Hauptoolith'. Arrow points to *?dichotomic* divergence of tubes. Thin section.
- Fig. 2. *Cayeuxia* sp. B is a very rare element and shows substrate preference to *Bacinella/Lithocodium* nodules. Thin section.
- Fig. 3. Polished hand specimen of thrombolite (darker coloured) in dendroid to reticulate growth form. Note sideward growth direction of thrombolite. Dolomitized allomicrite occupying cavities inside thrombolite framework.
- Fig. 4. Fine-agglutinating textulariid foraminifer resemble *?Placopsilina* fixed on *Solenopora* thalli. Thin section.
- Fig. 5. Detail of *Thamnasteria dendroidea*-thicket facies: *Thamnasteria dendroidea*-branch (tangentially cut) attached by serpulids. Strengthening of *Thamnasteria dendroidea* thicket by microbial crusts almost completely filling the interstices between the branches. Spicules in lower left part (black circles and needles) are remains of a decomposed siliceous sponge. Due to microbial activity which partly prevents the spicules from disarticulation they occur closely connected. The *Thamnasteria dendroidea* branch is leached (karst solution) and filled by detritical quartz grains and strongly dolomitized allomicrite. Polished slab.
- Fig. 6. Microproblematicum clinging to *Thamnasteria dendroidea* branches. Arrow indicate directed upward. Thin section.



extend to a maximum thickness of about 0.6 mm and wedge out towards the lateral edges. Laterally fused margins of adjacent ribbons occur, too. The systematic position of this microproblematicum remains uncertain, though it slightly resembles the red alga *Peyssonnelia*.

An encrusting organism atypical for this stage is *Solenopora*, one specimen has been observed on a coral branch.

Discussion: Usually borings and encrustation are only possible on a dead coral branch. Consequently, there is no encrusting activity in the well-illuminated upper living part of the coral thicket (FREIWALD et al. 1997). Branches inside the thicket with parallel surfaces shade each other, and coral soft tissues dies (NEIGEL & AVISE 1983).

Occurrence of boring organisms is restricted to this stage. Obviously, borings never penetrate even the thinnest microbial crusts which occur in the following stage of the community replacement sequence (stage 3). Hence, branches are bored prior to the development of coating microbialites (JONES & HUNTER 1991, MONTAGGIONI & CAMOIN 1993:152, BERTLING 1995). However, a penetration of certain endoliths into the tissue-covered branches can not be excluded (KLEEMANN 1994, OSCHMANN 1989).

Though boring organisms frequently play an important role in the destruction of corals (and coral reefs) (CHAZOTTES et al. 1985, HUTCHINGS 1986) and with regard to the modest intensity of bioerosion and subsequent framework destruction, the effect of bioerosion in the thicket is considerably small. This fact may be attributed to the following causes:

(1) In contrast to phaceloid- and dendroid-branched corals, the ramose morphotype possesses branches with coating and protective soft tissue (cf. FAGERSTROM 1987, FREIWALD et al. 1997, HIGHSMITH 1982).

(2) Bioerosion rate increases with ongoing exposure of a substrate (FÜRSICH & WERNER 1991, SCOFFIN 1972). In the examined case, coral penetrating endoliths are mainly restricted to stage 2, so the exposure seems to have lasted only for a short time.

(3) Intensive coalesced branches furtherly strengthen

the coral framework and protect it from bioerosive destruction.

The encrusting sponge assemblage directly inhabiting the branches indicates that it has been quickly established. According to REITNER (1993), the success of larval colonization is favoured by the presence of pre-existent microbial biofilms (see also FREIWALD et al. 1997).

The occurrence of encrusting foraminifers within sponges is a common feature (BRACHERT 1992, FÜRSICH & WERNER 1991, HITCHINGS 1980, LANG 1989, MATYSKIEWICZ & FELISIAK 1992, SCHMALZRIEDT 1991). However, it is not possible to decide if they had a mutualistic mode of life (space inside sponges offers protection) or settled on the meshwork post mortem. We interpret the foraminifer species as 'symbiotic' organism, as fast-growing microbialite quickly occupies cavities within the sponges (see Pl. 16/4 and KEUPP et al. 1990) even contemporaneously to the growth of sponges (REHFELD 1996, REITNER 1993, 1994).

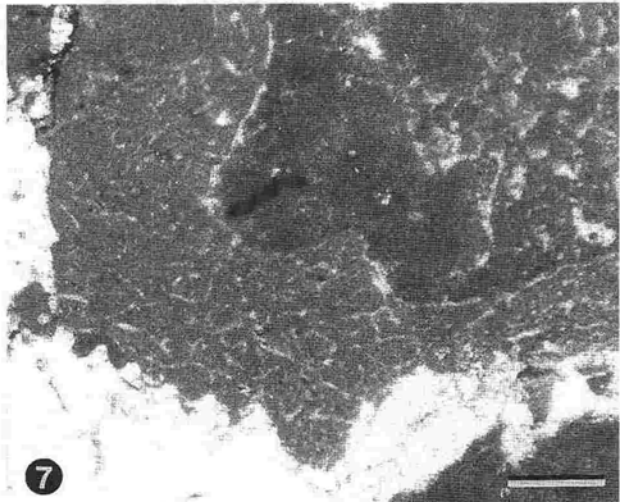
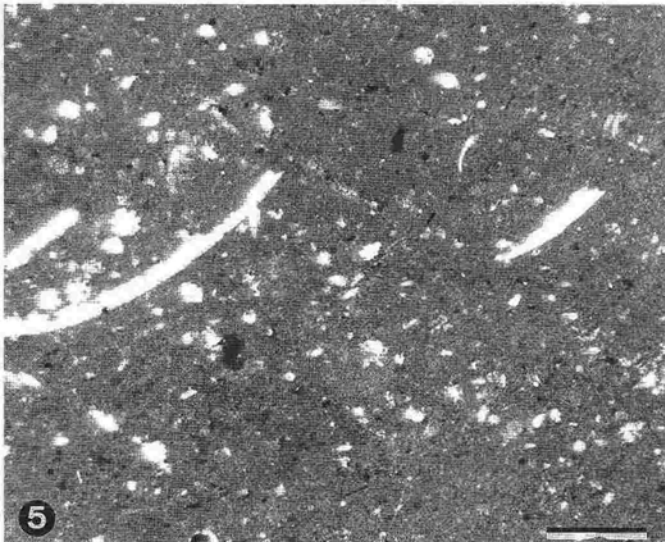
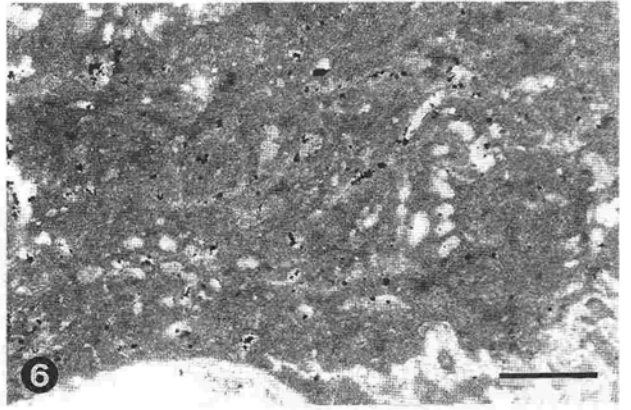
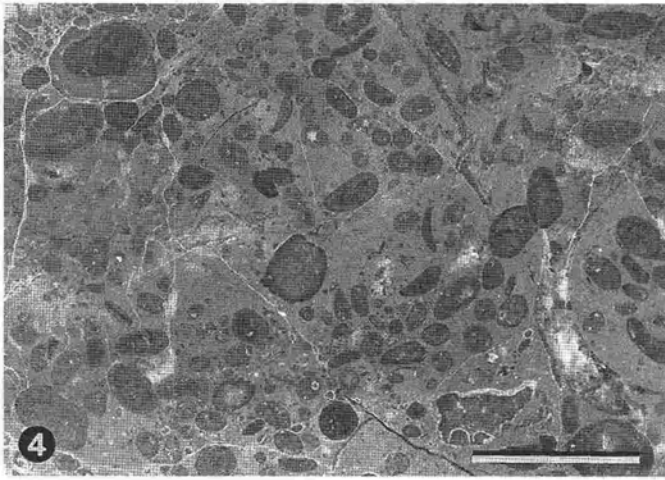
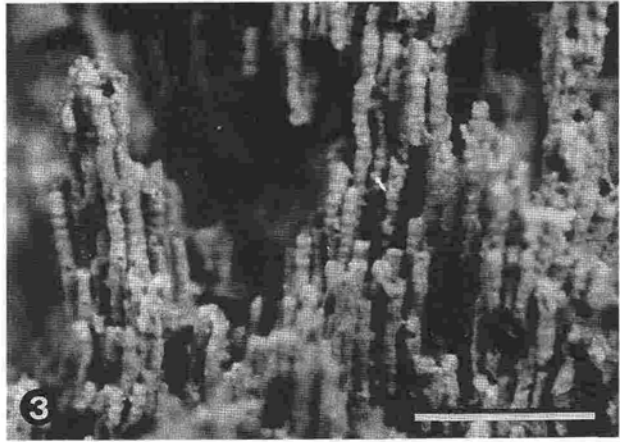
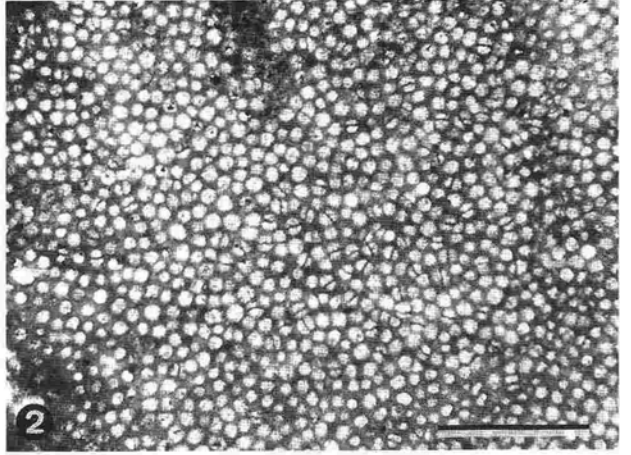
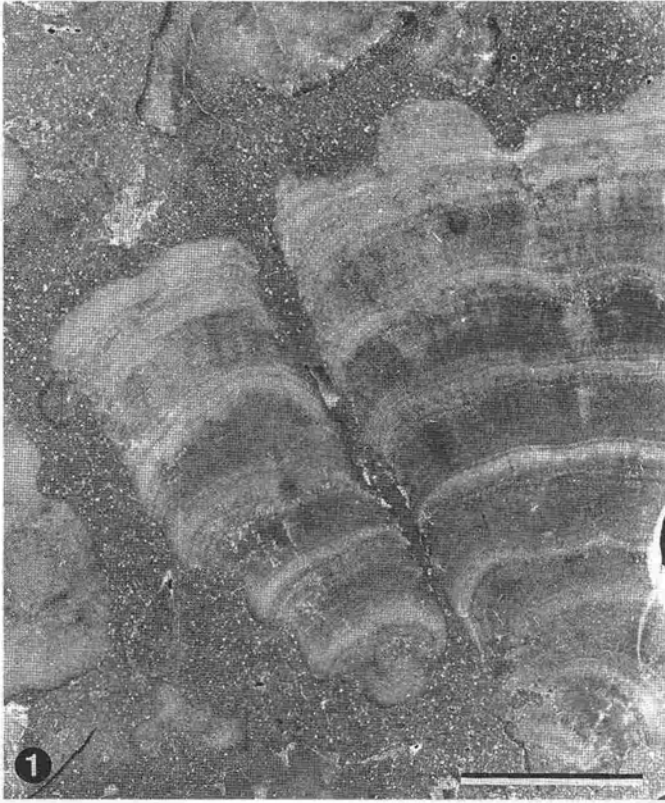
The bulk of serpulids are able to conquer living space very fast (JACKSON 1977). This fact explains their success in early colonizing hard tissues in the reef.

According to WAGENPLAST (1972) and AGER (1965), the presence of pedicle-attached reef dwelling brachiopods is an exception. In most cases, only micromorphic ecotypes are able to survive because of the restricted space conditions between phaceloid, dendroid and ramose branches of corals. AGER (1965) demonstrated the presence of micromorphic terebratulid and rhynchonellid brachiopods between dendroid *Dendrophyllia* colonies. WERNER (1986) and FEZER (1988) noted micromorphic '*Terebratula*' and *Loboidothyris* species inside phaceloid *Calamophyllia* colonies. Micromorphic brachiopods also occupying small niches inside sponge reefs (PALMER & FÜRSICH 1981).

Koskinobullina socialis referred to as rotaliid foraminifera (SCHMID 1996) is also restricted to this stage, but in the following stage, it is overgrown by microbial crusts or other encrusting organisms (Fig. 8, FÜRSICH & WERNER 1991) probably because of reduced growth rates (SCHMID 1996).

Plate 19 An Upper Jurassic coral-microbialite reef from the Süntel area, Lower Saxony.

- Fig. 1. Longitudinal section of bulbous thick-branched *Solenopora* thallus surrounded by allomicrite. Note sequence of thick dark layers and thin light layers. Polished slab. Scale of bar is 1 cm.
- Fig. 2. *Solenopora jurassica* in cross section showing numerous cell columns with cross-walls. Thin section. Scale of bar is 0.5 mm.
- Fig. 3. Etched specimen of *Solenopora jurassica*. Residue represents iron-impregnate cell columns. Note the pearl string-pattern of cell lumina. Thin section. Scale of bar is 0.5 mm.
- Fig. 4. Top of "Hauptoolith". Ooids, bioclasts, 'oncoids' and lithoclasts (white arrow) are scattered in micritic matrix. Numerous components are encrusted with *Cayeuxia* sp.-A (black arrows). Polished slab. Scale of bar is 1cm.
- Fig. 5. Thin section showing biomicrite with minor amount of *Acicularia* (arrows) and bivalve shells. Some ?spicules of sponges (white round spots) are scattered in the matrix (resemble spicules of geodiid sponges). Scale of bar is 0.5 mm.
- Fig. 6. Microbial crust with nubeculariid foraminifers. Thin section. Scale of bar is 0.5 mm.
- Fig. 7. Fungal borings in microbialite.



Stage 3: Large masses of microbialites with incorporated foraminifers and *Terebella lapilloides* encrusted the *Th. dendroidea* branches and abandoned borings during this stage. *Koskinobullina socialis* and pharetronid *Calcarea* II die while serpulids, surrounding sponges, and *?Juralina humeralis* persist until the end of this stage.

Microbial crusts exhibit lamellar growth form (Pl. 15/2-3). The following structural types (sensu SCHMID 1996) are developed: poorly structured thrombolite, layered thrombolite, micritic stromatolite, clotted leiolite, layered leiolite and pure leiolite. Small spherical micritic particles (peloids) can only be recognized when surrounded by sparry cement. This is mainly the case inside *?Juralina humeralis* shells which frequently exhibit geopetal infills. Lamination and additional textural features, e.g. growth direction, are rarely discernible except when encrusting elements exist (e.g. Pl. 15/3) which follow crypto-hardgrounds. Masses of microbial crusts commonly incorporate the frequent nubeculariid foraminifers (Pl. 17/1, 19/6). They outnumber other faunal elements by far occurring scattered to rarely enriched in clusters. Additional important parts of encrusting organisms during this stage are *Bullopore ?rostrata* (Pl. 15/2) and *Terebella lapilloides* as subordinate constituents. Other sessile foraminifers are textulariids (cf. Pl. 18/4) (*?Placopsilina*-species). Their tests are composed of numerous inflated, and finely agglutinated chambers, sometimes in clusters. Microbial crusts are populated by cementing thecideidnids in places.

Discussion: With the exception of addressed pharetronid *Calcarea* sp. B, sponge growth increases vertically and gains height (knobby morphotypes). According to JACKSON (1977) this is an 'escape in size'-strategy of clonal animals enabling them to avoid predation (e.g. resisting overgrowth by neighbors/microbialites: JACKSON & HUGHES 1985). Discussion on recent sponges focuses on toxic properties providing an important advantage in active competition for space (JACKSON & BUSS 1975). Taking this abilities into account, the survival of sponges until the end of stage 3 reflects the sponges' capability of well competing within restricted habitats and dominating 'older substrates' (JACKSON 1977). Because of the vertical upgrowth of sponges, space above is limited and sponges become attached to adjacent *Th. dendroidea* branches. Apart from coalescent coral branches, these bridges connecting adjacent branches add strength to the framework. After death of the organisms, these links remain almost strong due to microbial activity resulting in an early calcification (REHFELD 1996) and preservation of the shape of siliceous sponges (Pl. 18/5).

The preservation of the *Th. dendroidea* thicket can be attributed to the massive encrustation by microbial crusts during this stage. The community of this stage is characterized by a considerably lower faunal diversity similar to that of other Late Jurassic reefs (LEINFELDER et al. 1993). The close intergrowth of nubeculariid foraminifers and microbialites (SCHMID 1996, cf. FEZER 1988, LANG 1989, LEINFELDER 1994) led SCHMID (1996) to a discussion of symbiotic relationship between them. This assumption bases on the capability of foraminifers to support and

prevent underlying microbial films from predation. Corresponding feeding properties are proposed for *Terebella* (SCHMID 1996), a taxon able to stand even reduced oxygenation (LEINFELDER et al. 1993, LEINFELDER et al. 1994).

Stage 4: Microbial crusts established during stage 3 are penetrated by sponges (*Aka* sp.) and boring ?fungi. They penetrate microbialite coatings but have never been observed penetrating coral branches. Rarely, specimens of haplosclerid excavating sponge *Aka* occur. Due to indistinct outlines of *Aka* borings, their existence is only indicated when sponge remains (amphioxean spicules) are present. Probable fungi borings - identical to those described by REITNER (1994) and DELECAT (1996) - comprise a network of slender and branched boreholes (0.01-0.04 mm in diameter) filled with sparry calcite. They are restricted to leiolite surrounded *Th. dendroidea* branches.

Microbial crusts fill the remaining space inside the *Th. dendroidea* thicket during this stage and provide the substrate for new generations of fixed nubeculariid and textulariid foraminifers, *Bullopore ?rostrata* and *Terebella*. The separation of this stage from stage 3 is defined by a new entry of boring organisms penetrating the microbialite and the complete loss of the e.g. sponge fauna persisting to the end of the latter stage.

Discussion: Excavating sponge *Aka* is a prominent carbonate-destroyer in Late Jurassic reefal settings (BAUMGÄRTNER & REYLE 1995, HERRMANN 1996, KEUPP et al. 1990, LANG 1989, REITNER & KEUPP 1991, REITNER 1994). An endolithic network of fungi has only been reported from Lower Saxonian localities (DELECAT 1994, REITNER 1994). The destruction rate of the reefal structure by both boring organisms is of only modest importance in the outcrop studied.

By the end of this stage, the space between the coral branches is vastly occupied by microbialite. Thus, binding microbial crusts play the most important role in strengthening the *Th. dendroidea* thicket and create a rigid framework. Compared to structures with a similar stabilization by microbialite (DUPRAZ 1997, MONTAGGIONI & CAMONI 1993, NOSE 1995, RIDING et al. 1991, SCHMID 1996, LEINFELDER 1992:12), our example yields some substantial information. NOSE (1995) points out, that interaction between branched corals and coating microbial crusts may only be successful, when both possess the same growth capacity. Faster growing microbial crusts would overwhelm living tissue of branches. In contrast, due to reduced growing capacity of microbial crusts branched corals suffer biological and hydrodynamical destruction (e.g. TUNNICLIFFE 1981). An additional cause for successful interaction can be the distance between coral branches. Such a habitat is an excellent dwelling place for microbial crusts (RIDING et al. 1991). The narrow space between the branches hinders predators as grazing sea urchins, gastropods and fishes from their destructive activities (cf. LEINFELDER et al. 1993).

Stage 5: At the beginning of this stage, the *Th. dendroidea* thicket is vastly filled with microbialite. Therefore, an

ongoing development of the replacement sequence occurs outside the thicket. Characterizing this stage, *Rothpletzella* (Pl. 16/1) partly covers reefal surfaces of the coral-microbialite body (Pl. 17/1, Fig. 7). *Rothpletzella* is characterized by a few overlying sheets of juxtaposed scarce cells. They surround a central open cavity (diameter is about 0.05 mm) which is filled with sparry cement. Sheets are arranged in parallel lines. The foliose 'thalli' are up to 5 mm thick, wedging out at the margins. Observed lateral extension does not exceed a few centimeters. *Rothpletzella* laterally splits into several thin layers with intervening microbial crusts.

In outer regions of the *Th. dendroidea* thicket and partly covering *Rothpletzella* microbialitic laminar crusts grade into branched columns which digitate sideways to upwards.

Big and thick-shelled, byssate bivalves also contribute to this stage. They frequently grow in clusters adjacent to the reefal body or occupy intra-reef depressions. Specimens are articulated, and in life position. Largest forms extend up to 5 cm in length. Thin-sections revealed a shell structure similar to perterian bivalves figured by SCHMID (1996).

Discussion: Occurrence of the porostromate alga *Rothpletzella* (WOOD 1948) in the patch reef studied extends the stratigraphic range of this taxon into the Late Jurassic. Most data on its occurrence have been published from mid-Paleozoic settings (e.g. CHUVASHOV & RIDING 1984, FLÜGEL & WOLF 1969). ROTHPLETZ (1890, 1891) provided the first descriptions of post-Palaeozoic (Triassic) occurrences with a gap comprising Carboniferous to Permian. Possibly, Early Jurassic '*Osagia incrustans*' (WENDT 1970) may be placed in synonymy with *Rothpletzella*.

The systematic position of *Rothpletzella* remains unsettled. At times, they have been assigned to the Porostromata (PIA 1927) which are a systematically heterogeneous group (RIDING 1991, DRAGASTAN 1993) probably consisting of true cyanobacteria, chlorophyta or even rhodophyta.

During the Paleozoic *Rothpletzella* appears to have the same preferences concerning substrate and environment. It is an important encrusting organism binding and stabilizing both reefal framework and detrital sediments (FAGERSTROM 1987) in shallow low-energy lagoonal reef and backreef settings (TSIEN & DRICOT 1977).

During the Cretaceous porostromate algae tend to decline (RIDING 1991) and since the Upper Cretaceous coralline algae conquered the niche formerly occupied by *Rothpletzellans* and other porostromate algae (LEINFELDER 1994, STENECK 1985).

Investigations on growth rates of microbialites are still in progress (REITNER 1993, SCHMID 1996). The following results add data to this topic:

(1) Split margins of *Rothpletzella* interfere with microbial crusts (mutual biomuration) (Pl. 17/1). Hence, growth of microbial crusts kept space with that of *Rothpletzella*.

(2) Before overgrowing each other, serpulids (-agglomerates) are coated by a thin microbial film which is intercalated between the tubes.

The growth rate can only be estimated. We assume

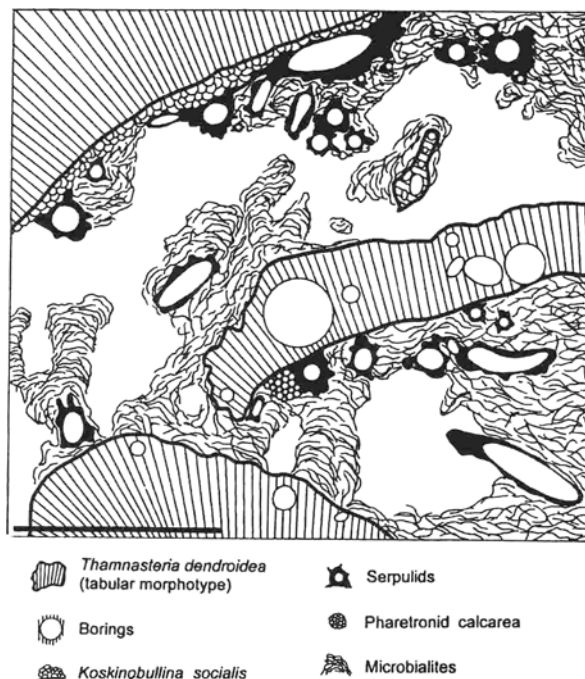


Fig. 8. Detail of thrombolite facies (drawing of thin section). Ragged outlines of *Thamnasteria dendroidea* (massive morphotype) are under-crustured by *Koskinobullina socialis*, subsequently overgrown by serpulids. Serpulids are also crustose elements on coral and microbialite. The latter fill large parts between coral plates. Remaining space is filled with (pel)micrite. Scale of bar is 1 cm.

values of 0.1-1 mm per year. A comparison with other reefal settings is not easily possible, since microbial crusts can be formed by the activities of completely different organisms (e.g. cyanobacteria and other bacteria, algae, fungi; SCHMID 1996). Our assumption on microbial growth rates largely corresponds to those of SCHMID (1996) concerning Late Jurassic Tethyal shallow water reefs, but contrast to those of REITNER (1993) on microbialites in recent cryptic reef caves (0.05-0.1 mm/year).

Among the bivalves as reef-dwellers, oysters are generally lacking. The observed bivalves settle on the reef body only by byssate attachment. It is assumed that this taxon prefers positions elevated above the surrounding seafloor (NOSE 1995).

6.4 Thrombolite facies

The thrombolite facies is composed of huge masses of microbialite in growth position exhibiting numerous reef cavities and is associated with a sparse fauna. Its lateral extension is figured in Fig. 3.

According to SCHMID (1996), four structural types of microbialite can be differentiated within this facies: pure clotted thrombolite, layered thrombolite, poorly structured thrombolite and clotted leiolite. Microbialite commonly exhibits staining by iron minerals. Comparable microbialite structures are figured by LEINFELDER et al. 1993, SCHMID 1996, NEUWEILER 1993).

The dendroid growth form (Pl. 15/4) predominantly consists of irregular-shaped slender microbialite sticks about 0.5 cm in diameter. Sticks digitate and coalesce

during growth, or grow in a sideward direction (Pl. 18/3). Linked to the dendroid growth form, clotted thrombolite structures occur (GYGI 1992; SCHMID 1996; LEINFELDER et al. 1993).

Less frequently, columnar growth forms occur. They resemble the dendroid growth form except for the diameter of columns (> 1 cm) and the presence of a convex-upward lamination (layered thrombolite predominate) (Pl. 15/1; cf. SCHMID 1996).

A third growth form (reticulate growth form) is rare in this facies. It is characterized by a grid-like construction of platy elements arranged in vertical and horizontal directions. All transitions towards dendroid and columnar growth form exist (cf. KENNARD & JAMES 1986; SCHMID 1996).

Numerous cavities are present within the loosely digitating and anastomosing microbialites (Pl. 15/4). Cavities are partly filled with geopetal limemud (allomicrite) which can be weakly to strongly dolomitized. Remaining shelter pores are filled with blocky calcite (Pl. 15/1). Frequently, microbialite/allomicrite boundaries are intensified by the formation of solution seams.

Microbialites can build knobs up to several decimeters in diameter. They resemble vertically arranged inverted cones positioned closely to each other (cf. NOSE 1995; SCHMID 1996). A process of roofing-over between these knobs (GARRETT et al. 1971, ZANKL & SCHROEDER 1972) leads to the development of voluminous reef cavities (submarine caves sensu TAYLOR & PALMER 1994) with an extension of several decimeters across (distribution pattern is shown in Fig. 3). The sediments inside the cavities consist of heavily dolomitized allomicrite.

This facies is characterized by a considerably lower faunal diversity when compared to the *Th. dendroidea* thicket facies. Associated biota are lithified in growth position and randomly distributed.

The macrofossil content is restricted to a few massive *Th. dendroidea* colonies (up to 30 cm in lateral and 8 cm in vertical direction) that partly mould its paleorelief and partly must have raised above thrombolite because of the extensive encrustation by epiliths on coralline underplates (*Koskinobullina socialis*, serpulids, sponges, e.g. Fig. 8; cf. INSALACO 1996a).

Thrombolite is profusely encrusted with numerous nubeculariid foraminifers and fine-agglutinating micritic *Terebella lapilloides* tubes which delineate former microbialite surfaces. For the complete fauna compare Tab. 1. Apart from encrusting organisms, also two ichnogenera have been identified in the thrombolite facies (?*Trypanites*, ?*Gastrochaeonolites*, Pl. 15/1)

Discussion: The existence of borings (e.g. NEUWEILER 1993), cryptohardgrounds (FLÜGEL & STEIGER 1981), development of submarine relief (LEINFELDER et al. 1994), and growth cavities (e.g. LEINFELDER 1992) are diagnostic criteria for early lithification of thrombolites. The fauna distinguished in this section resemble those of the "*Terebella-Tubiphytes*-association" (sensu SCHMID 1996). According to him, the occurrence of this community in shallow water setting indicates poor oxygenation.

6.5 *Solenopora* biostrome facies

Above and laterally adjacent to the reef core a paraautochthonous biostrome (sensu KERSHAW 1994) occurs mainly characterized by *Solenopora jurassica* moulding the surface of the reef core.

Sediments (biomicrite to biopelmicrite), macro- (gastropods, bivalves, brachiopods) and microfossil content (benthonic foraminifera, dasycladalean algae) equals that found in the adjacent deposits (Chap. 6.6, Tab. 1).

Solenopora thalli are the dominating component with only a small content of *Isastrea* colonies in this facies type. Associated encrusting biota are low diverse. *Solenopora* thalli are positioned closely to loosely spaced (Fig. 5). Eastwards, a continuous decrease in thalli size and population density occurs forming a graded transition into the adjacent deposits (Fig. 3).

Solenopora jurassica thalli have rigid skeleton. They are bulbous with a diameter of about 15 cm and a maximum height of 10 cm. Average diameters vary around a few centimeters. In larger thalli the multicolumnar growth form (Pl. 19/1) (thick-branched colonies sensu NOSE 1995) is developed. Frequently, thalli show alternating zonation of thicker dark layers (3-4 mm thick) and thinner light layers (1.5-3 mm thick) (Pl. 19/1). They consist of closely packed polygonal to circular cell columns filled with sparite (Pl. 19/2). Observed range of cell diameter (lumen) is about 0.025-0.05 mm; thickness of the wall ranges from 0.006 mm to 0.012 mm. The cell wall is frequently outlined by a dark coloured layer embedded in a lighter coloured micro-sparitic matrix. In a few *Solenopora jurassica* cross-sections numerous cells exhibit a wall in longitudinal direction releasing a division of the lumen into two equal parts (Pl. 19/2). In longitudinal sections parallel to the growth axis (Pl. 18/4), parallel juxtaposed to vertically radiating cell columns are visible. Cell columns are transversely by downward-convex cell walls irregularly distanced (0.05-0.1 mm). Cell walls of adjacent filaments are not positioned on the same level. In some etched thalli the internal morphology of cell lumina can be observed (Pl. 19/3). They consist of a series of globular bodies (0.02-0.04 mm long) arranged in a string-of-pearls pattern.

In distal parts of several *Solenopora* thalli, *Bacinella* threads are intervened. In distal direction, they successively grade into a bacinelloid fabric (HELM 1997).

Borings inside thalli are almost absent. Only some slightly to strong curved cylindrical borings 0.3 mm to 0.8 mm in diameter (referred to *Spirichnus spiralis* FÜRSICH et al. 1994) and a single penetration by *Troglotella incrustans* have been identified.

Patchy distributed *Isastrea* colonies (Fig. 3) grow as bubbles and with diameters up to 30 cm. They are modestly affected by cylindrical borings (Ichnogenus *Trypanites*).

Red algae and corals display only thin microbialite coatings distributed in patches which commonly provide a substrate for numerous generations of nubeculariid foraminifers. Hence within the biostrome, frame builders are not cemented to each other by microbialites and occur both in growth direction or toppled.

	Facies type					Guilds					
	Hauptoolith	Th. dendr.	Thrombolite	Solenopora	adj. Deposits	Builder	Baffler	Binder	Dweller	Destructor	Non-reefal
Cyanobacteria											
<i>Bacinnella irregularis</i>				**					#		#
<i>Cayeuxia</i> sp. A	*****			**					#		#
<i>Cayeuxia</i> sp. B				**					#		#
<i>Rothpletzella</i> sp.		***						#			
Chlorophyta											
<i>Solenopora jurassica</i>				*****	*****						#
<i>Acicularia</i> sp.	***			***	***						#
Dasycladacean algae indet.					**						#
Foraminiferida											
<i>Pseudocyclammina</i> sp.	**			?	?						#
<i>Everticyclammina</i> sp.	?			?	?						#
<i>Troglotella incrustans</i>	**			*	?				#		#
<i>Lithocodium aggregatum</i>		*		**					#		#
? <i>Placopilina</i> sp.		**							#		#
<i>Textularia</i> sp.	**				**				#		#
? <i>Textulariidae</i> indet.		**		*					#		#
<i>Nubeculariids</i> indet.	**	*****	*****	**					#		#
<i>Trocholina</i> sp.	**								#		#
? <i>Lagenina</i> indet.		***							#		#
? <i>Nodosaria</i> sp.					*						#
<i>Lenticulina</i> sp.	**			*	*						#
<i>Bulloporea</i> sp.		***	***						#		#
Porifera											
<i>Aka</i> sp.		**								#	
<i>Geodiida</i> indet.		**								#	
Siliceous sponges indet.		**						#			
? <i>Neuropora</i> sp.			**					#	#		
<i>Pharetronid calcarea</i> sp. A		***	**	**				#			
<i>Pharetronid calcarea</i> sp. B		**						#			
Scleractinia											
<i>Thamnasteria dendroidea</i> (ramose morph)	**	*****				#					
<i>Thamnasteria dendroidea</i> (tabular morph)			**					#			
<i>Stylosmilina</i> sp.		**					#				
<i>Isastrea</i> sp.				**				#			
Bryozoa											
Bereniccan bryozoans	*	*	**						#		
Brachiopoda											
? <i>Juralina humeralis</i> (micromorphic)		****							#		
<i>Juralina humeralis</i>					**						#
<i>Septaliphoria pinguis</i>	?				**						#
<i>Thecideidnida</i> indet.		***							#		
Polychaeta											
<i>Terebella lapilloides</i>		**	****						#		
<i>Glomerula gordialis</i>			****					#			
Div. serpulids indet.		****		**				#			
Bivalvia											
<i>Plagiostoma laevisculum</i>					**						#
<i>Astarte</i> sp.					***						#
<i>Camptonectes</i> sp.					****						#
<i>Inoceramidae</i> indet.					**						#
? Pteracean bivalve indet.		***						#			
Gastropoda											
<i>Nerinea</i> sp.					*****						#
? <i>Metriomphalus</i> sp.					*****						#
<i>Ampullina</i> spp.					**						#
<i>Proceranthium</i> spp.					****						#
<i>Gastropoda</i> indet.					**						#
Crustacea											
<i>Ostracoda</i> indet.	**			**	**						#
Echinoidea											
<i>Paracidaris florigemma</i>	?			**	***						#
<i>Echinoidea</i> indet.	****										#
Incertae sedis											
<i>Koskinobullina socialis</i>		**		***	**			#	#		#
"Krustenproblematikum"				**	**				#		?
Microproblematicum		**							#		
Ichnotaxa											
<i>Nygmites solitarius</i>		****	**							#	
? <i>Spirichnus spiralis</i>		***	?	*						#	
<i>Gastrochaenolites</i> sp.		***	?							#	
Boring fungi indet.		**								#	

Tab. 1. List of fossil with semiquantitative estimation of abundance indicated by number of small stars (* single occurrence; ** rare; *** abundant; **** frequent; ***** dominant) and guild position.

A common faunal component of microencrusters is *Koskinobullina socialis* building foliose to multilamellar layered sheets or dome-like, multibranched morphotypes up to 1 cm high. Frequently, *Koskinobullina socialis* fragments appear reworked in the surrounding sediments. These fragments are commonly intergrown or overlain by the 'Krustenproblematikum' (sensu SCHMID 1996) usually forming biogenic layers (Pl. 16/2). 'Krustenproblematikum' is composed of an indistinct meshwork of several small chambers up to 0.05 mm in length, that are fused and spindle-shaped in outline and grade into parallelly arranged, irregular forms surrounding microsparite filled centers. Chamber walls are constructed of structureless micrite. 'Krustenproblematikum' forms undulating laminae which horizontally extend between *Koskinobullina socialis* columns. Sometimes isolated to aggregated *Koskinobullina socialis* chambers are intercalated. Early lithification of the *Koskinobullina socialis* 'Krustenproblematikum' agglomerates is indicated by the presence of borings (HELM 1997).

Grain-supported oncoids occur restricted to lense-shaped bodies. The biggest forms exceed 5 mm in diameter; average is about 2 mm.

Some sharply outlined *Bacinella/Lithocodium* nodules (up to 8 mm in size) occur scattered in interreef depressions above the reef core. These nodules exhibit a core of *Bacinella irregularis* (Pl. 16/3) which is surrounded by *Lithocodium aggregatum* (Pl. 16/7). *Cayeuxia* sp. B (Pl. 18/2) also participates in the construction of *Bacinella/Lithocodium* oncoids. This rare porostromate alga consists of radiating, slightly curved, and closely joint tubes arranged in a parallel pattern. Diameter of tubes ranges between 0.02 mm and 0.03 mm. The maximum size of coherent algal bodies reaches 4 mm. A few *Koskinobullina socialis* chambers are also present within *B./L.* nodules. Attached to the exterior of such nodules, thecideidiniid brachiopods and serpulids have been observed.

Discussion: Thalli colonize the area above the reef core most densely in close to loose connection. Frequency and size of thalli decreases considerably in sideward direction. Therefore, the area above the reef core is assumed to be the original dwelling place of the thalli. Due to almost lacking microbialite envelopes, a connection between adjacent thalli is not developed. This type of framework is regarded as parautochthonous: few thalli are in upright growth direction, others toppled. Since thalli have a delicately preserved epifauna, transport probably occurred over a short distance.

The zonation in darker and lighter layers of *Solenopora* thalli is a commonly observed phenomenon (e.g. FÜRSICH et al. 1994., NOSE 1995), that indicates seasonal (=annual) growth (WRIGHT 1985). In addition, pearl-string pattern of lumina is interpreted as daily (?) growth rings, though the number of swellings in both a dark and a light zone does not exactly correlate to a 365 day cycle. This is probably attributed to a reduced growth rate during winter (light layer).

The occurrence of *Bacinella irregularis* in (structurae sui generis sensu MOUSSAVIAN 1989) or fixed on *Solenopora* is a frequently reported feature (FEZER 1988, HERRMANN

1996, LEINFELDER et al. 1993, NOSE 1995, SCHMID & JONISCHKEIT 1995). HERRMANN (1996) proposes, that previously described interspersing reflects an active decomposition act of *Bacinella irregularis*.

'Krustenproblematikum', first noticed by SCHMID (1996) in Late Jurassic reefal sequences of Portugal is a remain of an organism of uncertain systematic position. It resembles enigmatic ?algae figured by FEZER (1988). According to SCHMID (1996), 'Krustenproblematikum' it is similar to red algae, in particular *Lithoporella*, or porostromate algae *Spaerocodium* (= *Rothpletzella*). Enigmatic 'Krustenproblematikum' is developed in close connection with *Koskinobullina socialis* (SCHMID 1996, FEZER 1988). Boundaries between both fossil structures are frequently dissected and a grading transition occurs (interspersed marginal sections of *Koskinobullina socialis*?). These circumstances suggest a colonial plasticity within 'Krustenproblematikum' (a small chambered morphotype of *Koskinobullina socialis*). On the other side, evidence for the interpretation as two different organisms derives from the frequent intergrowth of *Koskinobullina socialis*-agglomerates with other organisms attributed to distinct taxa (FEZER 1988, GRÖTSCH & FLÜGEL 1992, DECROUEZ & MORYCOWA 1997). CHERCHI & SCHROEDER (1985) interpret this characteristic as mutual biomuration.

Much confusion has resulted from frequently figured co-occurrence of *Bacinella irregularis* and *Lithocodium aggregatum* (e.g. BAUMGÄRTNER & REYLE 1995, DECROUEZ & MORYCOWA 1997, HERRMANN 1996, NEUWEILER & REITNER 1992, NOSE 1995, SCHMID & JONISCHKEIT 1995). Discussion is in progress about specific alignment to a single or to two distinct species (BANNER et al. 1990, LEINFELDER et al. 1993, NEUWEILER & REITNER 1992, SCHMID & LEINFELDER 1996, NOSE 1995, SCHMID 1996). *Lithocodium aggregatum* now is regarded as loftusiid foraminifer (SCHMID 1996, SCHMID & LEINFELDER 1996) and *Bacinella irregularis* - enigmatic and difficult to distinguish - may belong to cyanobacteria (NOSE 1995). In the material studied, *Cayeuxia* sp. B is restricted to *Bacinella irregularis/Lithocodium aggregatum* nodules giving rise to the impression of three closely connected organisms. Similar mutual intergrowing and interspersing recognized HERRMANN (1996) and NOSE (1995).

6.6 Adjacent deposits

A complete continuum in facies transition exists between the *Solenopora* biostrome and the laterally developed deposits which are composed of massive micritic limestone (mudstone to wackestone or biomicrite to biopelmicrite respectively (Pl. 19/5)). Locally, the limestone displays fine lamination (Fig. 3) released by an interbedding of siliciclastics reaching a maximum thickness of 0.7 m. This horizon in one place erosively overlies a thrombolite-knob and gently dips on its flanks. Reefal debris is interspersed with the adjacent deposits successively decreasing with increasing distance from reef core.

Limestone of the reef-adjacent deposits is very rich in fossils (gastropods, bivalves, brachiopods, small *Solenopora* thalli, echinoid remains). Rare, small colonies of *Th.*

dendroidea in growth position up to a few decimeter in diameter are also present adjacent to the reef core.

Up-section following the *Solenopora* biostrome, the number of *Nerinea* specimens successively increases forming a 'Nerinea bed' in the topmost part of the *florigemma*-Bank. The 'Nerinea-bed' moderately elevates above the reef core and the *Solenopora* biostrome, and is partly eroded in this position. To the E its thickness increases, but does not exceed 0.5 m.

Echinoid spines - *Paracidaris florigemma* which added its name to the *florigemma*-Bank - is only present in small numbers. In a sideward direction distal to the reef the number of spines increases. In the bedded limestone areas most macrofossils disappear and *Camptonectes lens* becomes predominant.

Microfossil remains comprise foraminifers (*Textularia*, *Lenticulina* and lituolids), variable amounts of sponge spicules derived from geodiid sponges, patchy distributed dasycladalean algal fragments (e.g. *Acicularia*). Ostracodes are also present within this facies but are of minor importance.

6.7 Diagenesis

Dolomitization: Noteworthy dolomitization documented by the presence of euhedral dolomite rhombs took place only in intra-reef cavities (submarine caves). This process totally included the original deposits (allomicrite) with the exception of some scattered bioclasts. Considerable amounts of dolomite crystals also developed in allomicrite 'baffled' between branched thrombolite fabrics (Pl. 15/1, 4). Weakly dolomitized allomicrites also occur, but are randomly and patchy distributed.

Surprisingly, microbialite and allomicrite surrounding the reef core are almost free from dolomitization (Pl. 19/5). These rocks contain only a few dolomite rhombs which are scattered throughout the matrix especially within the allomicrite.

Discussion: The selective distribution of dolomite crystals is controlled by facies factors as reported from other reefal buildups, e.g. 'massive limestone' (LEINFELDER et al. 1994). These authors point out, that during early diagenesis, dolomitization only affects the allomicrite. In contrast, the bulk of microbialites and sponges incorporated by microbialite are more resistant to dolomitization (LEINFELDER et al. 1994. KOCH & SCHORR (1986) discuss, that dolomitization in Jurassic 'sponge-algal reefs' always starts within the most porous and permeable parts of the reef. Initial dolomitization also seems to be a result of clay mineral distribution as Mg-ions suppliers (LEINFELDER et al. 1994).

Diagenesis of corals: Three different preservation types for corals have been observed:

(1a) At the top of the *florigemma*-Bank *Thamnasteria dendroidea*, *Isastrea* sp. and *Stylosmilia* sp. (and other aragonitic taxa) exhibit selective leaching. Biomoulds are infilled with oncoids, limemud, siliciclasts and partly are stained with iron oxides (Pl. 14/1-7).

(1b) Aragonitic skeletons are dissolved. Granular blocky calcite occupies the resulting space. All structures are completely destroyed. Especially *Th. dendroidea* is affected by this kind of preservation. Its diagenesis appears to equal Type 1 preservation of TALBOT (1972).

(2) Aragonite is substituted by calcite crystals in a mosaic pattern. Fine inclusions within the blocky calcite outline the former skeleton. Among the corals, only *Isastrea* sp. and massive *Th. dendroidea* colonies exhibit this preservation type. Features presented here, resemble Typ 3 preservation of TALBOT (1972).

6.8 Environmental reconstruction

Observations in the Süntel outcrop lead to the conclusion that the patch reef grew up in a well-illuminated moderate to low energy lagoonal environment of a few meters water depth (?5-10 m) and under a modest rate of background sedimentation.

Salinity: The presence of stenohaline groups (corals, sponges, brachiopods etc.) indicates normal salinity and open marine conditions.

Sedimentation rate: Microbialites establish and flourish when the background sedimentation rate tends to zero (KEUPP et al. 1993, LEINFELDER 1993, SUN & WRIGHT 1989) due to the inability of the benthic microbial community to survive high sedimentation rates (SCHMID 1996). Taking all the dendroid, columnar, and reticulate growth form into account which create a bafflestone-fabric, we assume, that the patch reef developed under slow rates of accumulation (SCHMID 1996). This conclusion can be derived from the reduced capability of the bafflestone-fabric to keep space with sedimentary influx during its growth.

Illumination and water depth: In marine environments light intensity and water depth are closely connected limiting environmental factors. The occurrence of phototrophic organisms (dasycladalean algae, *Solenopora*) indicates very shallow and clear water. Late Jurassic *Solenopora* species prefer water depths of about a few (ca. 10 m) meters according to FÜRSICH et al. (1994), GEISTER & LATHUILLIÈRE (1991), HARLAND & TORRENS (1982), INSALACO (1996a), NOSE (1995), RONIEWICZ & RONIEWICZ (1971). *Acicularia* and other dasycladalean algae also inhabited very shallow environments (FEZER 1988, GIELISCH 1994, HERRMANN 1996, LEINFELDER 1992, LEINFELDER et al. 1994).

Thamnasteria dendroidea is a coral species with a considerable ecomorphic plasticity. INSALACO (1996b) demonstrated that branching morphotypes are limited to very shallow and quiet water-settings (cf. BERTLING 1995, GEISTER & LATHUILLIÈRE 1991, INSALACO 1996a:) where light available is abundant. Similar relationships in shallow water-setting (foliaceous morphotype of coral species in low-illuminated settings grades to branched morphotypes in well-illuminated settings) were demonstrated by JAUBERT (1977).

Bacinnella/Lithocodium nodules have a very restricted bathymetric distribution. They only flourish in very shal-

low water (DUPRAZ 1997, FOOKES 1995, LEINFELDER et al. 1993). A shallow water environment is also indicated by the frequency of *Koskinobullina socialis* (NOSE 1995, SCHMID 1996). A notable exception is the occurrence of *Terebella*, usually observed in deeper environments (e.g. DUPRAZ 1997, NOSE 1995, cf. SCHMID 1996). If in contrast the occurrence of this taxon depends on the absence of turbulence, protected places as available in cryptic habitats appear favoured by this organism even under shallow water conditions.

Water energy: Combining paleontological and sedimentary features, the water movement was modest to moderate. Macrofossils are dispersed throughout the sediments and lack damage by transportation. Due to a missing apron of reef debris around the reef core, a high level of water energy must be refused. In contrast, toppled *Solenopora* thalli above the reef core indicate a development towards a higher energetic environment after reefal growth ended.

Layers rich in nerineid gastropods usually developed in highly turbulent water environments (e.g. TIEDT 1958). In contrast, BAUMGÄRTNER & REYLE 1995, FOOKES (1995) and NOSE (1995) show that rich assemblages of *Nerinea* also occur under calmer conditions, e.g. in restricted lagoonal settings.

According to SCHMID (1996), *Bacinella/Lithocodium* nodules imply moderate water energy conditions, but they also proliferate in restricted lagoons (NEUWEILER 1997).

Low water energy is also supported by the predominant existence of dendroid thrombolite growth forms (SCHMID 1996).

6.9 Classification and comparison with other Late Jurassic reefs

Following reefal classification published by LEINFELDER (1993) and LEINFELDER et al. (1994), the patch reef examined belongs to the 'coral-thrombolite reefs in (pel)micrite matrix'. The *Solenopora* biostrome up section is considered as 'homogenous autoparabiostrome' as defined by KERSHAW (1994).

Apart from *Th. dendroidea*, additional frame builders are rare or absent. This fact indicates a considerable misfit in reef classifications given by INSALACO et al. (1997). A transition between the reef types III ('thickets dominated by tall dense phaceloid colonies developed within pure carbonate muds') and IV ('microbial-coral reefs dominated by massive, branching and phaceloid colonies') as defined by the above authors can be considered similar to the studied reef. In contrast, the above reef types generally display a coral fauna with remarkably higher faunal diversity in comparison to our reef.

Similar reefs mainly built by ramose *Th. dendroidea* accompanied by *Stylosmilia*, *Solenopora* and microbialites are well known from the northeastern Paris Basin, Oxfordian in age (BERTLING 1995, GEISTER & LATHUILLIÈRE 1991). In addition, coral-microbialite reefs overlain by low-diversity biostromes are described by SCHMID (1996) from Upper Jurassic reefal sections of Spain.

7 EMERSION, PALEOKARST FEATURES

The top of the *florigemma*-Bank is developed as erosional surface. The upper part of the patch reef and adjacent deposits are subject to karst solution (HELM in press). Karst features include the presence of anastomosing karst solution cavities parallel to the bedding plane and selectively leached corals up to 70 cm below the disconformity. In a single place, surface fragmentation reworking resulted in the formation of collapse breccias. *Thamnasteria dendroidea* branches frequently exhibit mouldic porosity. Moulds are filled with blocky calcite replacing former aragonite, which indicates the influence of meteoric water, and siliciclastics or ooids.

Discussion: Karst features in the outcrop indicate emergence from shallow, but marine environment to sub-aerial exposure. The karstic relief at the top of the *florigemma*-Bank is referred to as 'Hauptemersionsfläche'. This disconformity only rarely developed as a true emersion horizon can be traced over several tens of kilometers throughout the Lower Saxony Basin (HELM in press). MÖNNIG & BERTLING (1995) report the occurrence of palaeosoil in connection with this disconformity.

According to STINDER (1991), the stratigraphic lacuna comprises a 'gap' of 2 foraminifers/ostracods-biozones in the Süntel area. Taking the modest intensity of karst penetration into account, duration and/or intensity of karst processes must have been comparatively moderate. Nevertheless, the amount of erosion of now missing sediments can only be estimated.

Karst features, documented by the presence of coral moulds with siliciclastics or other infills equal those described from Late Jurassic reefal sequences in Portugal (LEINFELDER 1992, 1994). Similar phenomena are known of Late Jurassic reefal sequences of Poland (RONIEWICZ & RONIEWICZ 1968).

8 CONCLUSIONS

The patch reef studied comprises a fast growing reef core composed of ramose *Th. dendroidea* as main frame-builder with considerable amounts of microbial crusts and thrombolite additionally strengthening the reefal framework. Comparable reefal units are known from the north-eastern Paris Basin (BERTLING 1995, GEISTER & LATHUILLIÈRE 1991). A low-diverse *Solenopora* biostromal unit overlies the reef core. Similar reef successions are published by SCHMID (1996) and GEISTER & LATHUILLIÈRE (1991) from the Late Jurassic of Spain and the Paris Basin respectively.

The occurrence of reef biota typically associated with conditions up to now only known from the Tethyal realm has been observed within the Lower Saxony Basin which, in contrast, is positioned in higher paleolatitudes. In addition, a community replacement sequence has been reconstructed, that not yet reported from Tethyal reefs, although faunal composition is rather equivalent.

Microbial coatings play an overwhelming role in stabilizing and strengthening the small patch reef, even though corals are needed for the establishment of an initial habitat

for microbial dwelling. This study may also give rise to a new discussion about the role of microbialites in reef biota documenting their guild position (cf. LEINFELDER et al. 1996).

The occurrence of *Rothpletzella* in post-Triassic times has been discussed.

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