

Contribution of Microbial Mats to Sedimentary Surface Structures

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SUMMARY

This paper summarizes studies of sedimentary surface structures in which microbial mats play a role. Intertidal/supratidal transitions of tidal fiats of the North Sea coast, and shallow hypersaline water bodies of saherns (Bretagne, Canary and Balearic Islands), and Gavish Sabkha (Sinai) reveal a multitude of sedimentary surface structures which can be grouped into two categories: primary physically controlled and primary biologically controlled structures. Physically controlled surface structures include shrinkage cracks, erosion marks, deformation structures caused by water friction, gas pressure and mineral encrustation. S hrinkage cracks in microbial mats reveal the following features: (i) horizontally arranged cauliflower pattern that differs from the usually orthogonally regular crack morphology in clay, (ii) rounded edges and pillow-like thickening along the crack edges, caused by the growth of mats into the cracks. Criteria of erosion are pocket-like depressions and ripple marks on the thus exposed non-stabilized sand, and residual stacks of microbial mats. Deformation structures are due to water friction causing flotation of loosely attached microbial mats which fold and tear. Gas migration from deeper layers causes domal upheaval, protuberance structures, folds and "fairy rings". Protuberance structures are caused by the rupture of gas domes and rapid escape of the enclosed gas. The sudden drop of pressure forces sediment to well up from below through the gas channels and to fill the internal hollow spaces of the domes. "Fairy rings" are horizontal ringshaped structures. Their center is the exit point of gas bubbles which escape from the substrate into the shallow water. The bubbles generate concentric waves which cause displacement of fine muddy sediments at the

sediment-water interface. Such gradual displacement guides mat-constructing microbes to grow concentrically. The "fairy rings" are crowned by pinnacle struc-

tures of bacterial and diatom origin. Pinnacles, "fairy rings" and pillow-like coatings of crack margins are biogenic structures which have to be genetically separated from purely physically controlled structures.

1 INTRODUCTION

Microbial mats are fibrillar, slime-supported, coherent coatings of sedimentary and rocky surfaces, which by their morphology, physiology, and arrangement in space and time interact with the physical and chemical environment to produce a laminated pattern (KRUMBEIN 1983). Fossil records of these laminated buildups initiated the term stromatolite (KALKOWSKY 1908). Cyanobacteria constitute the predominant organisms in most microbial mats, although diatoms and fungi may also be present.

Microbial mats form on bedding surfaces. Most have a characteristic filamentous morphology, the filaments having rigid cell walls and polymeric sheaths. Laminations develop from the interaction of the microbes with the environment of deposition. Of main importance is the capacity of the mat-constructing biota to migrate vertically to escape burial by sediments and to recolonize the newly deposited surface. Such biolaminated stacks can reach several centimeters and even decimeters in thickness.

The laminated patterns of stromatolites record the history of actively growing benthic systems. PETTIJOHN $&$ POTTER (1964) used the term "growth bedding" to visualize that organisms can produce bedding. Furthermore, micro-

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bial mats contribute to the shape of sedimentary surface structures, because they act as elastic tissues which influence surface forms (REINECK et al. 1990).

The purpose of this paper is to summarize studies of sedimentary surface structures controlled by microbial mats. This study focusses on field observations in modern peritidal environments. In these environments, physical processes shaping the sedimentary record include evaporation and desiccation, erosion, water friction, and gas pressure resulting from decay of organic matter.

The following sedimentary systems have been studied: (i) Tidal flats of the southern North Sea coast; (ii) Salterns of Bretagne, France, (iii) salterns of Lanzarote, Canary Islands, (iv) salterns of Formentera, Balearic Islands; (v) Gavish Sabkha, southern Sinai, Egypt.

On the tidal flats of the southern North Sea coast, tidal flushing allows for the formation of microbial mats only in areas which lie within the spring-tide flooding cycle. Here, microbial mats interact with abundant siliciclastic sedimentation. The salterns studied are protected against ocean dynamics by partially artificial bars. Sedimentation is largely reduced. The Gavish Sabkha lagoon represents a natural salina within a depression protected behind a coastal bar and fed by seepage of seawater from the nearby Gulf of Aqaba (GAVISH et al. 1985). In all the salterns studied and in Gavish Sabkha, standing water, prevailing low energy and low sedimentation rates provide excellent

2 SOURCES OF DATA Table 1. Study sites referred to in the text, and references.

conditions for prolific growth of microbial mats. References for more detailed descriptions of study sites are listed in Table 1.

3 MICROBIAL MAT TYPES

In the microbial mats referred to in this paper, the bulk of biomass is built by cyanobacteria. Abundant are both filamentous and coccoid forms (PI. 11/1-2). Filamentous forms belong mainly to the genera *Oscillatoria, Microcoleus. Spirulina* and *Phormidium.* Predominant forms of coccoid cyanobacteria belong to Pleurocapsaleans, *Synechocystis, Synechococcus* and *Gloeothece.* Diatoms of various species are associated, the most abundant forms belonging to the genera *Nitzschia, Navicula, Amphora,* and *Mastogloia.*

We observed two types of biolaminated buildups. The

- Fig. 1. Characteristic fibrillar meshwork of filamentous cyanobacteria and diatoms. Arrows: bundles of the cyanobacterium *Microcoleus* sp. surrounded by sheaths of extracelluar polymeric substances (EPS). SEM-photography, scale: $100 \mu m$ long
- Fig. 2. Colony of unicellular cyanobacteria surrounded by rigid capsules of EPS (extracellular polymeric substances). SEM-photography, scale: $1 \mu m$ long
- Fig. 3. *Microcoleus-dominated* surface mat covers and penetrates siliciclastic grains of North Sea tidal flats, illustrating biostabilization of sedimentary surfaces. Scale: $100 \mu m$ long
- Fig. 4. Vertical section of grain-supported biolaminated buildup showing sharply projecting microbial mats buried several times by siliciclastic sediments. Section 1-1': Higher sedimentation rate buried microbial mats (note current ripples). Section $2-2$: Lower sedimentation rate allowed mat-forming microbes to escape from burial, to migrate to the new sediment surface and to form new mats. Length of core: 30 cm.
- Fig. 5. Biolaminations, initially made by predominance of filamentous and coccoid cyanobacteria (the latter not visible). Coccoids form cell clusters in the interspaces and internal microfabrics. The buildup is impregnated by extracellular polymeric substances (EPS). SEM-photography, scale: $100 \mu m$ long.
- Fig. 6. Vertical section through two pinnacles. Benthic diatoms *(Nitzschia sp.) are* floating in the supernatant water (arrow). Pinnacle walls are stiffened by filaments of cyanobacteria and EPS. Internal space: graycolored EPS visible (compare with SEM photography in Pl. 11/7). Scale: 500 μ m long
- Fig. 7. Interior of a pinnacle showing diatoms *(Nitzschia* sp.) in living position. Typical wedged arrangement of diatom frustules. Diatom frustule architecture may stabilize the vertical buildup and serve as solid substrate for the attachment of bacteria. SEM-photography, scale: $100 \mu m$ long

first is quartz grain-supported (GERDES et al. 1985a, 1985b) and occurs predominantly on open tidal flats of the southern North Sea (Pls. 11/3,4). Lamination is created by mats of filamentous cyanobacteria intertwined with mineral grains (P1. 11/3). Several species of the constructing organisms are capable of a rapid gliding mobility, probably via gel excretion which allows them to escape burial. By this means, the organisms migrate from buried mats to the freshly sedimentated new surface, where they grow and multiply to form a new mat (P1.11/4). Reduced availability of light induced by burial serves as a trigger mechanism.

The second type of buildup forms without the aid of sedimentation and occurs predominantly in the protected hypersaline basins of salterns and Gavish Sabkha (PI. 11/ 5). In response to seasonal fluctuations of environmental conditions (e.g. light intensity, salinity), microbes override the topmost mats to gain optimal environmental position. In summer, coccoid cyanobacteria form the active surface layer. These organisms are able to produce large amounts of extracellular polymeric substances (EPS). Layers built by coccoid cyanobacteria are swollen by water-saturated viscous gel. In winter, filamentous cyanobacteria are dominant at the surface. This type of alternating couplets of coccoid and filamentous cyanobacteria is termed "biogenic varvite" (GEROES et al. 1991). Its internal fibrillar meshwork exhibits irregular-sized and -distributed pores and cavities, impregnated by large amounts of EPS. Commonly, carbonate particles also grow withtin these mats, caused by chemical gradients around physically defined nucleation centers (e. g. small grains, organisms, or gas bubbles; DAHANAYAKE et al. 1985).

Both mat types contribute to the sedimentary surface patterns referred to in the next sections.

4 PHYSICALLY CONTROLLED STRUCTURES IN WHICH MICROBIAL MATS PLAY A ROLE

As already mentioned, microbial mats embedded in sedimentary surfaces act as a kind of soft tissue which effectively alters the properties of surface structures (REINECK et al. 1990). In the study sites listed in Table 1, bedding surfaces subsequently are influenced by a variety of physically controlled processes such as desiccation, erosion, and gas pressure. From the interplay between these forces and the biogenic material, specific surface markings and deformation structures evolve. These structures are now briefly described and their genesis discussed.

4.1 Shrinkage cracks **(comparative studies)**

Sites of observation were two different types of basins of Bretagne salterns: (i) hypersaline ponds in which microbial mats flourish; (ii) abandoned seawater reservoirs of normal salinity in which clay is deposited. The clay sediments were bare of microbial mats, possibly because faunal bioturbation and grazing was taking place under these normal salinity conditions.

(i) Crack morphology in microbial mats: Shrinkage is marked by polygonally arranged cracks with short incomplete sub-fractures which results, in plane view, in cauliflower patterns (Fig. 1, PI. 12/1). Some cracks tend to be widely spaced, others are narrow. Edges of cracks are rounded since cracking enables the mat-forming microbes to overgrow the margins and migrate into the cracks. Overgrowth of margins results in pillow-like structures (PI. 12/4).

(ii) Crack morphology in mineral clay: Shrinkage is marked by polygonally arranged cracks of the classical V-

- Fig. 1. Shrinkage cracks: small-scale sub-fracturing of crack margins and splitting of larger cracks into smaller ones is controlled by fibrillar microbial mats producing characteristic cauliflower-like patterns. Upper part: transition towards smooth angular cracks indicating decrease of influence of microbial mats. Scale: 5 cm long
- Fig. 2. Shrinkage cracks in clay-rich sediment bare of microbial mats: Shrinkage cracks are not devided and have sharp edges. Center: tracks (taphoglyph) and body of a crab (Carcinides *maenas)* visible. The animal track appears to have controlled the form and direction of cracking (Schäfer 1954b). Scale: 5 cm long
- Fig. 3. Section of a sediment core (same setting as in P1. 12/1) showing widely spaced shrinkage crack with pillow-like structure. Top: stack of microbial mats (indicating re-wetting of locality). Scale: 1 cm long
- Fig. 4. Microbial mat growing around crack margin producing pillow-like structures which prevent healing of cracks after re-wetting (compare PI. 12/3). Scale: 1,5 cm long
- Fig. 5. Surficial microbial mat, loosely attached to the substrate, folded and cracked after drying, cracks producing large openings. Cap: 5 cm in diameter
- Fig. 6. Submerged microbial mat, loosely attached to the substrate, folded and torn due to water movement. Scale: 5 cm long
- Fig. 7. Sectional view of sediment core showing upfolded mats. Upfolding may be produced by desiccation (compare P1. 12/5), water motion (compare P1.12/6), or gas pressure (compare PI. 13/5). Top: domed stack of biolaminations below evaporitic crust. Scale: 1 cm long

shape (SHINN 1983). In plane view, the crack margins are sharp and orthogonally regular (Fig. 1, P1. 12/2). Various crack-bound polygons occur, some of them recracked. Obvious is the rather strong linear course of cracks. In place, the cracks tend to be directionally oriented indicating the existency of a sloping water table, such as described by LACHENBRUCH (1962).

Fig. 1. Morphological change of shrinkage cracks noted in settings studied in this chapter (A and D: plane views, B and C: vertical sections). A: cracks typically developing in structurally homogenous substrate, e. g. clay-rich sediment: triplett fracturing and fissure intersection result in orthogonal polygons; B and C: sketches illustrating influences of microbial mats: B: the densely entangled meshwork of the mat causes tearing of mats like "blotting paper"; C: mat-forming microbes respond to cracking by active growth, since cracks provide additional space and probably favourable environmental conditions such as wetting and shading; D: typical cauliflower-like patterns of microbial mats, incomplete fissures due to the "blotting paper" effect, rounding of edges due to active growth of mats into the fissures. Classification according to LACHENBRUCH (1962): A: directionally oriented orthogonal polygons; D: irregular random polygons.

Discussion: Scale and character of polygon surfaces as well as cross sections are strikingly different between microbial mats and clay-dominated sediment. Most important criteria demonstrating the influence of a biogenic substrate are: (i) multiple incomplete sub-fracturing of crack margins, imparting cauliflower patterns to the sedimentary surface (Fig. 1), (ii) rounded edges and pillow

Plate 13 Sedimentary structures produced by gas production in the substrate (origin of samples: Formentera saherns: 13/1; Lanzarote salterns: 13/2-6; Bretagne salterns: 13/7-8)

- Fig. 1. Mole-hill"-like surface of a saltern basin covered by microbial mats. Domal upheaval due to gas accumulation beneath the elastic and easily deformable mats. Subsequent encrustation of domes by gypsum and halite. Domes exhibit a hollow center and usually a rounded base (compare PI. 13/2). Scale: 20 cm long
- Fig. 2. Sectional view of gypsum-encrusted dome. Microbial mats still live in the gypsum crust and display a colorful zonation of bluegreen cyanobacteria, purple sulfur bacteria and black sulfate-reducing bacteria. Hollow space of the dome partially filled with water-saturated and reduced muddy sediments. This accumulation have been initiated by destroying of the dome (see protuberance structures, Fig. 3). Pen: 14 cm long.
- Fig. 3. Cabbage head structure produced by microbial mats which after flooding overgrew a dome. Scale: 2 cm long
- Fig. 4. Vertical section of a sediment core showing internal protuberance structures created by gas pressure. Coarser (light areas) and finer material (dark areas) were pressed upwards. Lower right: Fungal-like structure resembling protuberance structure as schematically presented in Fig. 3. Scale: 1 cm long.
- Fig. 5. Submerged fold, rounded crest produced by gas accumulating and migrating beneath the surface mat. Scale: 20 cm long
- Fig. 6. Fold with cracked crest produced by continued precipitation of gypsum crystals causing lateral surface expansion which thrusts the limbs of folds upwards. Scale: 15 cm long.
- Fig. 7. Juvenile "fairy ring" in plane view on a submerged muddy surface formed around the exit point of gas penetrating through the sediment-water interface. The gas generates concentric waves which displace soft surface sediments and stirr up reduced sediments (viz. dark rings). Compare with Fig. 4 and Pl. 13/8: reaction of mat-forming microbes. Scale: 15 cm long.
- Fig. 8. Submerged microbial mat surface with "fairy rings", illustrating local growth of microbial mats in concentric patterns. Microbes react to concentric physical disturbances of the muddy sub-layer (P1. 13/7). Slight irregularities of ring margins (upper part right) may refer to niveau changes in microscopic scale. Lower part left: Closely situated tings touching each other with ring boundaries indicating simultaneous gas escape. Scale: 5 cm long.

Fig. 2. Schematic presentation of areas of the upper intertidal zone showing microbial mat-stabilized surfaces in which two different kinds of erosion marks occur: erosion pockets with ripples (obstacle markings; drawn from Reineck (1979) and erosion remnants (residual stacks of microbial mats (drawn from Krumbein 1987). Erosion pockets at the intertidal/supratidal transition indicate that mats are thin, subject to abundant waves and currents, and easily eroded where obstacles cause the injury of the surface. Erosion remnants on higher-lying flats indicate that mats increase in toughness and are eroded only during storm tides.

structures. The invasion of cracks by organisms from the surface mat may be induced by more humidity in the cracks, or even by the increase of substrate available for attachment. The intensive growth of microbial mats around crack edges prevents healing of cracks (PI. 12/3) which after wetting is not unfrequent in clay-rich sediment (see also Friedman & SANDERS 1978: Figs. 11-43, 11-44).

LACHENBRUCH (1962) distinguished orthogonal polygons as "random" or directionally oriented, random systems being either regular or irregular (Neal et al. 1968). This classification also appears applicable in describing differences between polygons in microbial mats and claydominated sediment (Fig. 1). Our study of the shapes noted on microbial mat-stabilized surfaces reveals that the type of random orthogonal polygons is predominant in microbial mats, but primary and secondary cracks are irregularly shaped like fissures in blotting paper, and secondary cracks which tend to intersect the primary cracks at right angles usually are incomplete. The fibrillar network of filamentous cyanobacteria may support both the irregularity and the incomplete splitting of crack edges (compare mat structures in P1. I1/1 with crack morphologies in P1. 12/1).

According to SHINN (1983) the rule that thick layers result in large cracks, and thin layers form smaller cracks, holds not true where microbial mats are abundant. We observed that thin microbial mats produce extraordinarily wide cracks. This may correspond to the degree by which the mat is fixed to the underlying sediment. For example, smooth gypsum mush effectively prevent attachment. After shrinking and tearing, the loose surficial biofilm produces large fractures (P1.12/5). Upcurling of the margins of the drying monolayered mat and desintegration is frequent, giving rise to chip and flat-pebble formation (VolcT 1972; FAGERSTROM 1967). Very bizarre fossil-like structures may thus be generated and preserved. Also, finally, it should be mentioned, that the mats interact with the evaporation potential considerably.

4.2 Erosion pockets and ripples, erosion remnants

Study sites were the upper parts of open tidal flats of the North Sea coast where sediments are stabilized against tidal currents and wave action by the binding activities of bacteria and diatoms (P1.11/3, 4).

Description of structures (Fig. 2): (i) erosion pockets: usually rounded depressions of about 10 to 50 cm diameter, margins sharp or gradual. (ii) ripples: minor wavelike features which form on the non-stabilized bottom of the erosion pockets. Crests of the ripples merge laterally with the non-eroded surface. (iii) erosion remnants: topographic features a few centimeters high, representing residual stacks of microbial mats left after destruction of the former biostabilized surface layer.

Discussion: The pockets evolve from tide-controlled wave and current energy which acts upon the sedimentary surface. Although microbial films and mats coat and glue together the fine sandy sediments and attenuate the effects of erosive forces, the protective biofilm is frequently destroyed where obstacles (e.g. hard parts of molluscs or other objects) lying in the path of tide currents cause vortices and small-scale rip currents. The shape of such erosional pockets is strikingly different from obstacle marks which occur in sediments lacking biofilms or mats (compare REINECK & SINGH 1986: fig 117).

REINECK (1979) compared the modern erosion pockets to fossil structures found in outcrops of the Dakota Sandstone (MACKENZIE 1972). On the first view, the fossil structures may suggest that weathering laid free a rippled, non-cohesive sediment. However, the modem analogues indicate that currents or waves eroded a formerly cohesive, biostabilized surface, and subsequently, produced ripple marks on the non-cohesive sediment.

Reworking of surface layers is also indicated by erosion remnants of the former biostabilized surface layer.

On the open tidal flats referred to in this chapter, erosion is a common feature. Sediment-stabilization by microbial mats starts in the upper intertidal zone and increases towards the supratidal zone. Erosion pockets develop in the upper intertidal zone where the microbial mat is juvenile, flocculous and loosely attached to the sediment grains. Erosional remnants occur, on the other hand, towards supratidal zone. This zone is mainly controlled by storm waves and associated currents. The mat is tough and eroded only during storm tides. Usually, the versicolored vertical succession of oxygenic and anoxygenic phototrophs and sulfate-reducing bacteria occur beneath the surface. Fig. 2 illustrates the distribution of erosion pockets and erosion remnants in relationship to topography and consistency of mats.

4.3 Deformation structures

Both tidal flats and shallow hypersaline basins reveal a variety of surface deformations. Common deformational processes are wind and water friction, and gas formation in the substrate.

4. 3.1 Wind and water friction

Sites of observation are the shallow basins of salterns. Loosely attached gelatinous surface mats established atop slippery sediments such as gypsum mush or clay tend to be easily moved across the substrate, folded and torn by even weak currents (Pl. 12/6). Similar structures have been described by GAWSH et al. (1985), REINECK et al. (1990), BERNIER et al. (1991), and GALL (1989). Photosynthetically produced oxygen bubbles from the mats support the floating of loosely attached mats.

4.3.2 Gas formation in the substrate

Domes, "protuberance structures", folds, and "fairy rings" referred to in this section are products of gas formation in the substrate.

Domes (sites of observation: all study sites listed in Table 1).

Domes form elevations 2 to 15 cm high and 5 to 30 cm

in diameter, composed of microbial mats or mat-stabilized sediments, with a hollow center and usually circular shape (PI. 13/1,2). Lower supratidal flats of the North Sea coast are in places covered with domes of about 5 - 10 cm in diameter. The hollow spaces are filled with methane. The gas migrates from deeper, buried organic deposits through internal gas channels toward the surface. Here, the cohesive microbial tissues inhibit escape of the gas into air or water. When accumulating beneath the surficial mat, gas pressure leads to doming of the mat. In the arid settings studied, soft substrate domes are immediately encrusted by gypsum (Pl. 13/1, 2). After re-wetting, domes are frequently overgrown by microbial mats. Repeated overgrowth results in structures resembling cabbage heads $(PI. 13/3).$

Discussion: Several authors report doming due **to gas** pressure. TRUSHEIM (1934) described small elevations of sandy beach surfaces of the size and shape of watch glasses. The author explained these structures as a result of air entrappment in the swash zone similar to the formation of keystone vugs (see also SHEPARD 1967). HANTZSCHEL (1941) described gas pits found in mud, produced by escaping gas. According to this author, a substrate promoting the formation of such pits should be fine-grained, water-saturated and easily penetrated by the gas. **These** conditions differ considerably from the fibrillar and sticky conditions by which microbial mats are able to bind sediment. In conclusion, the kind of deformation structure may vary according to texture and property of the material, while the shaping process (e. g. gas pressure) may be the same.

The massive gypsum encrustation of domes in arid environments (PI. 13/1, 2) is favoured by a repeated change between flooding and subaerial exposure of the sedimentary surfaces. Such rapid changes between wetting and drying have a considerable influence also on the microbiology of the area, inasmuch as wetting enables microbial mats to form new surface layers, and desiccation adds new evaporite crusts to the mats. Due to these processes, domes are overgrown by a multitude of microbial mats $(Pl. 13/3)$.

Base areas of domes from the North Sea coast usually

Fig. 3. Sketch of a gas dome in a microbial mat-stabilized sedimentary surface. Gas pressure from the zone of gas production (commonly methane) and pressure drop in the hollow space of the dome **after** cracking forces soft sediments to well up to the surface beneath the domed mat (protuberance structures; modified after GOEMANN 1939).

were only 2 to 5 cm high and reached 5 to 10 cm in diameter. The gypsum-encrusted domes of arid environments reached values of 30 cm in diameter and 15 cm high crests.

Protuberance structures (sites of observation: Lanzarote salterns).

Cracking of the domes and rapid escape of the enclosed gas causes a short drop in gas pressure. This enables deeper buried sediment to well upwards through gas channels and fill the internal hollow spaces of the domes (Fig. 3, P1.13/2). After burial, such internal protuberance structures typically exhibit mushroom-like patterns. The migrating gas is also able to cause the displacement of internal sediment (PI. 13/4).

GOEMANN (1939) made similar observations on tidal fiats of the North Sea where he studied the regular distribution of biostabilized domes. The domes were filled with methane, and almost each individual dome related to a small channel visible in the substrate. The channels led into the lower-lying reduced sediments. When the author punctured the domes, reduced sediments welled up through the gas channels and filled the internal hollow spaces of the domes. These studies coincide with our observations (Fig. 3, PI. 13/2, 4).

Table2. Classificationofpetees (antiform strutures in microbial mats) and tepees (antiform structures in mineral crusts lacking mats)*

*modified after REINECK (1990)

Sediments affected by biofilms and microbial mats and enriched in reduced sulfur compounds (e.g. in estuarine, salt marsh and hypersaline settings) are known for their high production potential of methane (KIENE et al. 1986). Methane formation is a form of anaerobic respiration in which $CO₂$ is frequently the terminal electron acceptor. Instead of $CO₂$ also organic acids, methanol or methylamines serve as electron accepter (for detailed description of bacterial reaction pathways see EHRLICH 1990).

Folds (sites of observation: all hypersaline water bodies studied).

Gas from the substrate migrates horizontally beneath loosely attached mats causing folds (PI. 13/5, 6). These can be linear and branched, and tend to merge with gas domes. Similar to domes, vertical sections of folds appear as inverted "U's" (Table 2). In the arid settings studied, folds become gypsum-encrusted. Continued crystal growth causes cracking of crests, due to the lateral expansion of surface lay-

ers which presses the limbs against each other. Overthrusting of limbs also takes place (P1.13/6).

Discussion: In the shallow water basins of the salterns, two different processes may lead to the generation of folds: (i) surface expansion by gas pressure, (ii) lateral compression of surface crusts due to crystal growth (Reineck et al. 1990). The latter process is particularly active at zones of weakness, causing buckling and folding of the surface crust (ASSERETO & KENDALL 1977; KENDALL & WARREN 1987). Resulting sedimentary surface structures are termed tepees or petees. Tepees are fractured folds in abiogenic surface crusts which in cross section appear as an inverted "V" (ADAMS & FRENZEL 1950). Petees are modified tepees with a biogenic matrix which in cross section appear as an inverted "U" (GAWsH et al. 1985; REINECK et al. 1990). In the fossil record, petee structures may not be uncommon, however, they are described as tepees. Reineck et al. (1990) proposed the following genetic differentiation of petees: upfolding through gas pressure or water friction, rounded crest: alpha-petee. Same process as before, ruptured crest: betapetee. Upfolding primary through lateral expansion pressure: gamma-petee (Table 2).

Crystal growth usually generates ruptured folds in consolidated crusts. Gas accumulation beneath surface mats

usually generates folds in soft substrate prior to consolidation. In the sedimentological record, folds originating from one or the other process may hardly be differentiated (P1. 12/7). Another aspect is that mat-forming microbes usually are opportunistic species capable of taking benefit from short-term wetting of evaporite crusts. Thus, between petee and tepee developments, there may be a lot of transitional stages.

"Fairy rings" (sites of observation: Bretagne salterns).

Ring-shaped structures occur on sedimentary surfaces of basins where the water is extremely shallow (about 1- 2 cm). The center of the rings usually is the exit point of gas bubbles from the substrate. The center is surrounded by one or several circles, displaying a regular spacing of about 1-2 mm. The total diameter may reach 5 to 15 cm. Rings occur in soft muddy sediments and in microbial mats (PI. 13/7, 8). In microbial mats, the rings are stipped with numerous micro-pinnacles making them look like a pin cushion. The pinnacles are 5-10 mm high (Pls. 11/6, 7). Ring structures usually are restricted to the sediment surface. So far, sediment cores and thin sections yielded no clearly discernible rings or related internal structures (open space structures?) in the subfossil or fossil record.

Discussion: Concentrically structured bodies are not uncommon where microbial mats and biofilms are present (see e.g. biogenic ooids, oncoids, or cortoids; DAHANAVAKE ET AL. 1985, GERDES & KRUMBEIN 1987). In the context of this paper, however, the ring-shaped structures deal with a two-dimensional pattern which occurs on mat surfaces. These structures recall "fairy rings" as known from fungal growth. Their genesis is not clear until now, although we believe that "fairy rings" on microbial mat surfaces account to millimetre ripples which develop, according to SINGH & WUNDERLICH (1978), on a sediment surface covered by a 1-3 cm thin water fihn. Small internal waves produced within the water layer cause gentle ripple development on the sediment surface.

In the shallow water film of Bretagne salterns, the sequence of events starts with the exit of gas from the substrate which causes concentric wave propagation in the water. This may lead to concentric millimetre ripples on the soft muddy surface (P1.13/7). The microbiology of the sedimentary surface reacts to this physical pattern by concentric organisation of individually adapted species, responding to minute chemical gradients.

Experimental studies of SCHAFER (1954a) underline our assumption. The author led gas through muddy sediments from deeper layers towards the surface. These experiments produced similar concentric oscillation patterns with centers where the gas bubbles penetrated the sediment-water interface.

5 PINNACLE STRUCTURES

(sites of observation: Bretagne salterns)

The "fairy rings" in microbial mats are crowned by numerous micro-pinnacles. These are composed of a mixed framework of cyanobacterial and diatom ceils, embedded in extracellular polymeric substances (EPS) of bacterial and diatom origin. The diatoms predominantly belong to *Nitzschia.* In the internal fabric of the pinnacles, the spindle-like frustules of these organisms often stand in vertical and diagonal positions. This typical situation of *Nitzschia* may stiffen the pinnacle architecture (PI. 11/7). In the depressions between the pinnacles, large amounts of EPS of bacterial and diatom origin accumulate, resulting from gravity gliding from the pinnacle wails.

Pinnacles contribute to the characteristic wavy appearance of biolaminations in microbial buildups. The underlying biological reason is not clear until now. *Nitzschia* often colonizes the outermost parts of mats floating in the water (Pl. 11/6). Due to this behaviour, the species may gain a certain distance to escape toxic substances inside the mat (e.g. H_2S). On the other hand, cyanobacteria and other organisms in the mats attach themselves to solid substrates, even to diatom frustules. The final effect may be a competitive growth between benthic diatoms and cyanobacteria which may be responsible for pinnacle formation. Since mainly the crests of millimetre ripples are crowned by pinnacles, this may indicate preferred colonization of gentle elevations by phototrophic framework builders of pinnacles, cyanobacteria and benthic diatoms.

6 DISCUSSION

Two different types of depositional settings were studied (i) tidal flats in temperate climate, and (ii) shallow hypersaline water bodies prone to desiccation. Tidal flats are typical transitional environments exposed to both tidal flushing and climate-related processes. Particularly open tidal flats lacking the protection by barrier islands undergo strong influences from tidal currents and wave action. Their sedimentary surfaces are affected by burial and erosion, evaporation and desiccation. In addition, tidal flats experience abundant accumulation of detrital organic matter. Its burial commonly results in decay, and methane production is copious. In these areas, biofilms and microbial mats commonly develop. Their fibrillar properties and extracellular products (commonly long-chain sugars and increasing concentrations of uronic acid; DADE et al. 1990) increase surface stability.

In tidal flats, biostabilized surfaces experience a variety of deformation events. Resulting structures are erosion pockets and erosion remnants caused by water shear, shrinkage cracks caused by desiccation and dewatering, domes caused by gas pressure. Rare, however, are surface structures which need subaqueous conditions for their development, such as folds caused by water friction, "fairy rings" and pinnacles. These structures are limited to shallow water bodies such as basins of salterns. Salterns are models for extremely quiet shallow water environments. The accumulation of abundant organic matter is made possible by the laterally and vertically extensive growth of microbial mats (GERDES et al. 1991, CORNEE et al. 1992). Approximately similar natural environments are closed peritidal lagoons on microtidal coasts (e.g. Laguna

Mormona, Gulf of Mexico, Gavish Sabkha, Sinai coast). Ancient examples may be shallow water environments described by WARREN (1986) and organic-rich biolaminated facies from a Kimmeridgian lagoonal environment in the French Southern Jura mountains (TRIBOVILLARD et al. 1992).

In the salterns studied, a variety of physical processes act upon the biostabilized surfaces and initiate deformation. Crack formation encompasses at least four different processes: volume change as a result of drying, water friction, gas pressure, and crystallization pressure. Folds were found to develop from at least three different processes: water movement, gas accumulation beneath the mat, and lateral pressure by evaporite crystal growth in surface crusts.

Other crack origins not discussed in this chapter include those induced by thermal contraction of salts (TuckER 1981), by salinity changes (VAN STRAATEN 1954), and by ice melting-off (REINECK 1956). Finally, various observations have been done on cracks which originate subaqueously as a result of synaeresis (JUNGST 1934). Such cracks have been produced experimentally in subaqueous sediment as a result of compaction of rapidly flocculated clay layers (WHITE 1961). Whereas DONOVAN & FOSTER (1972) assumed the formation of synaeresis cracks at sediment-water interface, PLUMMER & GOSTIN (1981) suggested that a majority of synaeresis cracks originate substratally.

Experimental work on the formation of subaqueous cracks at the sediment-water interface was also carried out by SCHÄFER (1954a) in a completely different set of conditions. The author led gas from below through mud using steam, compressed air, and finally methane from a deeper buried zone of decay. From these experiments, the author revealed structures which he termed "expansion cracks" (Dehnungsrisse). This type of cracks is genetically related to deformation structures which result from gas pressure as described in the present paper (domes, folds, protuberance structures, "fairy rings"). Expansion cracks induced by gas pressure may form where clay-rich sediment without biofilms or microbial mats occurs; domal upheaval, folding, and internal protuberances induced by gas pressure may develop where surfaces, stabilized by biofilms or microbial mats, are able to offer stronger resistance against expansion.

Formational processes of cracking discussed above encompass various different possibilities. For facies diagnosis it may be important that some of these processes are related to subaerial settings (e.g. desiccation, thermal

Table 3. Summary of sedimentary surface structures studied, and figure references

contraction, ice-cracking, salinity changes, crystallization pressure), however, other processes are not restricted to subaerial settings but are also subaqueous phenomena (e.g. shrinkage due to dewatering, expansion of surfaces due to gas pressure).

Folds generating from mineral encrustation and overthrusting seem to be typical for subaerial conditions in an arid climate (AsSERETO & KENDALL 1977; KENDALL & WARREN 1987). However, folding of biostabilized surfaces due to gas pressure or water friction suggest that also surface folding may have various origins.

Considering the various origins of cracks and other deformation structures, the problem in environmental reconstruction becomes evident. Thus, it is suggested to use such structures as diagnostic of subaerial or subaqueous conditions only in association with other structures typical of a specific depositional environment.

Besides physically controlled surface markings and deformation structures, primary sedimentary structures also include biogenic structures (REINECK & SINGH 1986). In this overview, four biogenic structures occur (Table 3): (i) growth bedding, (ii) pillow-like overgrowth of crack margins, (iii) concentric growth following the sediment displacement by internal waves ("fairy rings"), (iv) pinnacles, These biogenic structures produced by microbes are induced by motion (taxis), growth and multiplication of mat-constructing bacteria and diatoms in response to stimuli which are physical, physicochemical or interspecific in origin.

Under certain conditions, growth bedding is able to form even under subaerial exposure. This was observed on sandy tidal flats, where sedimentation provides microbial cells with solids for attachment, and where capillary transport of groundwater takes place which maintains the surface wet enough for microbial growth.

All the other types of biogenic structures referred to in this overview (mat overgrowth without sedimentation, pillow-like growth around crack margins, cabbage head structures, pinnacles and "fairy rings"), indicate at least periodic flooding, as overgrowth can only proceed in water.

Considering the good fossilization potential of the structures studied, shrinkage cracks are known from a great number of outcrops (e.g. SHINN 1983). The example of the Dakota Sandstone also shows fossil erosion pockets (MAc-KENZIE 1972, REINECK 1979). The fossilization of expansion structures in soft substrates (e. g. domes, folds) may be low. The chance that structural remnants may be preserved by burial, increases with the stabilizing effect of microbial mats. Mineral encrustation of domes and folds may also increase the preservation potential. Several fenestral structures (e.g. birdseyes) indicate the former presence of gas bubbles (TEBUTT et al. 1965, SHINN 1983). Also, folds are not uncommon in the fossil record (BERNtER et al. 1991, Gall 1989, VAI & RICCI LUCCHI 1977, HAUSCHKE 1987). Several so-called tepees, however, may be petees in origin (Table 2). The fossil record also includes the characteristic wavy appearance of laminations in stromatolites which is assumed to relate to pinnacles. Fossil cabbage head patterns are reported by FRIEDMAN & SANDERS (1978: fig. 5-11).

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REFERENCES

- ADAMS, J.E. & FRENZEL, H.N. (1950): Capitan barrier reef, Texas and New Mexico. - J. Geol. 58, 289-312, Chicago
- ASSERETO, R.L.A.M. & KENDALL, C.G.ST.C. (1977): Nature, origin and classification of peritidal tepee structures and related breccias. - Sedimentology 24, 153-210, 31 Figs., 5 Tables, Amsterdam
- BERNIER, P., GAILLARD, C., GALL, J.C., BARALE, G., BOURSEAU, J.P., BUFFETAUT, E. & WENZ, S. (1991): Morphogenetic impact of microbial mats on surface structures of Kimmeridgian micritic limestones (Cerin, France). - Sedimentology 38, 127-136, 11 Figs., Amsterdam
- CORNEE, A, DICKMAN, M. & BUSSON G. (1992): Laminated cyanobacterial mats in sediments of solar salt works: some sedimentological implications. - Sedimentology 39, 599- 612, 12 Figs., 3 Tables, Amsterdam
- DADE, W.B., DAVIS, J.D., NICHOLS, P.D., NOWELL, A.R.M., Tms-TLE, D., TREXLER, M. & WHITE, D.C. (1990): Effects of bacterial exopolymer adhesion on the entrainment of sand. - Geomicrobiol. J. 8, 1-16, 4 Figs., 3 Tables
- DAHANAYAKE, K., GERDES, G. & KRUMBEIN, W.E. (1985): Stromatolites, oncolites and oolites biogenically formed in situ. - Die Naturwissenschaften, 72, 513-518, Berlin
- DONOVAN, R.N. & FOSTER, R.J. (1972): Subaqueous shrinkage cracks from the Caithness Flagstone Series (Middle Devonian) of Northeast Scotland. - J. Sed. Petrol. 42, 309-317, 9 Figs., Tulsa
- EHRLICH, H.L. (1990): Geomicrobiology. 2nd ed., 646 p., Decker Inc., New York
- FAGERSTROM, J.A. (1967): Development, flotation, and transportation of mud crusts - neglectecd factors in sedimentology. - J. Sed. Petrol. 37, 73-79, 7 Figs., Tulsa
- FRIEDMAN, G.M. & KRUMBEIN, W.E. (1985, eds): Hypersaline ecosystems: The Gavish Sabkha. - Ecological Studies 53, 246 Figs., Berlin (Springer)
- FRIEDMAN, G.M. & SANDERS, J.E. (1978): Principles of sedi $mentology. - New York (Wiley)$
- GALL, J.CL. (1989): Die Grabungsstelle der oberjurassischen Plattenkalke von Cerin (Südjura, Frankreich). - Archaeopteryx $7, 1-11, 16$ Figs., Eichstätt
- GAVISH, E., KRUMBEIN, W.E. & HALEVY, J. (1985): Geomorphology, mineralogy and groundwater geochemistry as factors of the hydrodynamic system of the Gavish Sabkha. - In: Friedman, G.M. & Krumbein, W.E. (eds): Hypersaline ecosystems: The Gavish Sabkha, Ecological Studies 53, 186- 217, 24 Figs., 1 Table, Berlin (Springer)
- GERDES, G. & KRUMBEIN, W.E. (1987): Biolaminated deposits. -In: BHATrACHARJI, S., FRIEDMAN, G.M., NEUGEBAUER, H.J. & SEILACHER, A. (eds): Lecture Notes in Earth Sciences 9, 183 pp., 43 Figs., 11 Tables, Berlin (Springer)
- GERDES, G., KRUMBEIN, W.E. & REINECK, H.E. (1985a): The depositional record of sandy, versicolored tidal flats (Mellum

Island, southern North Sea). - J. Sed. Petrol. 55,265-278, 13 Figs., 1 Table, Tulsa

- GERDES, G., KRUMBEIN, W.E. & REINECK, H.E. (1985b): Verbreitung und aktuogeologische Bedeutung mariner mikrobieller Matten im Gezeitenbereich der Nordsee. - Facies 12, 75-96, 4 Figs., 2 Tables, 2 Plates, Erlangen
- GERDES, G., KRUMBEIN, W.E. & REINECK, H.E. (1991): Biolaminations - ecological versus depositional dynamics. - In: EINSELE, G., RICKEN, W. & SEILACHER A. (eds.): Cycles and events in stratigraphy, 9 Figs., Berlin (Springer)
- GIANI, D., SEELER, J., GIANI, L. & KRUMBEIN, W.E. (1989): Microbial mats and physicochemistry in a saltern in the Bretagne (France) and in a laboratory scale saltern model. -FEMS Microbiol. Ecol. 62, 151-I62, 8 Figs., 2 Tables, Amsterdam
- GOEMANN, H.B. (1939): Entgasungs-Kuppen auf den Sedimenten der Nieder-Weser. - Natur u. Volk 69, 508-512, 4 Figs., Frankfurt a. M.
- HÄNTZSCHEL, W. (1941): Entgasungs-Krater im Watten-Schlick. - Natur u. Volk 71,312-314, 1 Fig., Frankfurt a. M.
- HAUSCHKE, N. (1987): Knollige und tepeeartige Strukturen Indikatoren flit die friihdagenetische Bildung yon Ca-Sulfaten unter Playa-Bedingungen im Unteren Gipskeuper (km 1) des Lippischen Berglandes. - N. Jb. Geol. Paläont. Abh. 175, 147-179, 16 Figs., Stuttgart
- JONGST, H.(1934): Zur geologischen Bedeutung der Synaerese. Geol. Rundschau 25,312-325
- KALKOWSKY, E. (1908): Oolith und Stromatolith im norddeutschen Buntsandstein. - Z. Deutsch. Geol. Ges. 60, 68-125, Berlin
- KENDALL, C.G.ST. & WARREN, J.K. (1987): A review of the origin and setting of tepees and their associated fabrics. -Sedimentology 34, 1007-1027, 20 Figs., 2 Tables, Amsterdam
- KIENE, R.P., OREMLAND, R.S., CATENA, A., MILLER, L.G. & CAPONE, D. (1986): Metabolism of reduced methylated sulfur compounds by anaerobic sediments and a pure culture of an estuarine methanogen. - Appl. Environm. Microbiol. 52, 1037-1045
- KRUMBEIN, W.E. (1983): Stromatolites the challenge of a term in space and time. - Precamb. Res. 20, 493-531, 16 Figs., 2 Tables, Amsterdam
- (1987): Die Entdeckung inselbildender Mikroorganismen. -In: GEaDES, G., KROMaEm, W.E. & REmeCK, H.-E. (eds): Mellum, Portrait einer Insel.- 62-77, 6 Figs., Frankfurt a.M. (Kramer)
- LACHENBRUCH, A.H. (1962): Mechanics of thermal contraction cracks and ice-wedge polygons in perma-frost. - Geol. Soc. America Spec. Paper 70, 69 p.
- MACKENZIE, D.B. (1972): Tidal sand deposits in lower Cretaceous Dakota Group near Denver, Colorado. - The Mountain Geologist 9, 269-277, 8 Figs., 1 Table
- PETTIOHN & POTTER, P.E (1964): Atlas and glossary of primary sedimentary structures. - 370 p., 117 Pls., Berlin (Springer)
- PLUMMER, P.S. & GOSTIN, V.A. (1981): Shrinkage cracks: desiccation or synaeresis? $-$ J. Sed. Petrol. 51, 1147-1156, 11 Figs., Tulsa
- REINECK, H.E. (1956): Abschmelzreste von Treibeis an den Ufersäumen des Gezeiten-Meeres. - Senck. leth. 37, 299-304, Pts. 5 Plts, 1 Fig., Frankfurt a.M.
- (1979): Rezente und fossile Algenmatten und Wurzelhorizonte. -Natur u. Museum 109, 290-296, 11 Figs., Frankfurt a. M.
- (1990): Aktuogeologie. Cour. Forsch.-Inst. Senckenberg 127, 365-374, 13 Figs., 2 Tables, Frankfurt a. M.
- REINECK, H.E. & SINGH, I.B. (1986): Depositional sedimentary environments. - 2nd ed. corr. 2nd print., 551 pp., 683 Figs., 38 Tables, Berlin (Springer)
- REmECK, H.E., GERDES, G., CLAES, M., DUNAJTSCHIK, K., RIEGE, H. & KRUMBEIN, W.E. (1990): Microbial modification of sedimentary surface structures. - In: HELING, D., ROTHE, P.,

FÖRSTNER, U. & STOFFERS, P. (eds): Sediments and environmental geochemistry. - 254-276, 9 Figs., 1 Table, Berlin (Springer)

- SCHÄFER, W. (1954a): Dehnungsrisse unter Wasser im meerischen Sediment. - Senckenbergiana Ieth. 35, 87-99,12 Figs., Frankfurt a. M.
- (1954b): "Geführte" Trockenrisse. Natur u. Volk 84, 14-17, Frankfurt a. M.
- SHEPARD, F.P. (1967) : The earth beneath the sea. -242 p., 113 Figs., Baltimore (John Hopkins)
- SHINN, E.A. (1983): Tidal flat environment. In: SCHOLLE, P.A., BEBotrr, D.G. & MOORE, C.H. (eds): Carbonate depositional environments, AAPG Mem 33, 172-210, 51 Figs., Tulsa
- SINGH, I.B. & WUNDERLICH, F. (1978): On the terms wrinkle marks (Runzelmarken), millimetre ripples, and mini ripples. - Senckenbergiana maritima 10, 75-83, 2 Pls., Frankfurt
- TEBUTT, G.E., CONLEY, C.D. & BOYD, D.W. (1965): Lithogenesis of a distinctive carbonate rock fabric. - Contrib. Geol. 4, 1- 13, 1 Plate, Wyoming
- TRIBOVILLARD, N.P., GORIN, G.E., BELIN, S., HOPFOARTNER, G. & PICHON, R. (1992): Organic-rich biolaminated facies from a Kimmeridgian lagoonal environment in the French Southern Jura mountains - A way of estimating accumulation rate variations. - Palaeogeography, Palaeoclimatology, Palaeoecology 99, 163-177, 5 Figs., 4 Tables, Amsterdam
- TRUSHEIM, F. (1934): Eine bedeutsame Schichtfläche aus dem Muschelkalk und ihre Auswertung durch die Meeresgeologie. - Natur u. Volk 64, 333-340, 6 Figs., Frankfurt a. M.
- TUCKER, R.M. (1981): Giant polygons in the Triassic salt of Cheshire, England: A thermal contraction model for their origin. - J. Sed. Petrol. 51,779-786, 6 Figs., Tulsa
- VAI, G.B. & RICCI LUCCHI, F.R. (1977): Algal crusts, autochthonous and clastic gypsum in a cannibalistic evaporite basin: a case history from the Messinian of Northern Apennines. - Sedimentology 24, 211-244, 21 Figs., 1 Table, Amsterdam
- VAN STRAATEN, L.M.J.U. (1954): Composition and structure of recent marine sediments in the Netherlands. - Leidse Geol. Mededel 19, 1-10
- Voigr, E. (1972): Tonrollen als potentielle Pseudofossilien. -Natur u. Museum 102, 401-410, 10 Figs., Frankfurt a. M.
- WARREN, J.K. (1986): Shallow-water evaporitic environments and their source rock potential. - J. Sed. Petrol. 56, 442-454, 9 Figs., 2 Tables, Tulsa
- WHITE, W.A. (1961): Colloid phenomena in sedimentation of argillaceous rocks.- J. Sed. Petrol. 31,560-570, Tulsa

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