

Evidence of epibenthic microbial mats in Early Jurassic (Sinemurian) tidal deposits, Kulla Gunnarstorp, southern Sweden

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Cover Picture: Close-up of microbially induced wrinkle structures, long side of figure corresponds to 1.5 cm.

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Abstract: Wrinkle structures, a type of microbially induced sedimentary structures (MISS) were found in Jurassic tidally deposited heterolites of Kulla Gunnarstorp, southern Sweden. Wrinkle structures are characterized by minute, commonly elongate crinkles on the upper bedding planes of fine grained arenites. These structures, as well as MISS in general, form in siliciclastic sediments due to bacterial secretion of extracellular polymeric substance (EPS), which is strongly cohesive. The wrinkle structures of the present study originated as thick epibenthic microbial mats, and are of the non-transparent type, meaning that underlying bedforms are completely concealed by the bacterial remains. Where the mat grew, EPS hindered erosion of the substrate, thus changing the premises of the physical distribution of sediments.

The wrinkle structures were exclusively found on the upper bedding planes of wavy bedded micaceous arenites whose bioturbation indices range from 2–4. Microbial mat formation and preservation was facilitated since bioturbation and grazing was restricted by the fluctuating conditions (for instance regarding salinity) in the tidal depositional environment.

Keywords: Wrinkle structures, microbially induced sedimentary structures, Jurassic, Kulla Gunnarstorp, Sweden.

Supervisor: Mikael Calner

Subject: Bedrock geology

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Bevis på epibentiska mikrobiella mattor i tidala avlagringar från äldre jura (Sinemurian), Kulla Gunnarstorp i Skåne

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Sammanfattning: Skrynkelsestrukturer, en typ av mikrobiellt inducerade sedimentstrukturer (MISS) har återfunnits i jurassiska tidalt avsatta heteroliter i skånska Kulla Gunnarstorp. Skrynkelsestrukturer kännetecknas av små, ofta avlånga veck på överytan av finkorniga sandstenar. Dessa strukturer, liksom MISS i allmänhet, bildas i siliciklastiska sediment under inverkan av bakteriellt utsöndrad extracellulär polymerisk substans (EPS), vilket är starkt kohesivt. Skrynkelsestrukturerna i den aktuella avhandlingen härrör från tjocka, epibentiska bakteriemattor, och är av den icke-transparenta typen, vilket innebär att underliggande bäddformer helt täcks av de bakteriella lämningarna. Där mattan växte hindrades erosionen av EPS och på detta vis ändrades premisserna för den rent fysiska distributionen av sediment.

Skrynkelsestrukturerna återfanns uteslutande på det övre bäddplanet glimmerrika areniter, vilkas bioturbationsindex varierar mellan 2–4. Bildning och bevaring av bakteriemattan möjliggjordes då bioturbation och betning hölls nere av de fluktuerande förhållandena (avseende bl. a. salthalt) som rådde i den tidala bildningsmiljön.

Nyckelord: Skrynkelsestrukturer, mikrobiellt inducerade sedimentstrukturer, Jura, Kulla Gunnarstorp, Sverige.

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1 Introduction and aims

Microbes dominate the Precambrian stratigraphic record, but with the evolution of grazing metazoans and increasing rates of bioturbation in the Phanerozoic, cyanobacteria became restricted to more marginal marine environments. However, at times of severe environmental stress, such as in association with mass-extinctions, microbes can spread over a wider extension of the shelf and re-appear as anachronistic facies (Sepkoski *et al.* 1991; Pruss *et al.* 2004; Calner 2005).

Microbial activity through a complex interaction with substrate, erosional processes and other environmental factors is preserved in different ways depending on the depositional context. In carbonate environments stromatolites or oncoids may be formed. These are rigid, normally easily distinguished structures with a long history of research behind them (e.g. Walter 1976; Tewari & Seckbach 2011). Their counterparts in siliciclastic sediments are less well known. Owing to the later cementation in siliciclastics as compared to the carbonate settings, the preservation potential of microbial activity is lower and identification is harder. This can lead to that these for paleoenvironmental reconstructions potentially very important structures are overlooked or misinterpreted. Nonetheless, over the past two decades a larger attention from the scientific community has been focused on traces of microbial activity in siliciclastic settings. The produced structures are known as microbially induced sedimentary structures, or MISS (e.g. Noffke *et al.* 2001; Noffke & Chafetz 2012).

Hypothesised to be of microbial origin, this paper describes and analyses minute wrinkled surfaces on the upper bedding planes of arenites belonging to the Sinemurian tidal deposits of Kulla Gunnarstorp, southern Sweden. The first findings from this locality were made by the laymen geologists of *Geologiklubben i Helsingborg* and the aim of the study is to confirm the affinity of the structures as MISS and to investigate their temporal relation to the late Triassic mass-extinction. Swedish MISS have until now only been documented in Palaeozoic strata (e.g. Martinsson 1965; Calner 2005; Calner & Eriksson 2011), meaning that the Early Jurassic structures discussed here would be the youngest so far described from Sweden.

2 Methods

The study was divided in two parts: one part included practical fieldwork and study of collected samples, whereas the other part was a literature study in order to put the collected information into a broader context. The latter has been focused on three main themes: the character and nature of MISS in general and its association with mass-extinction events; the global and regional record and causes for the late Triassic mass-extinction event and lastly: the regional and local stratigraphy of Triassic-Jurassic strata in Skåne and Kulla Gunnarstorp.

The depositional environment was studied in the field at the Kulla Gunnarstorp coastal cliff. A composite log could be made by following the dipping strata along the 250 m of exposure using standard stratigraphical techniques. To classify and to confirm biogenicity of the observed structures, six samples found in the beach rubble containing wrinkle structures were visually analysed and examined in a light microscope, as well as the one sample found *in situ*. The studied rock specimens are stored at the Department of Geology, Lund University. Noffke (2010) was mainly used as a source for classification of wrinkle structures.

3 Microbially induced sedimentary structures (MISS)

3.1 Biofilms

Bacteria are not planktonic blobs just randomly drifting around, waiting for the right light and nutritional conditions to reveal themselves. Rather, the individual bacteria work together, creating a higher level of organization in the form of biofilms (Costerton *et al.* 1995). A biofilm is the slimy substance encountered in everyday situations like when one opens a water bottle a month after having forgotten to empty it. In fact, biofilms can develop on almost any surface on earth and their complexity even resembles that of eukaryotic tissue, facilitating optimal temperature, salinity and nutrition levels for the constituent microbes (Costerton *et al.* 1995; Noffke 2010).

Bacteria switch between a planktonic lifestyle, where they can spread and proliferate, and the efficient and protected biofilm phase (Costerton *et al.* 1995). The formation and disintegration of a biofilm can be summarized in a few steps (*sensu* Stoodley *et al.* 2002) starting with the attachment of cells to a surface. Then the secretion of extracellular polymeric substance, or EPS, starts (Fig. 1). EPS is strongly adhesive, and can be formed by bacteria and archaeans, as well as many eucaryotes. Once the cells have attached themselves, a



Fig. 1. The cyanobacterium *Merismopedia punctata* in a scanning electron microscope. The pillow-shaped cells form clusters that attach to the sand surface by the sticky, threadlike extracellular polymeric substance (EPS). Scale unknown. Modified from Noffke (2010).

biofilm can start to mature; if the conditions are right, an organized architecture with transport channels and pores develops. Eventually however, due to nutrient scarcity or overpopulation, the biofilm will start to disintegrate, be transported away and possibly start a new colony.

An advanced biofilm forming a laterally extensive, organic layer can be called a microbial mat, a denomination that has come to replace the older term “algal mat” (Noffke 2010). Microbial mats in for instance tidal flats are divided into what can be compared to tiering levels. The topmost layer is occupied by photoautotrophic cyanobacteria which act as primary producers. As they die, their matter is decomposed by heterotrophic bacteria directly below them. Beneath them in their turn are chemolithotrophic bacteria which manage to live on the relatively energy-poor chemical compounds left over by the microbes above (Fig. 2).

Favourable conditions for microbial growth coincide with the depositional context of finely grained sand (Noffke 2010). The slight turbulence associated with fine sand deposition hinders mud (which would otherwise block sunlight) from settling, at the same time as currents are not strong enough to destroy the mat. Furthermore, the low cohesiveness of fine sand (as opposed to mud), allows bacteria to move through the sediments, while the grains are still small enough to be “embraced” by the cyanobacteria. The translucent quartz grains can also be incorporated in the biofilm itself and conduct light to the photoautotrophic bacteria. This is what Noffke (2010) refers to as ‘microbial mat depositional facies’.

As hinted in the beginning of this paragraph, microorganisms modify their environment to suit their own needs. Not only has the secretion of EPS the effect of hindering erosion by holding grains together,

the smooth upper surface strongly reduces the shear stress exerted by the eroding currents (Paterson 1994). However, if there is a rupture in the mat, erosion can get hold of the underlying sediments. This leads to the formation of erosional remnants or pockets (Fig. 3). The sedimentary surface in the erosional pocket is several centimetres lower than that of the mat. It often displays ripples, a stark contrast to the elevated, smooth mat surface and a clear indicator of a palaeobiomat (Bose & Chafetz 2009). Other ways microbial mats may be preserved as include wrinkle structures, which will be discussed below.

3.2 Wrinkle structures

Wrinkle structures are small scale, crinkled and commonly elongate ridges of microbial origin seen in siliciclastics, but the term has a somewhat complicated etymology.

‘Runtzelmarken’ (wrinkle marks) was introduced by Häntzschel & Reineck (1968), who compared the structures to the skin of an old, dried apple. The term came to be used for small scale irregularities on sand beds which may also have a purely physical origin (Porada & Bouougri 2007, and references therein). Another term for a similar phenomenon, ‘Kinneyian ripples’, is derived from the genus *Kinneyia* erected by Charles Walcott (1916). Walcott described small scale, subparallel ridges that he interpreted to be of algal origin. Martinsson (1965) studying minute irregularities in Cambrian siliciclastics similar to Walcott’s, did not take a definite position on whether the structures were of biotic or physical origin, but rather suggested the genetically neutral term ‘Kinneyian ripples’. Later, Hagadorn and Bottjer (1997) coined the term ‘wrinkle structures’ as an umbrella term for ‘runtzelmarken’ and ‘Kinneyian ripples’.

Nonetheless, Porada & Bouougri (2007) suggest

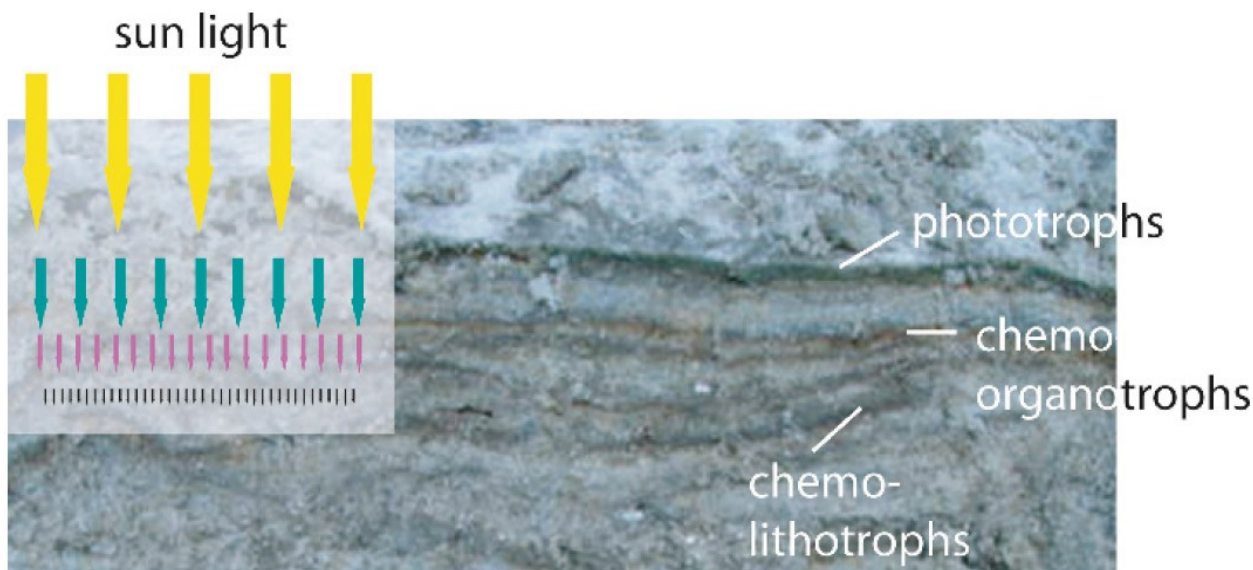


Fig. 2. Internal lamination of a biomat. Each layer is inhabited by different bacterial groups. Energy enters the system as sunlight. The phototrophic bacteria convert it into organic matter, which is later decomposed by the chemorganotrophic and chemolithotrophic bacteria. Scale unknown. From Noffke (2010).



Fig. 3. Erosional pockets in a recent microbial mat. Almost no ripples are discernible on the elevated and smooth surfaces where the microbial mats grow. The difference is stark to the topographically lower, mat devoid erosional pockets where physical processes can rework the sediment into ripples. From Bose & Chafetz (2009).

usage of the term wrinkle structure only if ‘microbial participation is likely but a clear classification is not possible’, and instead promote use of the long established ‘Kinneyian ripples’. Despite this, the newer term ‘wrinkle structures’ is now widely used and refers to structures of microbial origin (e.g. Pruss *et al.* 2004; Mata & Bottjer 2009; Calner & Eriksson 2011).

Several modes of formation of wrinkle structures have been proposed, but the common denominator is a microbial mat whose cohesiveness holds the sediment together. On one hand, there are those who mean that the crinkles develop after burial. For instance, Pflüger (1999) hypothesises a model with gas build-up beneath the sediments, while Noffke *et al.* (2002) and Noffke (2010) argues for post-burial deformation of the mat with overlying sediments exercising a shear stress on the mat, thus crinkling it. On the other hand, Hagadorn & Bottjer (1999) mean that wrinkle structures reflect the actual crinkled upper surface of a microbial mat, despite that Noffke (2010) and Porada & Bouougri (2007) mean that wrinkle structures have as yet not been observed in modern mats.

Noffke (2000) expanded the term by dividing it into the two types transparent and non-transparent. In a transparent wrinkle structure, the crinkles are superimposed on the other physically induced sedimentary structures, meaning that for instance ripples are still visible underneath the wrinkles. Beneath the non-transparent structures instead, the relief of ripples is

not discernable. Noffke (2010) relates this to the mat type giving rise to the structure originally.

Epibenthic mats are smooth, centimetres thick mats that grow on the sedimentary surface. Their thickness obscures any underlying bedforms, thus forming wrinkle structures of the non-transparent type. Endobenthic mats on the other hand are intrasedimentary, only visible on the surface as a discrete grain taint. This weaker mat produce the wrinkle structures of the transparent type.

3.3 Differentiation from abiotic structures

Microbially induced structures are not always conspicuous and can therefore be hard to find. But they are also easily confused with abiotic phenomena (Porada & Bouougri 2006). In order to be able to define a structure as MISS, Noffke (2009) list six typical features:

1. Strata should not be affected by metamorphism exceeding lower greenschist facies.
2. Associated with transgressions, with the creation of suitable environments for cyanobacteria.
3. Deposited in “Microbial mat depositional facies”, meaning fine grained sand, predominantly composed of quartz.
4. Main hydraulic pattern controls the distribution of MISS, for tidal flats this means that endobenthic

mats develop in the upper intertidal zone, while epibenthic mats belong to the lower supratidal zone.

5. Statistical analyses of erosional remnant slope angles and microbial levelling of surfaces are in accord with models of Noffke and Krumbein (1999).
6. In thin section, textures that are formed or associated with biofilms or microbial mats, such as wavy laminae, high porosity from gases that have gathered below the mat or the baffling of small grains.

3.4 The habitats of microbial mats through time

In the Precambrian, microbial mats dominated a wide spectrum of environments (Seilacher 1999). An example is the Archean Pongola Supergroup of South Africa with its 2.9 Ga old cyanobacterially induced sedimentary structures (Noffke *et al.* 2008). Starting in the Lower Cambrian, bioturbation rates began to increase with the evolution of skeletonised metazoans and their utilization of formerly unoccupied niches. Burrowing and grazing lead to the destruction of mats. This was followed by a second pulse of increased bioturbation in the Middle and Late Ordovician with increasing complexity in tiering structures (Droser & Bottjer 1989). Microbial mats, which had earlier dominated the shallow marine settings, became confined to stressed or marginal environments (Hagadorn & Bottjer 1999). However, in association with the late Devonian and end-Permian mass-extinctions they reappear as anachronistic facies in the shallow marine setting. Both these events can be coupled with widespread anoxic conditions which are lethal to metazoans but favourable for many groups of microbes (Pruss *et al.* 2004; Mata & Bottjer 2012). Pruss *et al.* (2004) estimate that this effect lasted for millions of years.

Modern microbial mats are once again restricted to marginal environments, such as tidal flats, sabkhas and salt marches. At such localities, rapid fluctuations in salinity, water depth, currents and temperature create unfavourable conditions for benthic organisms. This restrains burrowing and grazing which could otherwise destroy the microbial mats. For instance, Fenschel (1998) showed that a four month old mat can be completely ingested in a matter of weeks by gastropods

and other grazers. Post-burial burrowing also has the potential to obliterate mat laminae. Nonetheless, burrows need not be completely absent (e.g. Hagadorn & Bottjer 1997), but generally bioturbation is a limiting factor for mat preservation (Mata & Bottjer 2009).

Transgressions create favourable habitats for microbial mats, when the shelf is inundated and extensive shallow marine areas form (Noffke *et al.* 2006). In modern tidal flats, differing hydraulic conditions and moisture levels on the tidal flat will lead to the development of different types of MISS depending on which tidal zone (Fig. 4) they form in, growing thicker from land to the lower supratidal and upper intertidal area, only to decrease in size towards the subtidal area (Bose & Chafetz 2009). In fact, the lower intertidal area (which is only drained at neap tides) might seem to be almost devoid of microorganisms, but when examined closer, numerous microorganisms inhabit the sand, forming biofilms. However, these do not produce sedimentary structures with any preservation potential (Noffke 2010).

In the upper intertidal zone, which is inundated and drained once or twice every day, both the thick epibenthic and the weaker endobenthic mats may form depending on local conditions. In the storm prone and mesotidal North Sea coast, endobenthic mats dominate in the upper intertidal zone. They form quickly at the few hours of calm between the daily tidal currents, but tend to decompose in the autumn with increasing storm rate (Noffke & Krumbein 1999; Noffke 2010). Contrastingly, in the microtidally influenced and less agitated Texas coast, Bose & Chafetz (2009) reported 3 cm thick epibenthic mats from the same tidal zone.

The lower supratidal zone is only flooded by the spring flood, i.e. once every two weeks. This gives time for epibenthic mats to develop which do not decompose even when exposed to the North Sea winter storms (Noffke & Krumbein 1999). The lower supratidal is also where Bose & Chafetz (2009) report the thickest mat assemblages. They are initiated in the sheltered ripple troughs where moisture is retained, favouring bacterial growth. Eventually, the mat may completely cover the original rippled sediments, forming a smooth upper surface (Fig. 3). If preserved, it will give rise to what is known as a laminated levelling structure (Noffke *et al.* 2001).

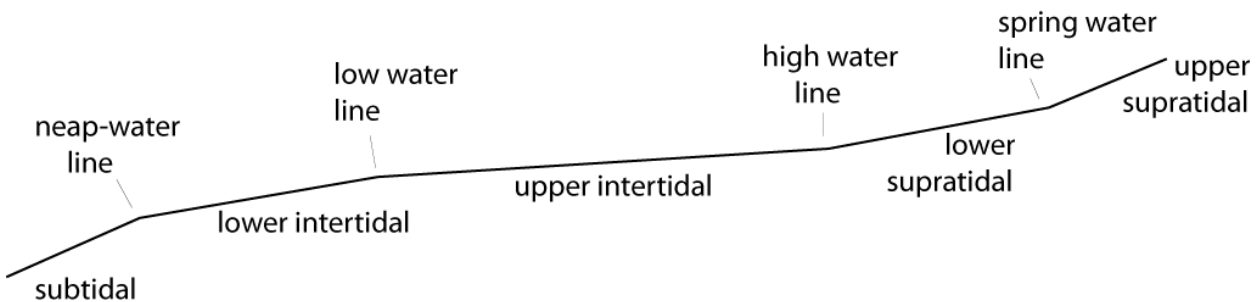


Fig. 4. Storms and tidal dynamics define the different tidal zones. The upper supratidal zone is only inundated by episodic storms, while the lower supratidal is submerged by the spring tide every two weeks. The upper intertidal is drained and flooded daily by tidal currents, while the lower intertidal is only dry during neap tides (also with a periodicity of two weeks). The subtidal zone is always below the water surface. Modified from Noffke (2010).

4 The late Triassic mass-extinction

The late Triassic mass-extinction (200 Ma) is regarded as one of the “big five” mass-extinctions (Hallam 1981; Raup & Sepkoski 1982) which not only led to a severe decline for ammonoids, brachiopods and conodonts among others, but also led to the dinosaur take-over of niches previously occupied by amphibians or reptiles (Tanner *et al.* 2004). However, the extinction appears have been a protracted one, with a gradual or intermittent extinction ranging throughout the Late Triassic (Hallam 2002).

Several extinction mechanisms have been proposed, for instance wide-spread volcanism (Central Atlantic Magmatic Province, CAMP) associated with the break-up of Pangea. Beerling & Berner (2002) mean that CO₂-emissions from the CAMP-volcanism lead to destabilization of ocean floor methane. This triggered a positive feedback-mechanism that lead to an accelerated global warming which severely challenged the land plants of the hot-house, late Triassic Pangean continent. Increased carbon-dioxide emissions also caused acidification of the oceans, inducing a crisis for calcifying marine organisms (van de Schootbrugge *et al.* 2007).

Other factors explaining the event include regional

sea-level fluctuations caused by thermal uplift or even meteorite impacts (Tanner *et al.* 2004). However, Tanner *et al.* (2004) argue that not one of these factors in itself was enough to trigger the extinction, but that it was the combination of all these circumstances that led to the major biodiversity decline. Nonetheless, unlike the end-Permian mass-extinction, a significant microbial response in not seen associated with the late Triassic mass-extinction (Mata & Bottjer 2012), despite a decrease in ichnofauna diversity and bioturbation rates in the Rhaetian (Twitchett & Barras 2004).

During a mass-extinction, niches are occupied by a few generalist taxa. Contrastingly, the recovery from a mass-extinction can be defined as the time when specialists have evolved and started to divide niches among them. The recovery interval differs between disparate taxa. For instance, ammonids needed the duration of the Hettangian (Lowermost Jurassic) to recover from the effect of the late Triassic mass-extinction, approximately 2 Ma (Schaltegger *et al.* (2008), while brachiopods had recovered already by the Middle Hettangian (Tomašových & Siblík 2007).

5 Field work

Field work was carried out in Lower Jurassic strata of the Höganäs basin in the north-western parts of the province of Skåne, southern Sweden (Fig. 5).

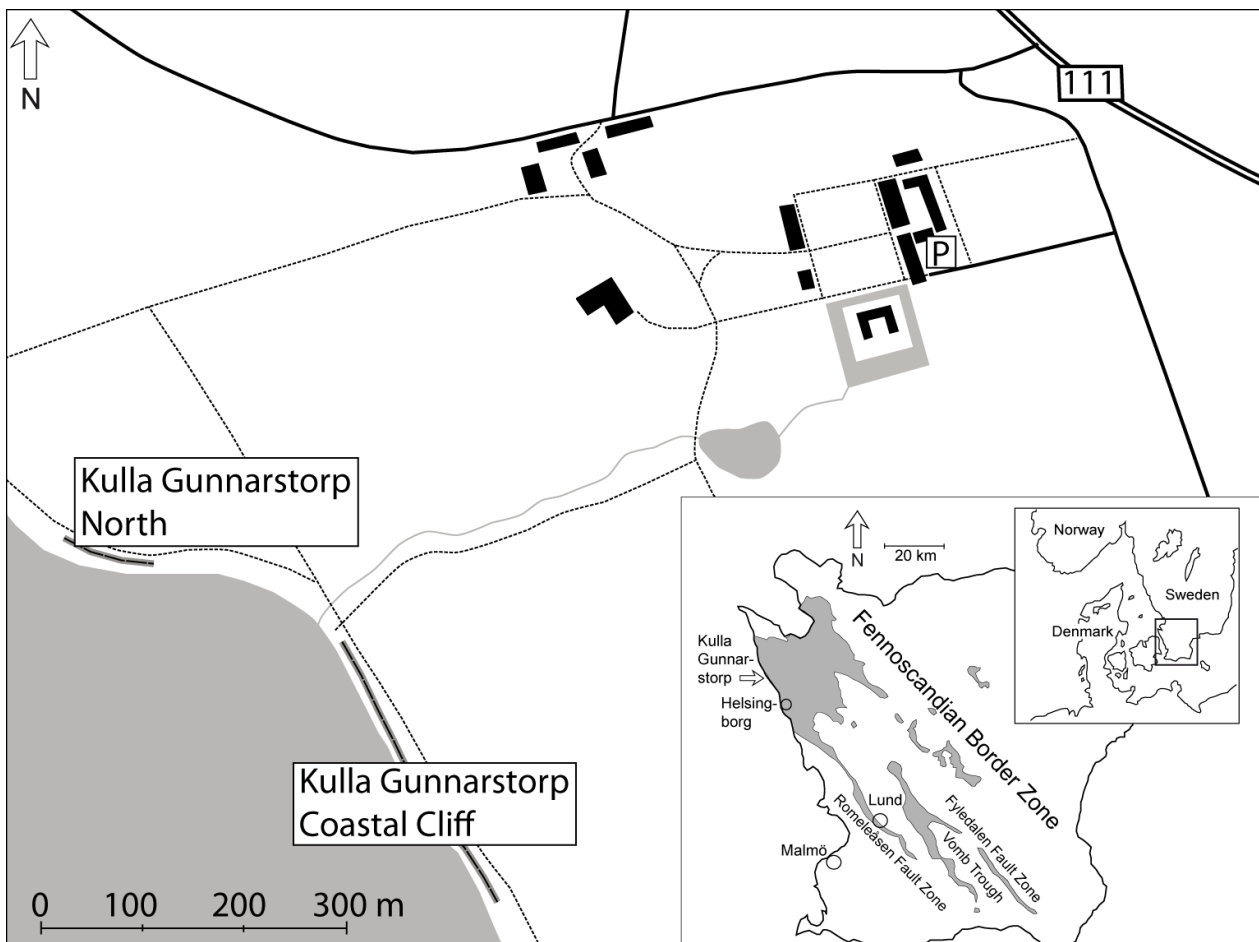


Fig. 5. Map of the studied area at Kulla Gunnarstorp and surroundings. Inset map shows the province of Skåne. Main tectonic elements are inferred, grey shade refers to Mesozoic strata.

5.1 Lithostratigraphy and geological setting

The main tectonic element of Skåne is the fault zone known as the Tornquist zone, which trends NW-SE and can be followed across Europe, from Romania through Poland and the Baltic Sea, through Skåne and eventually up into the North Sea. Following rifting and block faulting in the Upper Triassic, deposition of the Kågeröd and Höganäs formations (Fig. 6) was initiated in the Höganäs Basin (EUGENO-S Working Group 1988; Norling *et al.* 1993).

The Norian Kågeröd Formation is composed of arkoses and conglomerates, interpreted as continental redbeds that were deposited in an arid climate (Norling *et al.* 1993). The overlying Höganäs Formation is subdivided into three members, namely the Triassic Vallåkra and Bjuv members and the Jurassic Helsingborg Member, showing a sedimentary succession that reflects a variety of climates and depositional regimes.

The Vallåkra Member is mainly composed of clay stone, and reflects the transition from the arid Pangaean Kågeröd redbeds to more humid conditions. The Bjuv Member is composed of floodplain deposits and starts with a prominent coal-seam (known as the B-seam). Indeed, the Bjuv strata have been of great eco-

nomical importance, as signified by the local name “the mining beds”, or “gruvlagren” in Swedish (Sivhed 1986; Norling *et al.* 1993). Based on palaeobotanical studies by Lundblad (1959), its uppermost coal seam, the A-seam, marks the boundary to the overlying Helsingborg member, and has with that traditionally and arbitrarily also marked the lithostratigraphic base of the Jurassic in Skåne (Sivhed 1984).

However, more recent studies have slightly altered that division. The lowermost part of the Helsingborg Member, the coarse grained and poorly sorted sandstones of the Boserup beds, shows a transition from typical Rhaetian to typical Hettangian palynomorphs, and is thus inferred by Lindström & Erlström (2006) to include the T-J boundary. Overlying deposits reflect a transgressive phase and is predominately composed of deltaic sediments, with some tidal marine influences (Norling *et al.* 1994).

5.2 The Kulla Gunnarstorp coastal cliff section

The Kulla Gunnarstorp coastal cliff section is exposed along the shore some 10 km north of the town Helsingborg and belongs to the Helsingborg Member. The section has previously been described by Troeds-

		Ängelholm Trough	Helsingborg area	Landskrona Kävlinge SW Skåne	Central Skåne	Vomb Trough Fyledalen Fault Zone	
Cret.	Berriasian	Annero Formation		Annero Fm		Annero Formation	
	145.5						
Jurassic	Late						Tithonian
		Kimmeridgian					
		Oxfordian					
	Middle	Callovian	Rya Formation	Rydebäck Member (70)	Incomplete succession, not defined		Mariedal Formation
		Bathonian					
		Bajocian					
		Aalenian					
	Early	Toarcian	Höganäs Formation	Katslösa Member (40)			Röddinge Formation
		Pliensbachian					
		Sinemurian					
Hettangian							
176			Helsingborg Mb				
Triassic	Rhaetian	Höganäs Formation	Bjuv Member	Höör Sandstone		?	
			Vallåkra Member				
	Norian		Kågeröd Formation				

From Ahlberg *et al.* 2003; Bergelin 2009; Geological Time Scale 2009

Fig. 6. Mesozoic stratigraphy of Skåne.

son (1951), Pieńkowski (1991), Norling *et al.* (1993) and Ahlberg (1994b). Palynostratigraphical work has been carried out by Larsson (2009). Troedsson (1951) and Ahlberg (1994b) attribute the section to the Hettangian, whereas both Pieńkowski (1991; using sequence stratigraphy) and Larsson (2009; palynostratigraphically) conclude that the outcrop is of Sinemurian age. The assessment of Larsson (2009) builds upon pollen findings of the key taxon *Cerebropollenites macroverrucosus* and the spore *Retitriletes sinemurii*. The occurrence of the dinoflagellate *Dapcodinium priscum* further pinpoints the age of the deposits down to the early Sinemurian, since this taxon only ranges into the lower Sinemurian.

The section can easily be reached from the main road 111 between Helsingborg and Höganäs. A pathway leads from the Kulla Gunnarstorp estate along small rivulet developed in a fault zone (Fig. 5). The fault separates the slightly younger strata to the north from the slightly older strata to the south. In the gorge, herringbone cross-stratification can be seen. At the shoreline, a 2-3 m high exposure can be followed for 250 m southwards, where it due to the dip disappears below vegetation and quaternary deposits. 200 m to the north of the above mentioned fault zone, Sinemurian cross-bedded arenites of the Döshult Member (Rya Formation) can be observed along the beach (Norling *et al.* 1993). This outcrop is referred to as Kulla Gunnarstorp North in the map (Fig. 5).

The heterolithic strata are sloping at a low angle towards the south which approximately parallels the original depositional angle (Pieńkowski 1991). Nonetheless, one must bear in mind that the area has undergone some tectonism, as illustrated by the fault separating it from the Döshult rocks to the north.

The section is divided into the seven units depicted in the log (Fig. 7) and described below. Unit 1 and 2 of this publication together correlates to Unit 1 of Pieńkowski (1991), otherwise this publication follows his division (but as a consequence of the division, the names of the other units mentioned here have a numerical value of +1 as compared to his).

5.2.1 Unit 1

The unit is characterized by lenticular bedding (Fig. 8A), with 1-3 mm thick lenses of fine grained sandstone in which current ripples oriented in opposing directions can be observed. The strata are slightly bioturbated, with a bioturbation index of 2 (Droser & Bottjer 1986). One prominent horizon of 3D-rippled medium grained sand contains rip-up clasts similar to the underlying lithology, as well as traces of burrowing activities, where *Diplocraterion* is the most common.

5.2.2 Unit 2

Dominated by wavy bedding, the unit displays sand laminae, generally 2 cm thick (Fig 8B). The ripples show mud-draped foresets and are also here bi-directional. Several spindle and trilete shaped synaere-

sis sub-aquatic mudcracks (Fig. 8C) filled with fine sand from above or below can be observed, as well as iron-rich authigenic nodules. Bioturbation index is 3.

5.2.3 Unit 3

Lenticular bedding reoccurs at this level, with 3–7 cm long and 2–8 mm high sand lenses enclosed in the dark mud.

5.2.4 Unit 4

The unit is composed of wavy bedded heteroliths with 1–2 cm thick sand laminae. Ripple crests are oriented with their long axes in a E-W direction.

5.2.5 Unit 5

The strata consist of decimetre thick flasers, showing a distinct transition from the underlying beds. In the lower part of the unit, intraclasts of fine sand are embedded in the occasionally medium grained flasers, giving them a conglomeratic composition (Fig. 8D). Pieńkowski (1991) reported *Diplocraterion* and *Teichichnus* from this unit. The lithology is mineralogically immature, with high contents of mica.

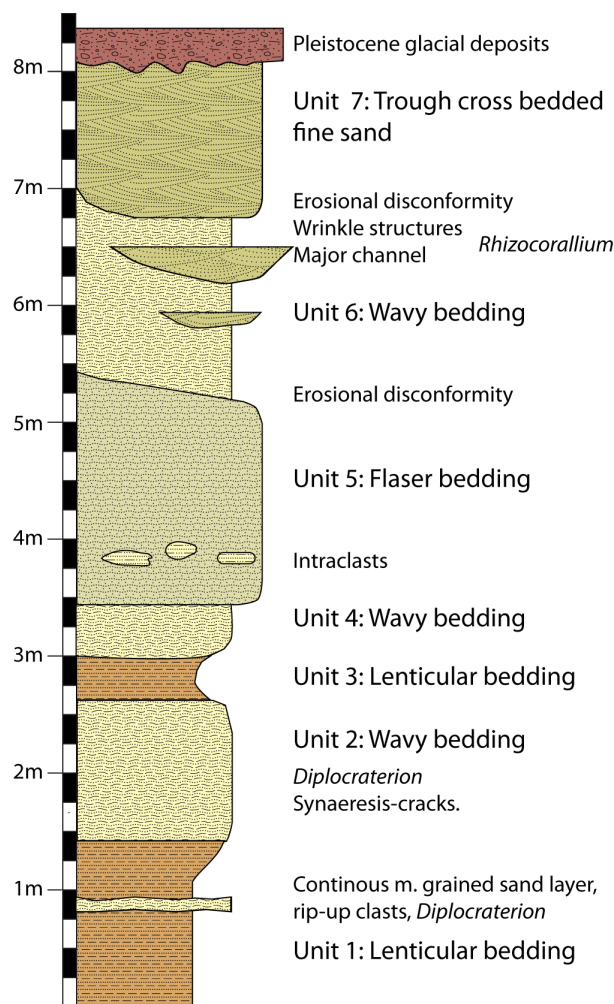


Fig 7. Schematic log of the Kulla Gunnarstorp coastal cliff.

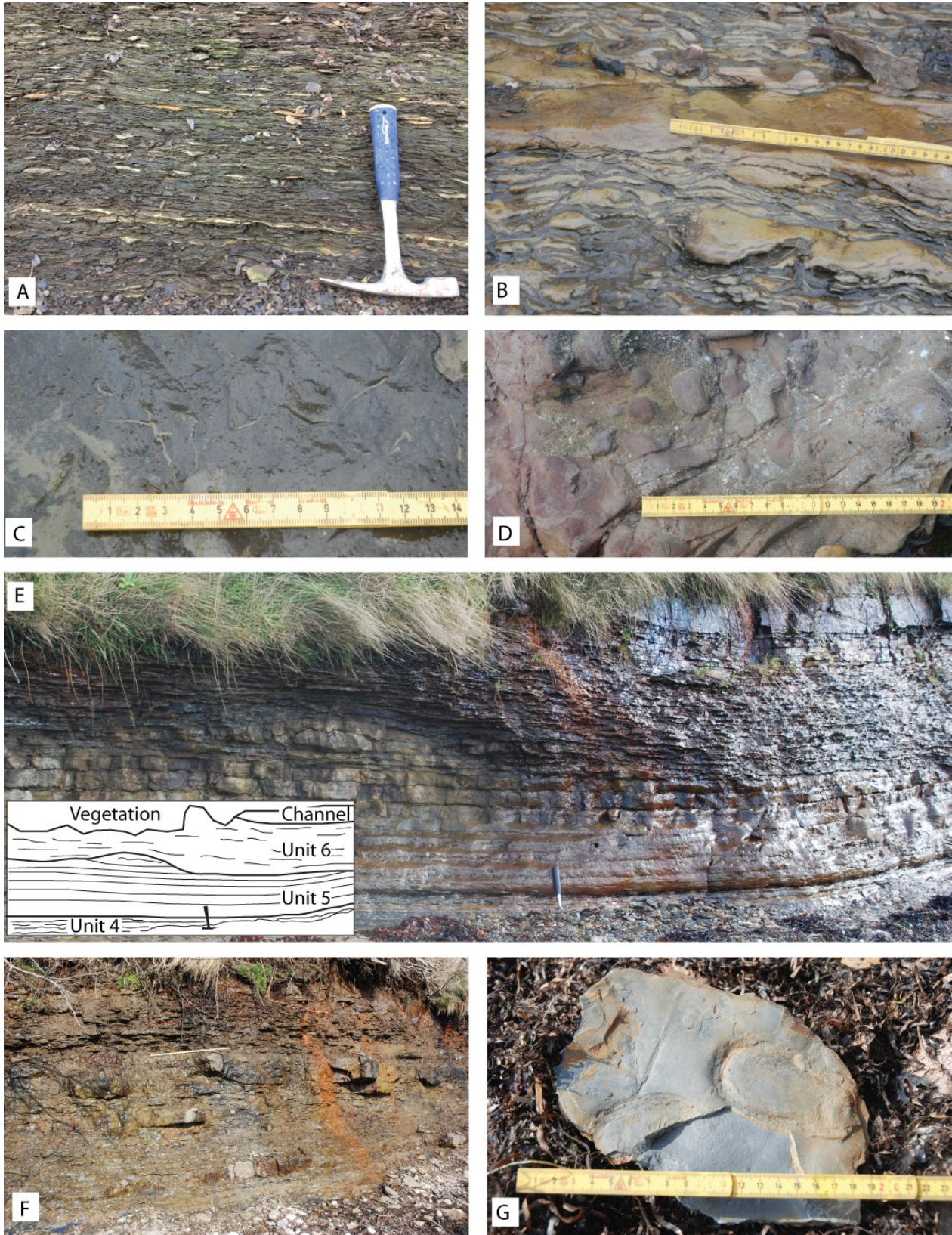


Fig. 8. Photographic plate from the Kulla Gunnarstorp coastal cliff section. **A.** Lenticular bedding, with isolated flat sand lenses enclosed in dark, organic rich mud. Hammer is approx. 30 cm. **B.** Wavy bedding. Note bi-directional ripple bundles indicating flood/ebb currents and the mud-draped foresets, deposited at slack water periods. Scale in centimeters. **C.** Synaeresis, or subaquatically formed cracks. **D.** Reddish intraclasts consisting of fine grained sand enclosed in coarser sand. **E.** The flaser bedded Unit 5 is not as easily weathered as the wavy beds below, giving the unit a bulging base. An angular disconformity separates units 5 and 6. **F.** Unit 6 hosts several drainage channels, indicating an intertidal setting. Ruler is 80 cm. **G.** *Rhizocorallium* and other trace fossils are abundant throughout the section. Photographs A and E courtesy of Mikael Calner.

5.2.6 Unit 6

Separated from the underlying beds by an erosional disconformity (Fig. 8E), the unit displays wavy bedding cut by several channel structures forming troughs normally 1–4 m wide (Fig. 8F). The channels are oriented in an E–W transport mode and the fine sand ripples show a N–S directed wave action. One channel is more than 50 m wide and can be observed almost at the top of the unit. Above the prominent channel, wrinkle structures were found *in situ*. The unit hosts several types of trace fossils (for instance *Rhizocorallium*; Fig. 8G), with a bioturbation index of 3.

5.2.7 Unit 7

The unit displays well cemented and well sorted fine sand, and shows an erosive contact to the underlying sediments. Ripples indicate a current direction from east to west. Small bivalves can be found, but no tangible bioturbation.

5.3 Wrinkle structures

The wrinkle structures in the studied section are of the non-transparent type and confined to 2–3 cm thick and highly bioturbated beds with epichnial, endichnial and hypichnial digging traces (Fig. 9A). Bioturbation indices range from 2–4. The individual rippled surfaces on the collected rock specimens cover areas ranging from 30–60 cm².

The wrinkle structures are all less than 1 mm high and are exclusively found on the upper bedding planes of ripple laminated, micaceous arenites. They either occur as elongate or pitted forms. The former features up to 1 millimetre wide, semi-continuous, commonly bifurcated and subparallel ridges which are separated by slightly wider (1–2 mm) round-based troughs (Fig. 9B). The crests are flattened with over-steepened slopes.

The pitted forms on the other hand, have round bases and are generally oval, with their short axes ≤ 1 mm and the long axes 1–3 mm (Fig. 9C). They are often slightly interconnected with each other, showing a transitioning to more elongate or kidney-shaped forms. Slopes are steep or overhanging, and the crests form an irregular network.

Smooth ripple foresets can be seen adjacent to the wrinkles, and the wrinkle structures completely or almost completely fill the ripple troughs, forming laminated levelling surfaces (Figs. 9D and E). In other words, underlying bedforms are indiscernible below the wrinkles, meaning that the wrinkle structures are of the non-transparent type formed by an epibenthic mat (Noffke 2010).

Wrinkles are not seen within the trace fossils; rather, these cut the wrinkle structures (Figs. 9A and F). This signifies that the burrows were constructed subsequent to wrinkling of the mat, and were later infilled by often coarser or finer material from overlying beds.

6 Discussion

6.1 Interpretation of the Kulla Gunnarstorp deposits

As indicated by the bi-directional currents and the heterolithic composition, the sediments were deposited in a shallow marine environment subjected to tidal processes. Sand was deposited by tidal currents, whereas the mud settled at the slack period in between tidal floods. Overall morphology of the sediments is concordant with that of a tidal flat.

Owing to decreasing energy across a tidal flat, sand dominates in the lower intertidal zone but gives way to mud higher up (Tucker 2001). The flaser bedding and the medium grained sand thus reflect the subtidal zone with its stronger currents whereas the fine sand and wavy bedding reflects the calmer conditions of the intertidal to lower supratidal zones. Additionally, the wavy bedding of Unit 6 is cut by ebb drainage channels, also indicating that the strata were deposited in the intertidal zone. The influence of these drainage channels increase going up into Unit 7, which is assessed by Pieńkowski (1991) and the author to consist entirely of amalgamated tidal channels. The erosive base of the unit indicate that the currents first went through a stage of substrate erosion before the deposition of the channel infill.

Roots, coals or desiccation cracks have not been observed, indicating that the supratidal zone never existed at this locality, or that it has been eroded subsequent to deposition (Pieńkowski 1991). Instead, the syaeresis-cracks observed in Unit 2 are a typical feature for the subtidal environment. They tend to form subaqueously when the sediments are contracted due to fluctuating water salinity (Tucker 2001; Collinson *et al.* 2006), but interestingly, deformation of microbially bound sediments may also be involved in syaeresis formation (Pflüger 1999). Seilacher (1999) points out that sand reacts to shrinkage stress by grain movement, unless its cohesion is enhanced by the sticky microbially secreted EPS. The formation and occurrence of intraclasts possibly relates to this as well. For the sandy sediments to behave cohesively, they were either cemented early on (which would be more typical for carbonate rich environments), or kept together by either mud or EPS.

The ichnofauna mainly speak for a marine palaeosetting, but Ahlberg (1994b) points out that the coexistence of pyrite and siderite reflect complex early diagenetic conditions. This combined with the observation of mainly terrestrial palynological indicators (Larsson 2009), as well as the tidal setting in itself, speak for brackish or fresh water influences.

6.2 Origin of wrinkle structures

Are the observed structures actual microbially induced wrinkle structures; why and how did they form and are they possibly related to the late Triassic mass-extinction? To answer the first question, they must be

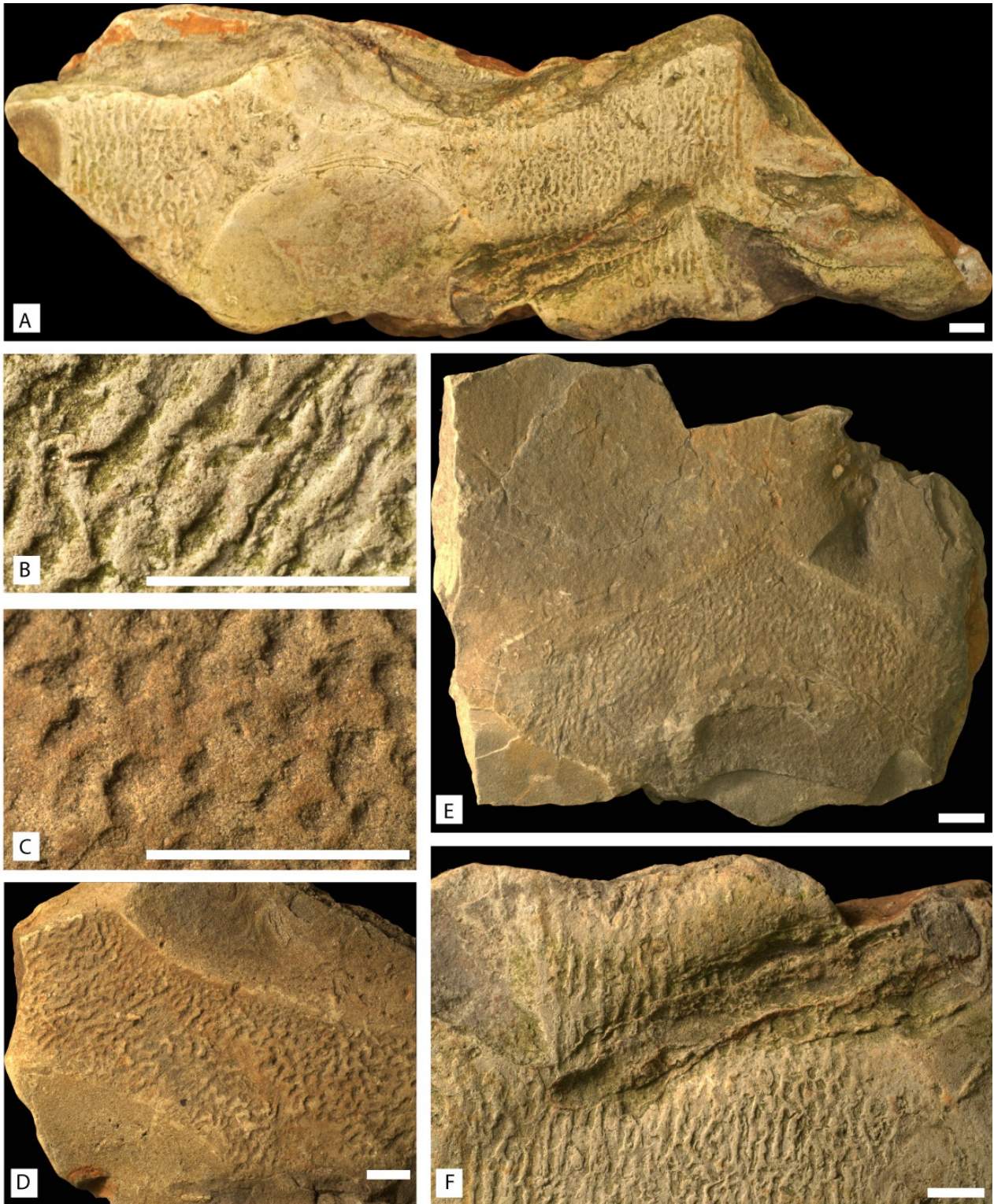


Fig. 9: Photographic plate of wrinkle structures found in Kulla Gunnarstorp. All scale bars represent 1 cm. **A.** Elongate wrinkle structures cut by epichnial tracefossils. Smooth area in the lower, middle part represents a ripple foreset, see also F. **B.** Close-up of elongate, subparallel ridges. Note the steep slopes of wrinkles, far exceeding the normal angle of repose for sand. **C.** Pitted and kidney shaped morphology. **D.** The wrinkle structure fills out the area between the ripple foresets, forming a leveling structure. **E.** The one specimen found *in situ*, also forming a leveling surface. The degree of bioturbation is not evident from the photo, but endichnial and hypichnial traces are abundant (bioturbation index 3). **F.** Close-up of epichnial trace fossil shown in A. Constructed by a vermiform animal, it cuts the wrinkle structure ridges. Photographs by David Åkesson.

scrutinized according to the criteria of Noffke (2009). To begin with, the strata have only undergone shallow burial, meaning that metamorphism cannot have given rise to the structures (Ahlberg 1994a). The timing and location is also concordant with what would typically be expected for MISS; they are formed during a transgression in a shallow tidal environment, with fine grained quartz rich sands.

Nonetheless, it must be stated that the lithology (with a rather high bioturbation, lack of rootlets etc.) indicate an intertidal setting, but the inferred mat morphology (epibenthic) is most common in, and would rather suggest a lower supratidal setting (Noffke & Krumbein 1999). Indeed, the one specimen of wrinkle structures found *in situ* belongs to Unit 6, a unit characterized by its cross-bedded channels. These structures formed as ebb tide drainage channels, signifying that these strata, including the wrinkle structures, were formed in the intertidal to upper subtidal zone. Furthermore, the lithology of specimens found in the beach rubble resembles the wavy, bioturbated horizons of Unit 6, indicating that they too belong to this unit or were formed under similar conditions. An epibenthic mat in the intertidal zone is seemingly contradictory, but as seen from the Texas coast example of Bose & Chafetz (2009), a low tidal range and storm rate can lead to the formation of thick microbial mats even in the intertidal zone. The lack of a preserved supratidal setting can also explain why wrinkle structures are so rare in the section.

Due to the few findings, statistical analysis of for instance microbial levelling could not be carried out, and due to practical obstacles, thin section studies were also unfeasible. The latter is a real impediment for this present study, as it could potentially reveal for MISS typical features such as microbial filaments or microscopic laminations arising from mat growth.

Nonetheless, the macroscopic morphology of the observed crinkles, with their oversteepened slopes (as compared to the normal angle of repose for sand) and minute scale can only have formed in the presence of cohesive, microbially secreted EPS. Wind and water alone cannot explain these observed shapes (Porada & Bouougri 2007). The flat levelling surface that the wrinkles form and how it relates to the current ripples also suggests a microbial origin, the mat forming in and filling out the sheltered ripple troughs. Following the establishment of a mat, erosion is hindered where it grows but not surrounding it, explaining the morphology with the elevated wrinkles surrounded by topographically lower ripple troughs. Additionally, the outcrop features synaeresis cracks, which also can be coupled to microbial activity. The sediments of Kulla Gunnarstorp would doubtless have been different had it not been for the microbes.

Phanerozoic MISS are associated with tidal deposits, where the fluctuating salinity and water levels restrain burrowing and grazing, thus facilitating the formation and preservation of microbial mats. In the aftermath of both the late Devonian and end-Permian

mass-extinction events however, microbial mats both spread into environments not occupied prior to the event, and started to dominate in the environments they already inhabited (Mata & Bottjer 2012). The Kulla Gunnarstorp strata were deposited in Early Jurassic, i.e. in relatively rapid succession of the late Triassic mass-extinction. The question posed here was whether the observed MISS could be associated with the mass-extinction or if they are just an artefact of the tidal depositional environment. Three facts support the latter: i) palynological evidence indicates early Sinemurian rather than the recovery interval of Hettangian age of the deposits; ii) bioturbation in the wrinkle structure horizon is substantial and iii) wrinkle structures in Kulla Gunnarstorp are, as indicated by the few findings, quite rare and by no means dominate.

7 Conclusions

Wrinkle structures form within the sediments owing to the extracellular polymeric substance (EPS) secreted by microbes, but the substance is influential also before burial. It hampers erosion and makes sand behave more cohesively than when subject to purely physical influences. Microbes may be small, but have the power to control behaviour and properties of the sediments, an aspect that is important to keep in mind when attempting palaeoenvironmental reconstructions.

The observed but rare wrinkle structures were formed as epibenthic microbial mats, growing in the intertidal zone. The sheltered positions in the ripple troughs offered favourable conditions for microbial growth, while bioturbation and grazing was restricted due to the (for metazoans) harsh tidal conditions.

In the Phanerozoic, microbial mats have been restricted to marginal environments except when the ecosystems are in a state of severe stress, such as in association with for instance the Permo-Triassic mass-extinction. At such times, microbially induced sedimentary structures (MISS) may reoccur as anachronistic facies due to lower grazing and bioturbation rates. The Upper Triassic does feature such a period of lower bioturbation rates, but the structures of the present study postdate both this period and the biodiversity recovery interval of the mass-extinction.

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