Cyanobacterial key to the genesis of micritic and peloidal limestones in ancient seas

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The origin of micritic and peloidal limestones comprising the bulk of many ancient marine carbonate deposits represents a major unsolved problem of carbonate sedimentology. Our studies of such limestones from a sequence of Late Jurassic open marine sediments exposed in central Poland revealed them as products of *in situ* calcified mats of benthic coccoid cyanobacteria. Remains of the cyanobacteria are visible in scanning electron microscope (SEM) images as characteristic patterns closely resembling the common mucilage sheaths of modern entophysalidacean and/or pleurocapsalean cyanobacteria comparable to those we found producing micritic and peloidal microbialites in Lake Van, Turkey. We suggest, by analogy, that many subtidal micritic and peloidal limestones common in the marine sedimentary record might be products of similar *in situ* calcified cyanobacterial microbiota. Such an intensive calcification of marine cyanobacteria could have proceeded only in environments more than modern seawater supersaturated with respect to calcium carbonate minerals. Advection of excess alkalinity, originating from deeper, anaerobic or dysaerobic zones to shallow water areas is proposed as the main factor enhancing colonization of extensive sea bottom areas by the alkaliphilic cyanobacteria and promoting their *in vivo* calcification.

Key words: Cyanobacteria, biocalcification, palaeogeomicrobiology, carbonate sedimentology, micrite, peloids.

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Introduction

Beginning with the early Proterozoic onward, the marine sedimentary record is punctuated with thick sequences of carbonate deposits organized usually in large lithological bodies known as carbonate ramps and platforms (Wilson 1975; Crevello *et al.* 1989; Tucker *et al.* 1990). A considerable part of them is composed of bedded or massive very fine grained deposits called commonly micritic limestones. They often contain various admixture of small subglobular bodies known as peloids which can be either scattered within the micritic matrix or may occur separately. According to Folk's (1959) classification of carbonate rocks, these limestones are termed pelmicrites and pelsparites, respectively. The origin of these sediments represents one of the puzzling and controversial problems of carbonate sedimentology and calls for urgent explanation (for review see Bathurst 1975; Flügel 1982; Tucker & Wright 1990).

Micritic (synonyms: cryptocrystalline, microcrystalline, aphanitic, lithographic, pelitic, calcilutitic) limestones are commonly regarded as product of calcium carbonate 'rain' caused by inorganic precipitation in the water column, comparable to whitings appearing in modern marine environments (for review see Bathurst 1975; Flügel 1982; Tucker & Wright 1990). For a long time whitings were regarded as a purely inorganic phenomenon (Shinn *et al.* 1989). Recently, a possibility of epicellular precipitation of calcium carbonate on living cells of a chroococcoid cyanobacterium (*Synechococcus*) has been considered as well (Robbins & Blackwelder 1992; Thompson & Ferris 1990; Davis *et al.* 1995). Unfortunately, neither of these processes, and/or the role of other bacteria, sponges, codiacean algae or seagrasses (Cloud 1962; Land 1970; Fütterer 1974; Reid *et al.* 1992) could have been confirmed as a crucial factor responsible for the origin of the fine grained aragonitic mud accumulating on the Great Bahama Bank (for recent discussion see Milliman *et al.* 1993; Milliman 1994; Friedman 1994) considered generally to be the best modern analogue of ancient carbonate platforms (Tucker & Wright 1990).

The peloidal (synonyms: clotted, pelleted, pelletoid, pseudo-ooid, 'grumeleuse') limestones, in turn, have been believed to be either defecation products (fecal pellets) of various invertebrates or result of chemical (Fåhraeus *et al.*; Macintyre 1985) and/or (eu)bacterially induced calcium carbonate precipitation (Chafetz 1986; Buczynski & Chafetz 1993).

The weakness of the above mentioned explanations of the genesis of modern carbonate muds and peloids for elucidating the origin of similar ancient marine sediments lies in the fact that they are hardly transposable on the fossil record (for discussion see Folk 1973; Bathurst 1975; Flügel 1982; Tucker & Wright 1990). It seems therefore, that credible modern analogues for the thick sequences of the ancient sea-floor accumulated micritic/peloidal limestones are lacking thus far. Little founded are also the numerous proposals implying 'microbial' or 'calcimicrobial' participation in the genesis of large masses of open marine fine grained nonskeletal

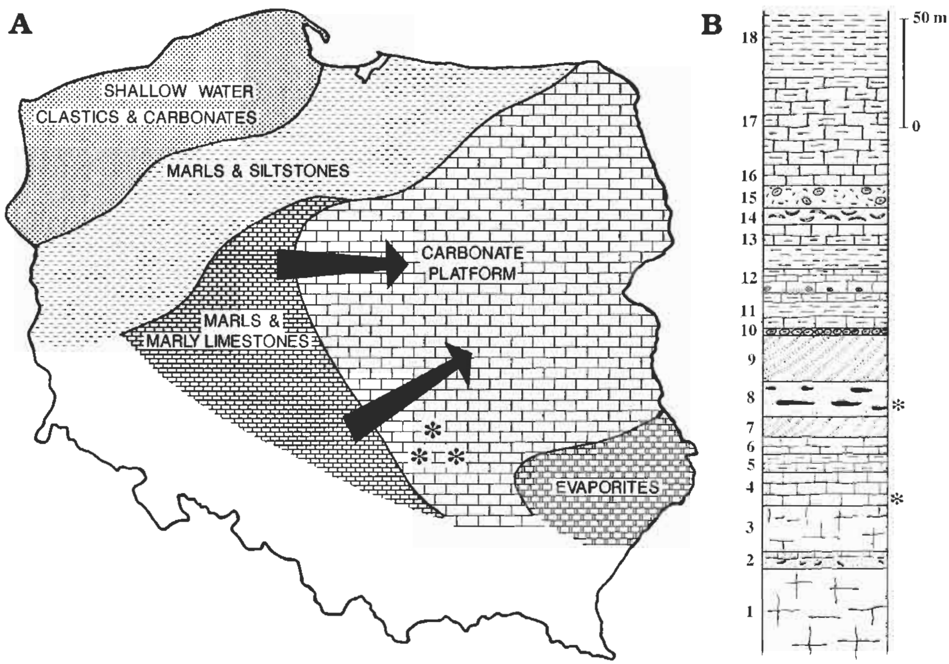


Fig 1. **A**. Early Kimmeridgian palaeogeography and facies in Poland (after Kutek *et al.* 1984). Starlets indicate sampling area (quarries: Malogoszcz, Gluchowiec, Skorkowska Góra) of the studied micritic and peloidal limestones in the SW Holy Cross Mts. Arrows denote direction of excessively alkaline and ^{12}C enriched water invasion from a deeper, dysaerobic or anaerobic zones of the sedimentary basin. **B**. Synthetic profile of the Early Kimmeridgian carbonate deposits in the SW Holy Cross Mts (after Kaźmierczak & Pszczólkowski 1968, modified). Starlets indicate the studied units composed of micritic and peloidal limestones. 1–3 – chalky limestones interbedded with oolitic biocalcarenites; 4 – platy micritic limestones; 5–6 – marly limestones and marls with overlayed with micritic limestones; 7 – oolites; 8 – banded micritic/peloidal limestones with cherts; 9 – oolites; 10 – oncolitic limestone; 11–13 – marly limestones and marls interbedded with micritic limestones occasionally with oncoids and ooids; 14 – oyster coquina; 15 – biocalcarenites with oncoids and oyster coquina; 16–18 – micritic limestones passing upwardly into marly limestones and clays.

limestones known from the geological record. This concerns particularly the 'cryptic microbial carbonates' (see Riding 1991 for review) believed to be the major component of the so-called mud mounds (e.g., Camoin & Maurin 1988; Monty *et al.* 1995; Pickard 1995). Unfortunately, most of these assumptions are not substantiated by direct evidences for the character and role of the alleged microbiota in the 'mud' formation.

Below, based on observations of fine grained Jurassic limestones from Poland and on comparative studies of modern cyanobacterial calcareous deposits from Lake Van (Turkey), we propose a radically new solution to that frustrating problem. The preliminary results of this study have been presented as abstracted lectures at the 14th International Sedimentological Congress (Kaźmierczak *et al.* 1994) and at the 10th Bathurst Meeting of Carbonate Sedimentologists (Kaźmierczak *et al.* 1995).

The Jurassic micrites and peloids

Setting. — The studied samples of fine grained limestones derive from 500 m thick sequence of Late Oxfordian–Early Kimmeridgian calcareous deposits cropping out in three large quarries (Małogoszcz, Głuchowiec, and Skorkowska Góra) in the SW part of the Holy Cross Mts, Central Poland (Fig. 1A). We have focused on two Early Kimmeridgian lithological units (Fig. 1B, units 8 and 4) belonging to the sequence (Kutek 1968; Kaźmierczak & Pszczółkowski 1968; Pszczółkowski 1970). In palaeogeographic terms (Kutek *et al.* 1984), the sedimentary area for these deposits was located near the basinward margin of an extensive carbonate platform covering during the Early Kimmeridgian central and eastern Poland (Fig. 1A). The open marine and subtidal position of this part of the sequence is indicated, beside palaeogeographic position, by findings of shark and skate teeth, locally abundant calcitized demosponge spicules (predominantly bean-shaped microscleres named rhaxes), and, occasionally, tiny pieces of brachiopods and echinoderms. Slump structures common in unit 8 (Kutek 1962) may be indicative for the foreslope location of the depositional environment. The limestone from the upper lithological unit (Fig. 1B, unit 8) is typically composed of irregularly alternating thin layers of micrite and peloids ('Banded Limestone member' in local lithostratigraphic scheme — see Kutek 1968), whereas the platy limestone from the lower lithological unit (Fig. 1B, unit 4) is a purely micritic rock.

Fabric. — Three microstructural categories can be discerned in light microscope examination of the Jurassic limestones (Figs 2A–D, 3A–B): (i) almost homogeneous micritic matrix (Fig. 2A), (ii) peloidal micritic bodies, 25–120 μm in diameter, passing often into the micritic matrix (Figs 2B–C; 3A–B), and (iii) subsphaerical voids, corresponding in size to the peloids, empty or filled with a sparry calcite mosaic (Figs 2C, 3A–B) and, occasionally, with mesh-like organic matter. Observations at contacts of micritic layers enclosing peloidal bodies with layers composed of pure peloids, show that the latter are just accumulations of peloidal bodies identical with those occurring rooted in the micritic matrix (Fig. 2D). Scanning electron microscope (SEM) examination of polished and EDTA-etched samples of micritic limestones showed a specific subpolygonal, spider web-like pattern both in the matrix and in the peloids (Figs 2E–F; 3C–D). The etched surface shows roundish or subpolygonal pits 5–10 μm in size (extremes 2 and 20 μm) separated by distinct walls of flaky shape. These consist of clay minerals, calcite crystals, and occasionally calcium phosphate, pyrite, and barite.

Isotopic and elemental results. — Measurements of carbon and oxygen stable isotopes using laser ablation sampler for stable isotope extraction (LASSIE) (Smalley *et al.* 1992) gave $\delta^{13}C$ values of -0.15‰ for the micritic framework and the peloids, and 0.15 to 0.34‰ for the spar filling the voids or occurring as cement in the pelsparites; $\delta^{18}O$ values are -7.07‰ and -7.81 to -7.89‰ respectively. Of interest are also the results

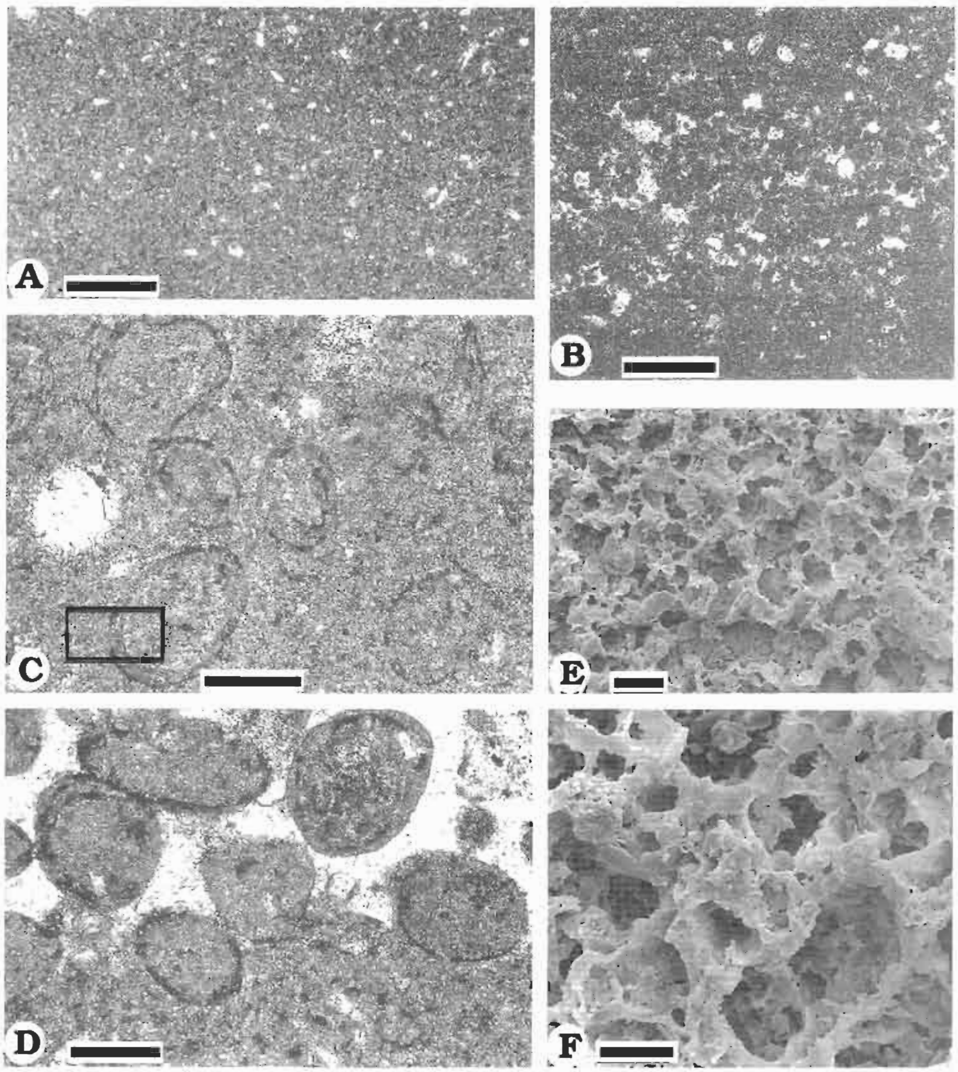


Fig. 2. Micritic and peloidal limestones from the Early Kimmeridgian of Central Poland (SW Holy Cross Mts, Małogoszcz quarry, unit 8). **A**. An almost homogenous micrite. **B**. Micrite grading into peloidal limestone. **C**. Fragment of a micritic layer enclosing a subglobular spar-filled void and micritic peloidal bodies grading in many places into micritic matrix (SEM magnification of the quadrangled area is shown in **E**). **D**. A contact between micritic and peloidal (pelsparitic) layer with some peloids still rooted in the micritic matrix. All transmitted light micrographs; scale bars for **A–D** are 100 µm. **E**. SEM picture (EDTA etching) showing continuity in the mesh-like pattern of the cyanobacterial glycocalyx remnants between the peloid and the micritic background (frames of this photograph correspond with the quadrangled area in **C**). **F**. A magnified portion of the above section showing the flaky appearance of the mineral substance replacing almost entirely the primary mucopolysaccharide glycocalyx; scale bars for **E** and **F** are 5 µm.

of elemental analyses for Sr and Mg content in the micritic matrix and in the spar filling the voids. The micrite shows relatively high amount of Mg in the micrite (4–8,000 ppm) and low of Sr (≤ 300 ppm), whereas Sr content in the spar (≈ 1,000 ppm) is combined with much lower concentration of Mg (≤ 2,000 ppm). The overall geochemical results suggest diagenetic imprint, emphasized particularly by oxygen isotopes and Sr content. However, we might believe micrite to have been originally composed of high Mg-calcite rather than low Mg-calcite or aragonite. On the other hand, calcite spar filling subglobular voids might be originally aragonite rather than high Mg-Calcite or low Mg-Calcite.

Modern analogues from Lake Van

Strikingly, the spider-web or honeycomb-like pattern found in Jurassic micritic and peloidal limestones is almost identical with that we observed in modern *in situ* calcified coccoid cyanobacterial mats occurring in the highly alkaline Lake Van, Turkey (Kempe *et al.* 1991). Lake Van is a large soda lake with a pH of 9.7–9.8, alkalinity of 152.5 meql^{-1}, and a salinity of 21.7‰ contributed to in equal shares by NaCl and sodium carbonates with minor contributions from sulphate, potassium and magnesium. Although the calcium concentration is very low (4.6 mgl^{-1}), saturation indices (SI) calculated for calcite and aragonite are quite high: $SI_{calcite} = 1.04$ and $SI_{aragonite} = 0.89$ (at temperature 20°C). Mg/Ca ratio is about 30.

The *in situ* calcifying cyanobacterial mats in Lake Van are composed of coccoid cyanobacteria (Figs 4B–C; 5A–C; 6A–B) which originally have been identified as *Entophysalis granulosa* Kützing (Gessner 1957). However, according to a new classification of cyanobacteria (Rippka *et al.* 1981), they can be classified, on the morphological basis, either as entophysalidacean members of the Chroococcales or as representatives of the pseudoparenchymatous Pleurocapsales. The definite taxonomic setting of these cyanobacteria cannot be with certainty established without knowing details of their mode of reproduction (sequential cell division in entophysalidaceans *versus* multiple successive division in pleurocapsaleans — compare Golubic 1976; Waterbury & Stanier 1978), which has not been studied thus far. Therefore, more general terms like 'benthic coccoid cyanobacteria' or 'entophysalidacean or pleurocapsalean cyanobacteria' are used for the purpose of the present paper.

The coccoid mats are participating in formation of large tower-like calcareous structures in places where calcium-rich ground waters enter the lake bottom resulting in very high calcium carbonate supersaturations in the mat ambience (Kempe *et al.* 1991). In sites where input of seepage calcium is high, the mats surface is strongly calcified (Fig. 4A). In places where seepage calcium supply is limited and the mat ambience is less calcium carbonate saturated, thin, weakly calcified crusts are produced or the mats remain uncalcified (Fig. 4D–E). Living coccoid mats have been observed in Lake Van from the water surface down to the depth of 25–30 m, where they grow almost in a darkness. This is not surprising since light

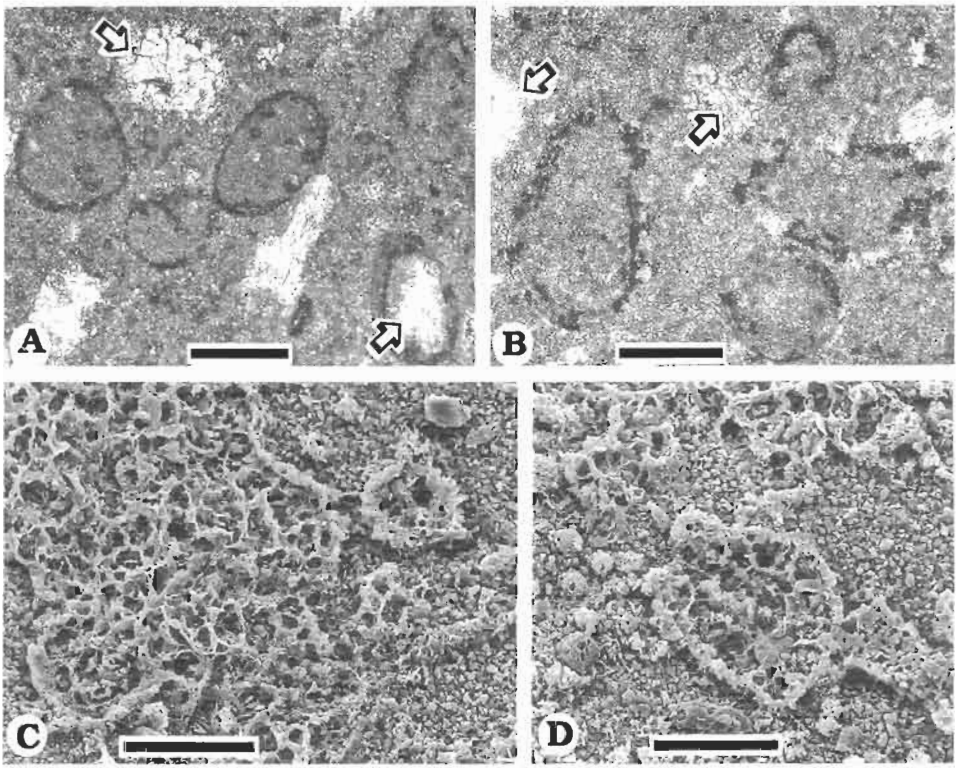


Fig. 3. Micritic and peloidal limestones from the Early Kimmeridgian of Central Poland (SW Holy Cross Mts, Głuchowiec quarry, unit 8). **A–B**. Transmitted light photomicrographs showing examples of peloidal bodies rooted in a micritic matrix. Note that in many places the peloids are grading into the matrix. Arrows indicate primary voids after decayed groups of coccoid filled later with sparry calcium carbonate. Recognizable remnants of cyanobacterial sheaths (glycocalyx) are preserved mostly in the darker rims surrounding the peloids and in the blackish parts of the micritic matrix. Scale bars are 100 µm. **C–D**. SEM images of EDTA-etched sections prepared from the same sample as above showing patterns recognizable as common mucilage sheaths (glycocalyx) of pseudoparenchymatous coccoid cyanobacteria very similar to those producing the Lake Van microbialites. Noteworthy is the gradual transition between the cyanobacterial glycocalyx and the surrounding micrite evidencing a genetic interrelationship between the glycocalyx and the microgranular calcareous material. Scale bars are 50 µm.

requirements of cyanobacteria are known to be limited and some of them can photoassimilate at very weak illumination (Van Liere & Walsby 1982; El Haq 1986; Couté 1982; Cox *et al.* 1989).

The mats are permineralized with microgranular (micritic) aragonite precipitating *in vivo* on and within the common mucilage sheaths (glycocalyx) surrounding individual cells and groups of cells (Fig. 4B–C). After the death of cells, the cytoplasm (Figs 5F; 6C) is decomposed and the remaining spaces are in the subfossil part of the microbialite filled with secondarily precipitated (?bacterially mediated) fine-grained aragonite or may remain empty for longer time (Figs 5G; 6D–F). As a result, the structure of such in part *in vivo* and in part early *post mortem* calcified mat is in some places homogenously micritic and in other porous (Fig. 6D–E). The porous parts of permineralized mat show in SEM pictures the characteristic, subpolygonal configuration of the glycocalyx.

The accretion of the microbialitic structure proceeds in a patchy manner and the intensity of calcification for particular groups of cells forming the mat may be different. Mats growing in a condition of high calcium carbonate supersaturation produce an almost homogenous micrite (Figs 4C; 5D; 6B, D–E). In less intensively calcified mats micritic peloid-like bodies are visible together with subglobular voids filled sometimes with sparry aragonite (Fig. 5B, D–E). The voids represent apparently spaces remaining after decay of particular groups of cells. Weakly calcified coccoid mats have been observed to occur usually on tops of the highest microbialitic towers where calcium carbonate saturation is lower because of the larger distance to the Ca-rich groundwater outflow. Such mats are composed of more individualized subglobular cell groups. Some of these groups display stronger calcification whereas other remain uncalcified. Mats of that kind are not very coherent and easily disintegrate into subglobular aragonitic peloidal bodies representing the permineralized groups of coccoids (Fig. 4D–E).

Comparison and discussion

SEM pictures of uncalcified (Figs 5F; 6C) and with aragonite permineralized (Fig. 5G) glycocalyx from Lake Van coccoid mats are almost identical with the patterns observed in the Jurassic limestones (Figs 2E, F; 3C–D). Comparison of the Jurassic spider web-like pattern with the structure of living coccoid mats suggests that the thicker outer mucilage sheaths (capsules) enveloping larger groups of cells are usually most resistant to degradation (Horodyski & Vonder Haar 1975; Kaźmierczak & Krumbein 1983; Krumbein & Swart 1983; Gerdes & Krumbein 1987; Kempe & Kaźmierczak 1993) thus may be easier preserved *post mortem*.

Average size of cell groups surrounded by the thick gelatinous envelopes correspond to the average size of peloids within both the Jurassic and Lake Van micrites. The average size of individual cells is much smaller, for instance, in the most common marine species *Pleurocapsa fuliginosa* 4–7 μm (largest 20–30 μm) (Bourelly 1972; Waterbury & Stanier 1978). It is, therefore, highly possible that the average size of the minimicrite (1–4 μm) (Tucker & Wright 1990) reflects just the average diameter of the pleurocapsalcan and/or entophysalidacean cells measured in thin sections or in electron microscope images.

The overall textural patterns of the examined Jurassic micrites and peloids suggests cyanobacterial origin. Organization of entophysalidacean and pleurocapsalean mats as agglomerations of smaller and larger cell groups (so-called *Gleocapsa*-like units) separated by thicker gelatinous

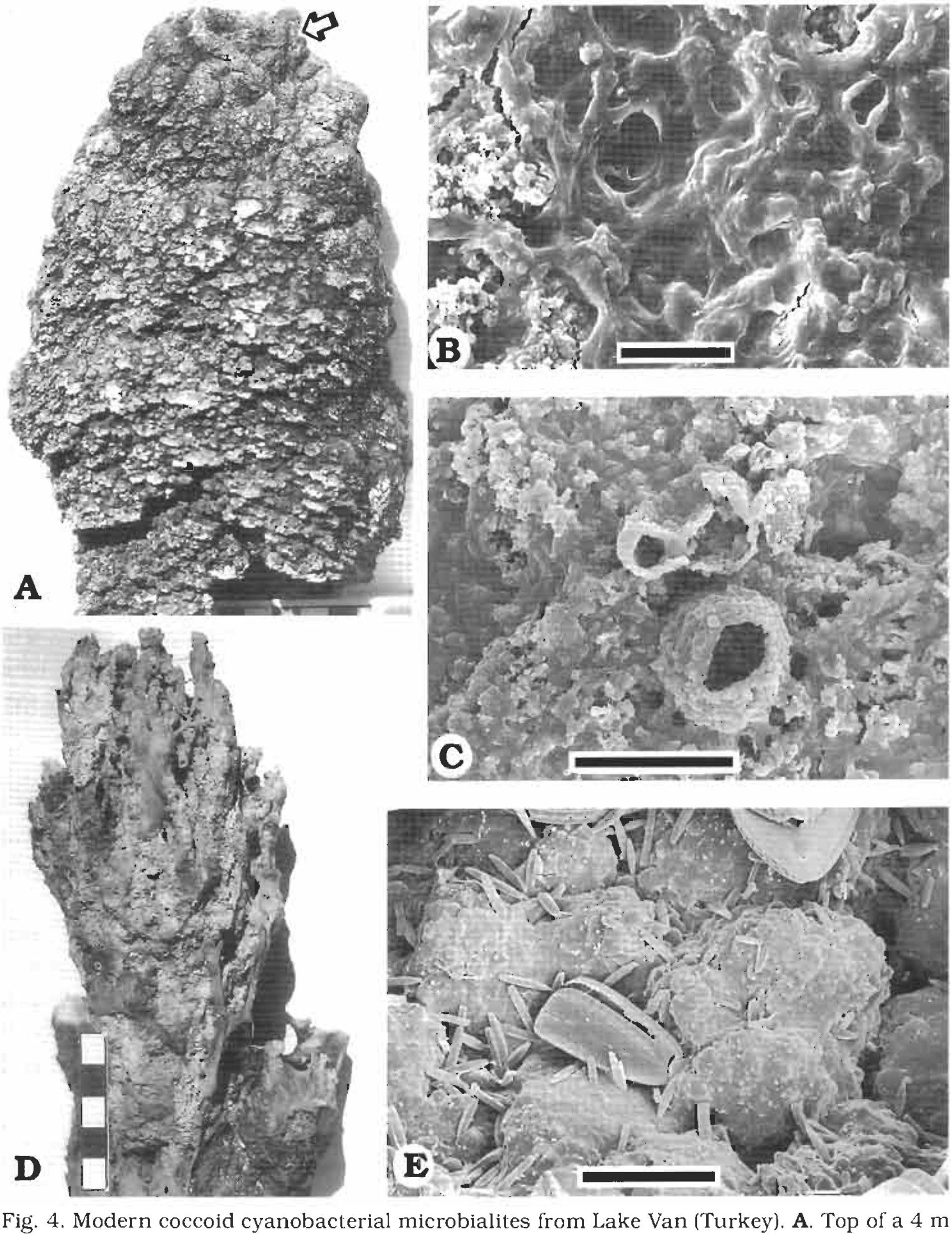


Fig. 4. Modern coccoid cyanobacterial microbialites from Lake Van (Turkey). **A**. Top of a 4 m high microbialitic column (arrowed) growing at water depth 18.5 m. In this case the coccoid mat is producing a hard, almost homogenous aragonitic micrite. Tatvan Bay; scale in cm. **B**. SEM view of a living coccoid mat from the surface of the column shown above covered with patches of *in vivo* precipitated aragonite granules; scale bar is 10 µm. **C**. SEM view of another fragment of the same surface heavily permineralized with microgranular aragonite. Two strongly calcified cyanobacterial capsules are visible in the middle of the micrograph; scale bar is 10 µm. **D**. Side branch of a microbialitic column growing at water depth 8 m. In this case the coccoid mat is weakly calcifying and produces predominantly peloidal bodies. Tatvan Bay; scale in cm. **E**. SEM view of peloidal bodies generated by a weakly calcified coccoid mat at water depth 15 m. Adilcevaz; scale bar is 50 µm.

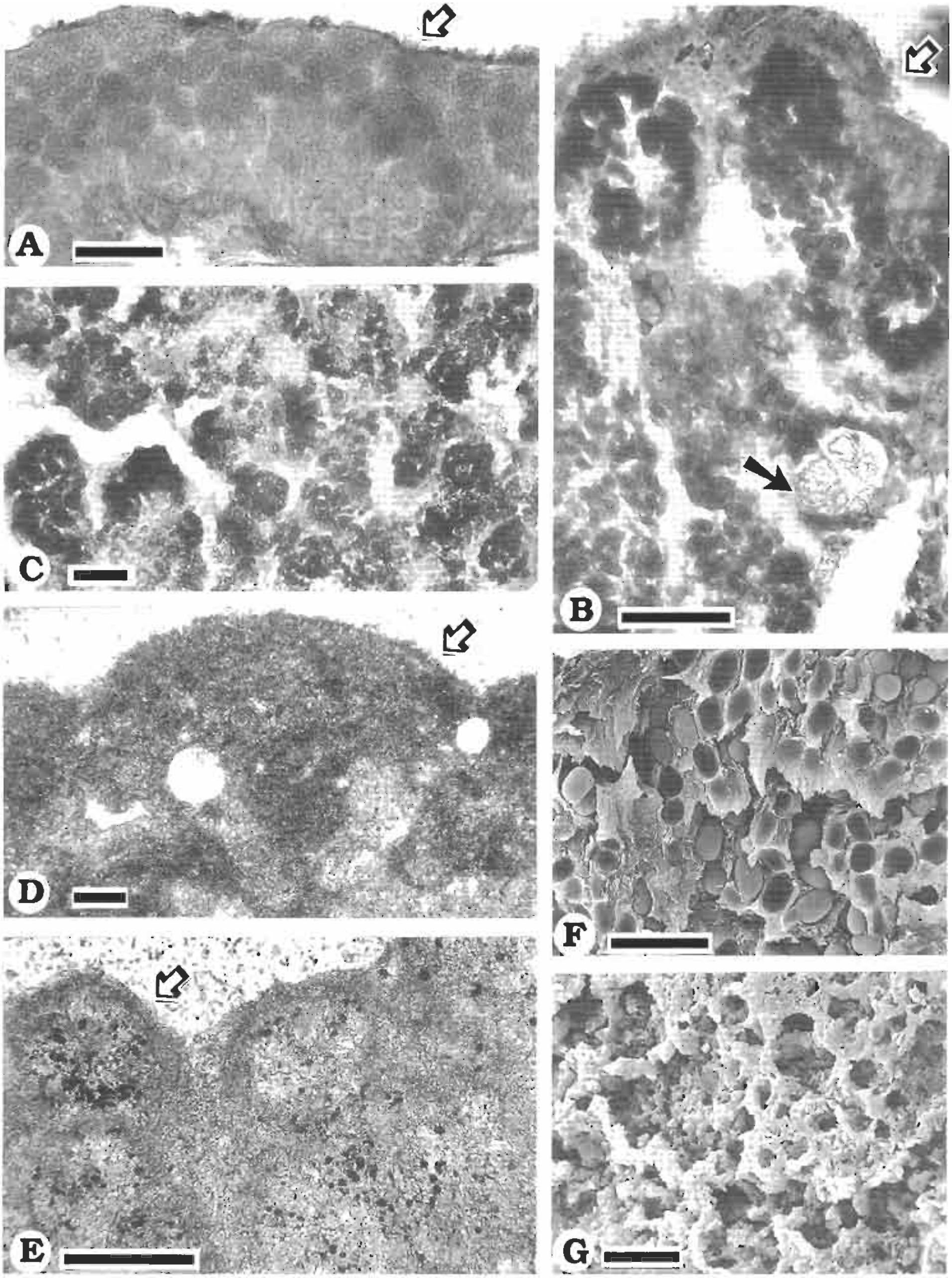
sheaths allows, particularly in a case of weaker, inhomogenous calcification, disintegration of slightly decayed mats into subglobular peloid-like units. As observed at contacts of the Jurassic micritic/peloid interlayers (Fig. 2D), hydrodynamic events, like a stronger bottom current, could tear out individual calcified cell aggregates from the mat or even destroy the whole mat. This resulted in myriads of subglobular particles which, as peloid grains, could have been transported and deposited elsewhere. Fig. 7 illustrates diagramatically the hypothetical stages in the formation of micritic and peloidal Jurassic limestones — products of varying intensity of *in vivo* calcification and *post mortem* decay of coccoid mats.

Micritic peloidal bodies (called also *in situ* grains and clots) reminiscent of those from Lake Van have been observed associated with cyanobacterial mats from hypersaline perimarine areas such as Baffin Bay (Dalrymple 1965), Shark Bay (Monty 1976) and Gulf of Aqaba (Friedman *et al.* 1973; Gerdes & Krumbein 1987). Their formation, however, has never been clearly ascribed to any definite group of cyanobacteria or other microbes.

The subfossil calcified mats from Lake Van microbialites contain still about 2% of organic matter (mostly remnants of the cyanobacterial glycocalyx) whereas the Jurassic limestones are almost free of organic carbon. Diagenetic alteration of the mucopolysaccharide glycocalyx material in the studied Jurassic limestones, mostly due to bacterial degradation, has apparently resulted in the formation of a whole spectrum of authigenic minerals replacing almost entirely the primary organics. Cyanobacterial sheaths and S layers (outermost cell surface components) are known to concentrate metals (Amemiya & Nakayama 1984; Lopes *et al.* 1986; Schultze-Lam *et al.* 1992; Schultze-Lam & Beveridge 1994; Merz & Zankl 1993) and mineral formation is often associated with bacterial decomposition (e.g., Ferris *et al.* 1989).

Thus, our studies indicate, rather surprisingly, that the thick series of the seafloor accumulated micritic/peloidal limestones from the Polish Late Jurassic find their close analogues in modern calcareous sediments produced by mats of coccoid cyanobacteria in the alkaline Lake Van. The exclusive role played by this particular group of cyanobacteria in the formation of micritic/peloidal limestones, known as perhaps the most common components of Jurassic carbonates (Dromart 1989; Sun & Wright 1989), is unexpected and requires further research. Although remnants of pleurocapsalean and morphologically similar entophysalida-

Fig 5. Modern coccoid cyanobacterial mats from Lake Van (Turkey) producing calcareous microbialitic structures analogous to those comprising the Jurassic micritic and peloidal limestones from central Poland. **A**. Vertical section of an uncalcified fragment of the coccoid mat composed of subglobular groups of cells separated by thicker sheaths of mucus. **B–C**. Surficial zone of weakly with aragonitic micrite permineralized coccoid mat showing groups of calcified cells forming smaller (15–30 μm) and larger (50–100 μm) subglobular peloidal bodies; voids resulting from *post mortem* decay of some uncalcified cell groups are often filled with early diagenetic aragonitic spar (thin arrow in **B**). Scale bars are 50 μm. **D–E**. Fragments of a strongly calcified mat showing various stages in the formation of voids and dark-rimmed



peloid-like bodies within the almost homogenous aragonitic micrite. Scale bars are 100 μm. Thick arrows in **A–B**, **D–E** indicate mat surface. **F**. SEM view of vertically sliced uncalcified portion of living coccoid mat showing subpolygonal to subcircular appearance of the sectioned common mucus sheaths (glycocalyx) enclosing blobs of shrunken cytoplasm. **G**. SEM picture of subfossil portion of *in vivo* with micritic aragonite calcified coccoid mat preserving the original form of the glycocalyx. Note the striking similarity of this pattern to that of the Jurassic specimen shown in Fig. 2E and F. Scale bars are 10 μm.

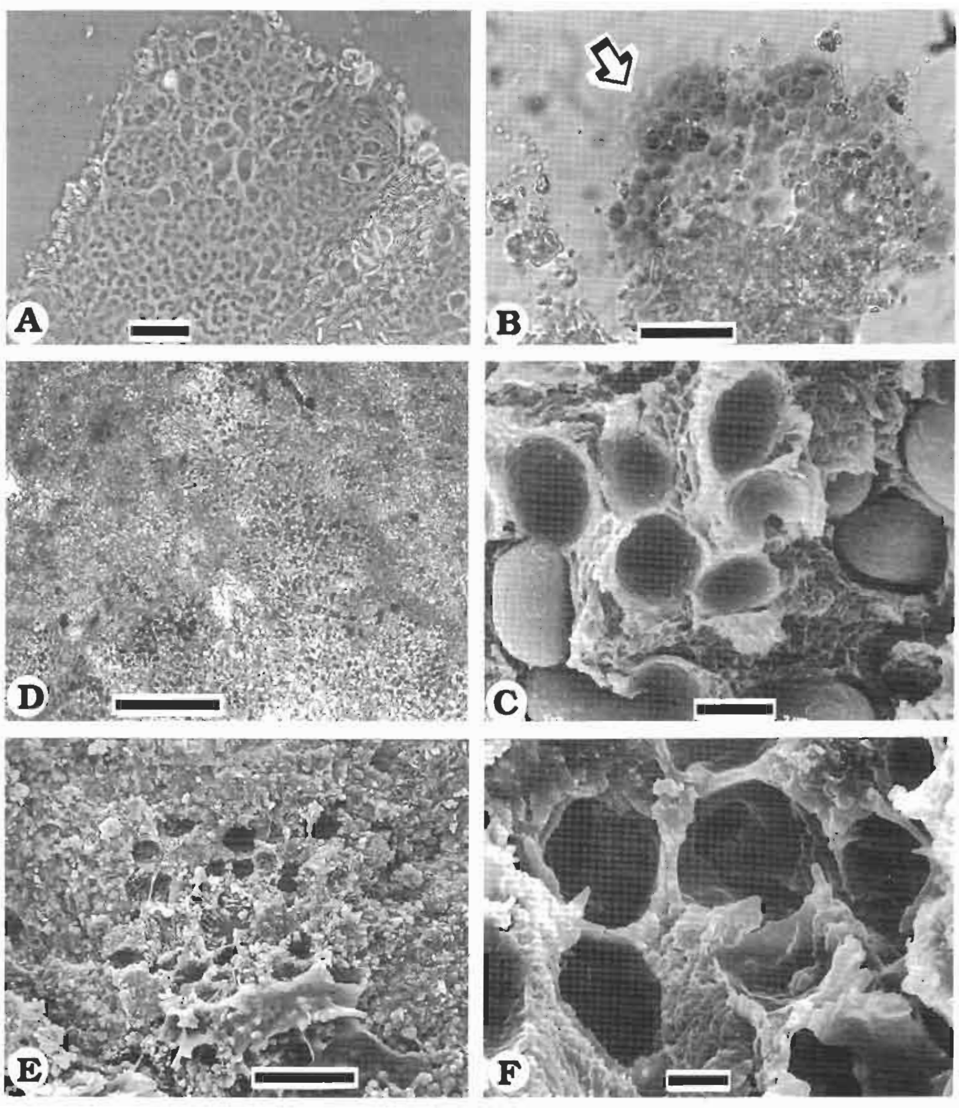
cean cyanobacteria have been noticed in the fossil record, mostly in association with Precambrian and Phanerozoic microbialites (e.g., Hofmann 1975; Knoll *et al.* 1975; Golubic & Hofmann 1976; Oehler 1978; Butterfield *et al.* 1994), their importance as major rock-forming agent has been largely overlooked.

In vivo and/or early *post mortem* calcified entophysalidacean or pleurocapsalean mats are not rare in modern perimarine, lacustrine (particularly alkaline and hypersaline lakes) and even some terrestrial (desert, caves) settings (Horodyski & Vonder Haar 1975; Halley 1976; Monty 1976; Krumbein & Cohen 1977; Krumbein & Giele 1979; Golubic 1982; Cox *et al.* 1989; Kempe & Kaźmierczak 1993). Although representatives of both cyanobacterial groups are also quite common in marine environment (for review see e.g., Kosinskaya 1948; Sieburth 1979), their *in vivo* calcification in normal seawater has not been noticed thus far. Moreover, members of both groups very rarely occur as monocultures and usually are associated with other coccoid and filamentous cyanobacteria and a variety of photo- and heterotrophic eubacteria. Two basic questions therefore arise: (i) why for a long time vast areas of the Jurassic sea bottom were colonized by such taxonomically uniform coccoid cyanobacterial strains, and (ii) what factor was responsible for the intensive and geologically longlasting calcification of these benthic coccoid mats in a subtidal marine environment?

According to recent hydrochemical estimations (Kempe 1990; Kempe & Kaźmierczak 1990, 1994; Kempe *et al.* in press), based on studies of modern environments sustaining *in situ* calcification of benthic cyanobacteria, calcium carbonate permineralization of coccoid mats sufficiently intensive to produce the huge masses of micritic/peloidal limestones observed in the fossil marine record could have proceeded only in environments more saturated with respect to calcium carbonate minerals than present-day seawater. Excess alkalinity transported by upwellings or diffusional processes from oceanic and/or epicratonic anaerobic or dysaerobic basins to shallow water areas has been recently proposed as the main factor responsible for the higher than today calcium carbonate saturation levels in the ancient epicratonic seas (Kempe & Kaźmierczak 1994).

Cyanobacteria are outstanding alkaliphiles (Brock 1973; Krulwich & Guffanti 1989; Kroll 1990) able to use HCO_3^- instead of CO_2 as a major source of carbon (Miller *et al.* 1989). Increased alkalinity input could therefore enhance colonization of large areas of the sea bottom located within the photic zone by coccoid cyanobacterial mats and their *in vivo* calcification. *In vivo* calcification of a cyanobacterial mat requires a significant calcium carbonate supersaturation in the mat (or cell) ambience (Simkiss 1986; Pentecost & Bauld 1988; Kempe & Kaźmierczak 1990;

Fig. 6. Coccoid cyanobacterial microbialites from Lake Van (Turkey). **A**. Subvertical section through a fragment of living uncalcified coccoid mat growing at about 14 m water depth in Tatvan Bay. Visible are mucilage sheaths surrounding subglobular groups of cells and numerous diatoms growing on the mat surface. Transmitted light micrographs (phase contrast);



scale bar is 50 µm. **B**. A group of weakly calcified cyanobacterial capsules from the living mat surface (arrow) grading into aragonitic micrite. Location as above; transmitted light micrograph (Nomarski illumination); scale bar is 50 µm. **C**. SEM view of a sectioned living group of coccoids showing outlines of individual cells (some still with cytoplasm blobs) and the large volume of the common mucopolysaccharide sheaths embedding the cells. Location as above; scale bar is 2 µm. **D**. Transmitted light micrograph of a subfossil portion of an aragonitic microbialite produced by the coccoid mat. Subcircular to subpolygonal outlines of the common mucilage sheaths are still recognizable within the mass of the otherwise almost homogenous micrite. Location as above, water depth 21.5 m; scale bar is 100 µm. **E–F**. SEM views of a fractured microbialite to show the micritic character of the *in situ* with aragonitic micrite calcified coccoid mat preserving in some places the subpolygonal pattern of the permineralized common mucilage sheaths (glycocalyx) with spaces occupied originally by cells not yet filled with the secondary calcium carbonate. Specimen same as above; scale bars are: 20 µm for **E** and 2 µm for **F**.

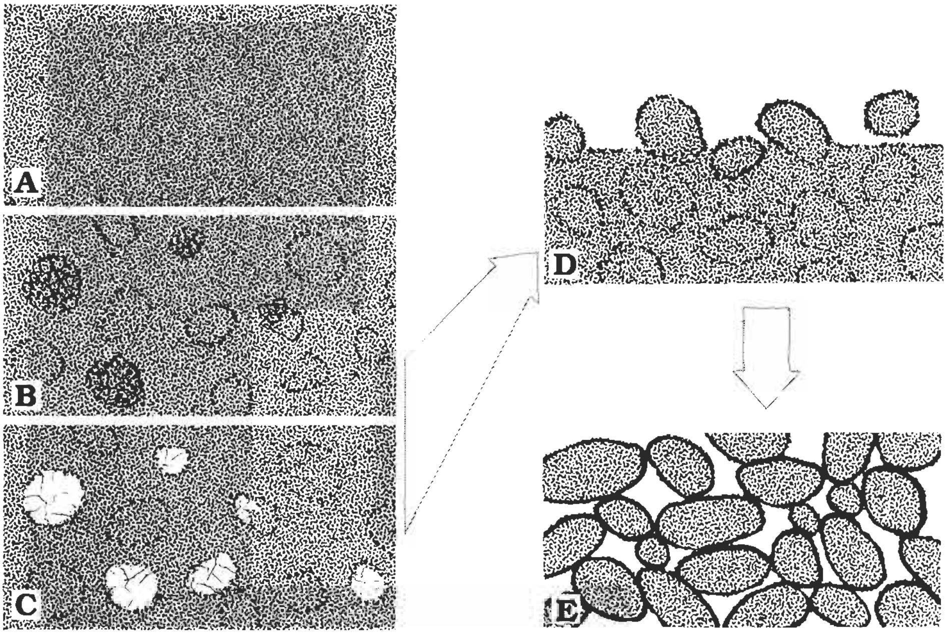


Fig. 7. Diagram illustrating main stages in the origin of micritic and peloidal open marine Jurassic limestones depending upon the intensity of *in vivo* calcification of a benthic coccoid mat controlled by the level of environmental calcium carbonate saturation. **A**. Intensive *in vivo* calcification produces an almost homogenous micrite. **B**. Due to weaker *in vivo* calcification of some cell groups surrounded by thicker mucilage envelopes the mat differentiates into homogenous micritic background and peloid-like bodies (pelmicrite stage). **C**. Very weak *in vivo* calcification may leave some groups of cells uncalcified; voids after early *post mortem* decay of such groups are filled with sparry calcium carbonate (originally probably aragonite) or remain empty. **D**. Mats in stage **B** and **C** can easily disintegrate into individual peloids. **E**. Accumulation of peloids can produce peloidal limestones (pelsparites).

Ferris *et al.* 1994; Kempe *et al.* in press). Calculations of supersaturation indices (SI) for calcite and aragonite made by Kempe & Kaźmierczak (1990, 1993) and Kempe *et al.* (1991, and in press) for several environments sustaining *in vivo* calcification of benthic cyanobacterial mats show that a supersaturation threshold of $SI_{Calcite}$ or $SI_{Aragonite} > 0.8$ (log $IAP/K_{mineral}$) in the mat ambience is indispensable to induce *in vivo* mineral precipitation on and within the cyanobacterial sheaths.

The excess alkalinity, associated probably with an input and temporal presence of some H_2S in the water column, was probably the main factor eliminating macrofauna from the ancient seafloor occupied by the calcifying cyanobacterial mats. This would explain the mostly faunistically barren thick series of the studied micritic/peloidal Jurassic limestones and similarly macrobiotically deserted fine grained limestones known from carbonate formations of other ages. Interestingly, at ambient H_2S level intolerable to many organisms cyanobacteria possess a powerful survival mechanism. They can effectively resist the inhibition of active CO_2 transport caused by hydrogen sulfide by switching from CO_2 to Na^+ -dependent HCO_3^- carbon source (Espie *et al.* 1989). Hydrochemical prerequisite, therefore, for survival of cyanobacterial mats in a H_2S-polluted environment is an alkalinity level supplying them with the required bicarbonate ions.

The $\delta^{13}C$ of calcium carbonate precipitated *in vivo* by a cyanobacterial mat, depending on the rate of photosynthetic activity of the cyanobacteria, can be heavier in relation to the dissolved inorganic carbon (DIC) of the ambient water by about 3 to 6‰ (Pentecost & Spiro 1990; Merz 1992). Fractionation of about +4‰ which has been measured between water DIC and the cyanobacterially precipitated aragonitic micrite at depth of 19 m in Lake Van fits well these observations. It is possible, therefore, taking into account the relatively deep-water location of the Jurassic mats during the generation of the micritic/peloidal sediments and hence their rather moderate photosynthetic rate, to reconstruct the $\delta^{13}C$ of the DIC in the ambient water as probably attaining value of -3 to -4‰, i.e. significantly lighter than for modern seawater. This would be in accordance with the light $\delta^{13}C$ values of the DIC known to be produced by sulphate reducing processes in modern anaerobic basins (e.g., Fry *et al.* 1991; Goyet *et al.* 1991; Kempe & Kaźmierczak 1994). The isotopically light DIC could have been, as alkalinity, transported to shallow areas. The light $\delta^{18}O$ values noticed in the micritic/peloidal limestones can be best explained by the relative enrichment of the mat ambience in ^{16}O due to preferential uptake of $HC^{18}O^{18}O^{18}O^-$ by photoassimilating cyanobacterial mats (Miller *et al.* 1989).

Conclusions

Further research will prove the relevance of our studies for explaining the origin of open marine micritic and peloidal limestones abundant in the sedimentary record of other geological ages. It seems to us, however, that the Phanerozoic carbonate ramps and platforms are simply a continuation of the pre-skeletal Proterozoic carbonate megafacies composed predominantly of micritic and peloidal limestones interbedded with stromatolitic structures (Grotzinger 1989). Although, starting from the early Cambrian, the skeletal eukaryotic organisms are participating in the formation of marine calcareous deposits, volumetrically their role in pre-Tertiary carbonate sequences, even in bioreefal deposits, is often quite subordinate, compared with micritic and peloidal components. Therefore, the absence of *in vivo* cyanobacterial calcification in modern marine environment is, geologically looking, a rather unusual phenomenon caused probably by generally lowered post-Cretaceous oceanic calcium carbonate saturation levels due to disappearance of large stagnant basins producing excess alkalinity. It can be concluded, a bit metaphorically perhaps, that the entophysalidaceans, pleurocapsaleans, and similar coccoid benthic cyanobacteria living in an uncalcified state in modern seas are waiting for the restoration of excessively alkaline environmental conditions to imprint again their micritic/peloidal signiture on widespread areas of the shallow seafloor.

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Cyjanobakteryjna geneza wapieni mikrytowych i peloidalnych w dawnych zbiornikach morskich

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Streszczenie

Geneza wapieni mikrytowych i peloidalnych, głównych składników większości kopalnych morskich formacji wapiennych, nie została do tej pory rozwiązana i od ponad stu lat jest jednym z bardziej kontrowersyjnych problemów sedymentologii i petrologii skał węglanowych. Przedstawione w pracy wyniki badań nad takimi wapieniami z utworów późnej jury (kimerydu) Gór Świętokrzyskich wykazały, że osady te są wytworem *in situ* zwapniałych bentosowych mat kokkoidalnych cyjanobakterii (= sinic). Szczątki tych mikroorganizmów widoczne są w skaningowym mikroskopie elektronowym w postaci charakterystycznych struktur, przypominających wspólne osłony śluzowe (*glycocalyx*) otaczające komórki i grupy komórek w koloniach dzisiejszych bentosowych kokkoidalnych cyjanobakterii zaliczanych do grup Chroococcales (szczególnie *Entophysalis*) i Pleurocapsales (*Pleurocapsa*). Szczegółowe badania porównawcze przeprowadzone zostały na dzisiejszych, w różnym stopniu zwapniałych matach takich cyjanobakterii występujących w alkalicznym (sodowym) Jeziorze Wan (wschodnia Turcja). Wyniki tych badań pozwalają wnioskować, że zarówno mikrytowe i peloidalne wapienie jurajskie, jak i miąższe serie podobnych morskich wapieni pospolitych w zapisie litologicznym innych okresów geologicznych są produktem *in situ* zwapniałych mat kokkoidalnych cyjanobakterii. Istnieją podstawy aby przypuszczać, iż tak intensywna kalcyfikacja morskich cyjanobakterii mogła odbywać się jedynie w środowisku, które w porównaniu z dzisiejszą wodą morską było bardziej przesycone w stosunku do produktu rozpuszczalności takich pospolitych minerałów węglanowych jak kalcyt i aragonit. Głównym czynnikiem utrzymującym wyższy od obecnego poziom przesycenia węglanem wapnia w dawnych środowiskach morskich był najprawdopodobniej napływ do fotycznej strefy zasiedlonej przez cyjanobakterie ekscesywnie alkalicznych wód pochodzących z głębszych, anaerobowych (stratyfikowanych) lub dysaerobowych partii zbiorników, których podwyższona alkaliczność była wynikiem metabolicznej aktywności bakterii redukujących siarczany w procesie remineralizacji substancji organicznej w strefach deficytu tlenowego.