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STROMATOPOROID STROMATOLITES: NEW INSIGHT INTO
EVOLUTION OF CYANOBACTERIA

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Common enigmatic fossils called stromatoporoids are recognized as calcareous stromatolitic structures build by coccoid cyanobacteria (= Cyanophyta). The diversified internal structures of stromatoporoids reflect various growth patterns of cyanobacterial cell aggregates or colonies preserved due to a rapid *in situ* calcification. Stromatoporoid stromatolites are evolutionary advanced descendants of early Precambrian stromatolites generated by weakly differentiated stratiform mats of coccoid cyanobacteria. The presence of stromatoporoid stromatolites in ancient subtidal environments, often in association with normal marine biota, is a non-actualistic phenomenon which needs to be explained in other than present-day ecological terms.

Key words: Cyanobacteria, evolution, stromatolites, stromatoporoids.

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INTRODUCTION

The discovery of cyanobacteria-like microfossils constituting the skeletal elements of the typical Devonian stromatoporoid *Stictostroma* Parks from the subsurface of southeastern Poland is reported. It confirms the recently proposed hypothesis (Kaźmierczak 1976) of the cyanophycean (= cyanobacterial) origin of true stromatoporoids, and negates previous interpretations (Lecompte 1956, and Galloway 1957, for review) of stromatoporoids as animal remains including recent attempts to relate stromatoporoids to living sclerosponges (Hartman and Goreau 1970) or other calcareous sponges (Stearn 1975; Wendt 1975). The surprisingly, but widely, accepted sclerosponge theory of stromatoporoid affinity is based on the incorrect comparison of extant sclerosponges with dubious Upper Palaeozoic and Mesozoic fossils misleadingly ascribed by some authors (e.g. Dehorne 1920; Yabe and Sugiyama 1935; Lecompte 1956) to stromatoporoids. Many of these fossils appear to be indeed sclerosponges or pharet-

ronids (Kaźmierczak 1974; Hartman 1978). The data presented below and similar discoveries in Devonian *Trupetostroma* and *Parallelopora* (Kaźmierczak, in press) show true stromatoporoids to be calcareous stromatolites formed by *in situ* calcification of a microbiota closely related to extant coccoid cyanobacteria (= Cyanophyta).

The described material is housed at the Institut of Paleobiology (Zakład Paleobiologii) of the Polish Academy of Sciences (abbreviated ZPAL).

OBSERVATIONS

The stromatoporoids with preserved biofabric come from the Devonian core of the borehole Płusy IG 1 (Lublin district, southeastern Poland) and have been found in black, bituminous calcispheric pelmicrite of Upper Givetian-Lower Frasnian age drilled at 1,314.2—1,318.3 m. From the internal morphology of several nodular specimens observed in thin section (pl. 1: *a*) they can be identified as *Stictostroma kolymense* (Yavorsky), known from the Middle-Upper Devonian of Eurasia (Yavorsky 1961; Kaźmierczak 1971). The skeleton is composed of distinct laminae and pillars. Laminae are interrupted in some places by subcircular openings covered usually by thin, upwardly convex plates. Pillars are cylindrical or spool-shaped and oriented normal or slightly oblique to laminae. They are often superposed. Darker (in transmitted light) interlayers of various thickness are irregularly distributed throughout the skeleton. They disorder the normal skeletal structure to an irregular meshwork (pl. 2: *a*, *b*) but are always in growth continuity with the under- and overlying skeleton.

The skeletal microfabric, as is typical for *Stictostroma* (St. Jean 1967), has a granular character with indistinct microlamination visible in the laminae. The granules, called also maculae or melanospheres (Stearn 1966; St. Jean 1967), are more distinct in darker skeletal interlayers (pl. 2: *a*) which are apparently enriched in organic matter (brownish). In normal, light-gray skeletal tissue they are less clearly seen and often obliterated to flocculent calcitic dust. The granules average 40—60 μm in diameter (extremes 15—110 μm). Depending on which theory on the affinities of stromatoporoids granules have been interpreted as traces of ectodermal calcification centres (coelenterate theory — Kaźmierczak 1971), spherulitic skeletal components (sponge theory — Stearn 1975) or remnants of coccoid cell aggregates (cyanobacterial theory — Kaźmierczak 1976). The last relationship has been inferred, in part, from the analogy with the microfabric of modern coccoid cyanobacteria (*Entophysalis*) calcified mats (Horodyski and Vonder Haar 1975).

Primary biofabric has been detected mostly within the darker skeletal interlayers as irregularly distributed aggregates of densely packed carbo-

naceous spheroids permineralised in carbonate and set within an amorphous organic matrix. The usually subglobular aggregates (pl. 1: b, e) enclose a few to several tens of individuals; chain-like clusters have also been observed (pl. 1: c). The spheroids average 7—8 μm or 10—16 μm in diameter with both size classes often mixed together in one aggregate. Some spheroids are paired (pl. 1: d). Globular pyritic inclusions are common within spheroids. The calcareous matrix surrounding the aggregates is often divided into globular units having the same size as the carbonaceous spheroids (pl. 1: b). This means that the presently isolated clusters of spheroids are remains of continuous and dense accumulations of spheroids forming originally the whole skeletal framework. The gradual transition of the darker skeletal tissue enclosing the majority of the aggregates of spheroids into the granular microfabric of the "normal" skeleton (pl. 2: a, b) is evidence that the granules (maculae) represent diagenetically altered groups of spheroids.

COMPARISON

Biologically, the aggregates of spheroids agree with some extant coccoid cyanobacteria. The pseudofilamentous arrangement of some spheroids (pl. 1: c) is similar to living pleurocapsalean cyanobacteria (Waterbury and Stanier 1978) and Precambrian microfossils interpreted as representatives of that group of cyanobacteria (Schopf and Fairchild 1973; Knoll *et al.* 1975). Strong similarity is also shown between the spheroids and modern chroococcalean cells, particularly colonies of *Entophysalis* known to form calcified crusts (Horodyski and Vonder Haar 1975) and soft mats (Horodyski *et al.* 1977) often in association with filamentous cyanobacteria. Unidentified, rare filamentous microfossils preserved either as nonseptate organic tubes, 20—25 μm in cross-section, or chains of pyrite grains, 3—6 μm in cross-section, penetrate interskeletal spaces of *Stictostroma kolymense*.

In extant *Entophysalis* mats only the outer sheaths surrounding groups of cells are preserved (Horodyski and Vonder Haar 1975). It is therefore not clear whether the spheroids building *S. kolymense* actually represent outlines of cells or rather their permineralised outer sheaths. Several examples of Precambrian coccoid microbiota strikingly similar to the cell clusters from *S. kolymense* can be given. They are usually interpreted as remnants of coccoid cyanobacteria. Many have been found in association with stromatolites, often as their integral components (Hofmann 1975; Schopf and Sovietov 1976). The most instructive examples are clusters of unicells described as *Myxococcoides minor* Schopf from the Upper Proterozoic Bitter Springs Formation of Australia (Schopf 1968) and

Mid-Precambrian Kasegalik Formation of Canada (Hofmann 1976), and as *Myxococcoides kingii* Muir from the Proterozoic McArthur Group of Australia (Muir 1976; Oehler 1977).

Stellate structures termed astrorhizae, characteristic of many stromatoporoids (e.g. Galloway 1957, for review), are not present in the studied specimens. However, the discovery of coccoid cyanobacteria-like cells building the skeleton of *Stictostroma kolymense* seem to confirm my previous suggestion (Każmierczak 1976), that astrorhizae are traces of young coccoid colonies that originated through germination of baeocytes (endospores) within the parental colony, and which have undergone less mineralization and early decay. This presumption was based on unusual astrorhizae found in Devonian *Parallelopora* aff. *planulata* filled with skeletal tissue structurally and microstructurally identical and continuous with the surrounding skeleton. *In situ* germination of baeocytes is known to occur irregularly in pleurocapsalean and chamaesiphonalean cyanobacteria (Fritsch 1945; Drouet 1951). The variable occurrence of astrorhizae reported in stromatoporoids (Galloway 1957; Kaźmierczak 1969) is in agreement with these observations.

IMPLICATIONS AND CONCLUSIONS

The detection of a cyanobacterial origin for stromatoporoids has several biological and geological implications. Stromatoporoids are a diverse group of about 2,000 species (Flügel and Flügel-Kahler 1968). Several examples of evolutionary lineages are described (Każmierczak 1971) demonstrating time-related trends within Palaeozoic stromatoporoids to rearrange the internal skeletal structure. The diversified structures of stromatoporoids reflect, in my opinion, various patterns of colony organization of coccoid cyanobacteria building the primary soft mats before their permineralization. Due to rapid and intensive calcification of the mats, probably by aragonite (Richter 1972), the primary structure of colonies has been preserved almost intact. This means that the final morphological expression of the calcified microbiota was directly related to its calcification potential and the availability of calcium in the environment. Growth disturbances observed commonly in stromatoporoids (Każmierczak 1971; St. Jean 1971), mostly as darker (in transmitted light) interlayers of irregularly woven or grumous tissue, is evidence that growth of stromatoporoids was to some extent controlled by abiotic environmental factors. For instance, the loosely arranged groups of coccoids observed in the darker interlayer of *Stictostroma kolymense* (pl. 2: a, b) may correspond, according to observations from recent coccoid cyanobacterial mats (W. E. Krumbein, personal communication, April 1979), to a period of temporary salinity increase causing

disintegration of dense coccoid aggregates into isolated small groups of cells surrounded by thicker than normal sheaths of mucous. Detailed recognition of the nature of growth disturbances and interruptions in stromatoporoid stromatolites makes them very sensitive potential palaeoecological indicators.

It can be concluded from the results of recent studies (Krumbein and Cohen 1977) on carbonate permineralization of cyanobacterial mats that similarly complex physiological and decompositional processes took place in the calcification of the stromatoporoid-generating coccoid mats. It means that only a part of the CaCO_3 actually forming the stromatoporoid "skeleton" was precipitated due to the photosynthetic activity of the cyanobacteria (CO_2 uptake); a considerable amount of CaCO_3 originated through the activity of aerobic and anaerobic heterotrophic bacteria, which as in modern mats (Krumbein 1979) were also responsible for the almost total degradation of the cyanobacterial cells. The darker, organic-rich interlayers in *Stictostroma kolymsense*, which are the main sites of preserved cyanobacterial cells, correspond therefore probably with periods of lower decomposing bacterial activity which, as in recent situation (Krumbein *et al.* 1977), may have been connected with a temporary, drastic increase in salinity.

The oldest unquestionable stromatoporoids are known (Galloway 1957) from the Ordovician (Middle Chazyan). However, many Proterozoic and Cambrian calcareous stromatolites (Walter 1972; Bertrand-Sarfati 1976) and doubtful stromatoporoids (Bain 1927; Vlasov 1961) have been reported characterized by distinct internal structures and granular microfabric (called thrombolitic, clotty or pelletoid), and very reminiscent of those found in stromatoporoids. I therefore postulate that the ancestors of stromatoporoids were weakly morphologically differentiated stratiform colonies of coccoid cyanobacteria as known already from Middle Precambrian deposits (Hofmann 1975). Some strains of these cyanobacteria apparently displayed a tendency to increase the level of colony organization, reflected in diversified internal morphologies seen in Upper Proterozoic and Cambro-Ordovician stromatolites. The stromatoporoid stromatolites with their often sophisticated internal structures appearing successively in relatively short time intervals (Kaźmierczak 1971) represent evolutionary the culmination of colony organization of benthic coccoid cyanobacteria. The question of what caused the modifications in colony organization and growth habit of the coccoid communities must remain, at present, open. Was it genetically controlled or rather dependant on environmental factors? Colony organization in extant coccoid cyanobacteria is insufficiently understood to answer these questions.

Stromatoporoids are important rock-building structures characteristic particularly of Lower Palaeozoic platform deposits. They commonly form extensive banks and mounds usually interpreted ecologically as reefs

(Laporte 1974, for review). The identification of the cyanobacterial nature of stromatoporoids means that the uniformitarian reef model (Klovan 1974) for stromatoporoid build-ups cannot be further applied. Coccoid cyanobacterial mats, either soft or calcified, are unknown from Recent shallow subtidal environments occupied in the past by stromatoporoids. A new ecological model for stromatoporoid facies should take into consideration such important and dominating non-actualistic ecological factors as unbalanced (schizohaline) and different from present-day salinities, temporarily stratified water column accompanied by oxygen deficiency, and higher trophogenic levels (eutrophication). Recently published geochemical and palaeontological data (Sandberg 1975; Kaźmierczak 1975; Degens and Stoffers 1976) strongly support these inferences.

The mass occurrence of stromatoporoid stromatolites in Lower Palaeozoic strata, often in concomitance with other micro- and macrobiota contradicts the commonly held view (Monty 1973, for review) that stromatolite-building cyanobacteria declined at the end of the Precambrian due to competition by better-adapted animals and eukaryotic algae. The early Palaeozoic vigorous evolution of stromatoporoids decelerated at the beginning of the Carboniferous and continued to do so though on a lesser scale, throughout the Mesozoic. They disappeared at the end of Cretaceous, but only from marine environments. Newly-collected materials (Hillmer and Kaźmierczak, in preparation) indicate the presence of stromatoporoid-like stromatolites within Tertiary and Quaternary lacustrine and brackish deposits from subequatorial Africa and the Phillipines.

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JÓZEF KAZMIERCZAK

STROMATOPOROIDOWE STROMATOLITY: NOWE SPOJRZENIE NA EWOLUCJĘ CJANOBAKTERII (= SINIC)

Streszczenie

Pospolite kopalne struktury organiczne zwane stromatoporooidami rozpoznano jako wapienne stromatolity utworzone przez kokkoidalne cjanobakterie (Cyanobacteria = Cyanophyta). Odkrycie to, dokonane w oparciu o unikalnie zachowane dewońskie

stromatoporoidy (*Stictostroma*) z głębokiego wiercenia Płusy IG 1 (Lubelszczyzna), potwierdza wcześniejszą hipotezę autora (Kaźmierczak 1976) o sinicowym pochodzeniu tych enigmatycznych skamieniałości, interpretowanych najczęściej jako szczątki stłbiopławów lub gąbek. Zróżnicowane struktury wewnętrzne charakterystyczne dla stromatoporoidów odzwierciedlają różne typy organizacji agregatów czy kolonii kokkoidalnych komórek utrwalone w rezultacie intensywnej kalcyfikacji. Stromatolity stromatoporoidowe są ewolucyjnie zaawansowanymi potomkami wczesnoprekambryjskich stromatolitów utworzonych przez słabo zróżnicowane, warstwowe agregaty kokkoidalnych cjanobakterii. Obecność stromatoporoidowych stromatolitów w subltoralnych strefach fanerozoicznych zbiorników epikontynentalnych, szczególnie charakterystyczna dla wczesnego paleozoiku (śr. ordowik — d. karbon), i ich częste współwystępowanie z normalnymi organizmami morskimi, jest zjawiskiem nie dającym się pogodzić z zasadą aktualizmu. Wyjaśnienie częstego występowania kalcyfikowanych mat cjanobakteryjnych w dawnych epikontynentalnych zbiornikach morskich wymaga przyjęcia niektórych dominujących w tych zbiornikach czynników ekologicznych zasadniczo różnych od znanych w dzisiejszych akwenach szelfowych. Wśród czynników tych szczególnie istotne były przypuszczalnie inne od dzisiejszych gradienty zasolenia, częsta stratyfikacja wód i związany z tym deficyt tlenowy, a także znacznie wyższa produktywność tych zbiorników, prowadząca w rezultacie do ich eutrofizacji.

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EXPLANATION OF THE PLATES 27—28

Plate 27

a Internal morphology of *Stictostroma kolymense* (Yavorsky) in vertical thin section; *b—e* aggregates of cyanobacteria-like coccoid microfossils forming the skeletal elements shown in *a* (arrowed). Note the pseudofilamentous arrangements of spheroids in *c*, and paired spheroids in *d*; transmitted light. Płusy IG 1 drilling, depth 1,314.2—1,318.3 m, thin section ZPAL St. II/2P/a.

Plate 28

a—b Photomicrograph and interpretation of vertical thin section of *Stictostroma kolymense* near basal portion. The light-gray basal layer (*bl*) in contact with the substratum (*s*) is followed upwards by darker interlayer (*di*) being the site of organically preserved coccoid microfossils; the darker layer passes gradually into the normal skeleton (*ns*); *c* an aggregate of coccoid cyanobacteria-like microfossils from the darker layer; transmitted light. Płusy IG 1 drilling, depth 1,314.2—1,318.3 m, thin section ZPAL St. II/2P/b.



