

Cyanobacterial origin of microcrystalline cements from Pleistocene rhodoliths and coralline algal crusts of Okierabu-jima, Japan

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Microcrystalline (micritic) Mg-calcite cements generated by *in vivo* calcified coccoid cyanobacteria have been identified in rhodoliths and coralline algal crusts from the Pleistocene Ryukyu Group of Okierabu-jima (Ryukyu Islands, Japan). The cements occur as: (i) fringes and festoons on ventral surfaces of *Neogoniolithon fosliei*, (ii) coatings on dorsal and ventral surfaces of *Mastophora pacifica*, and (iii) encrustations on tubular thalli of epiphytic and/or chasmolithic green algae. The calcification of the cyanobacteria colonizing spaces within the coralline algal framework was presumably enhanced by a local increase in calcium carbonate saturation due to CO₂ uptake by the living red and green algae strengthened by increased alkalinity resulting from decay processes in the framework. Many microcrystalline (micritic) cements described from other modern and ancient reefal limestones may, by analogy, be products of similar *in vivo* calcified cyanobacteria.

Key words: Cyanobacteria, coralline algae, reefs, biocalcification, carbonate cements, micrite, geomicrobiology.

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Introduction

The origin of microcrystalline carbonate (micrite) forming internal cements in reefal deposits is a fundamental problem of modern carbonate sedimentology (for discussion see Macintyre 1984; Friedman 1985; Milliman *et al.* 1985; Reid *et al.* 1990). Although in earlier studies on lithification of modern and fossil reefs microcrystalline carbonates have been thought to represent ooze deposition in quiet water (e.g., Folk 1959; Dunham

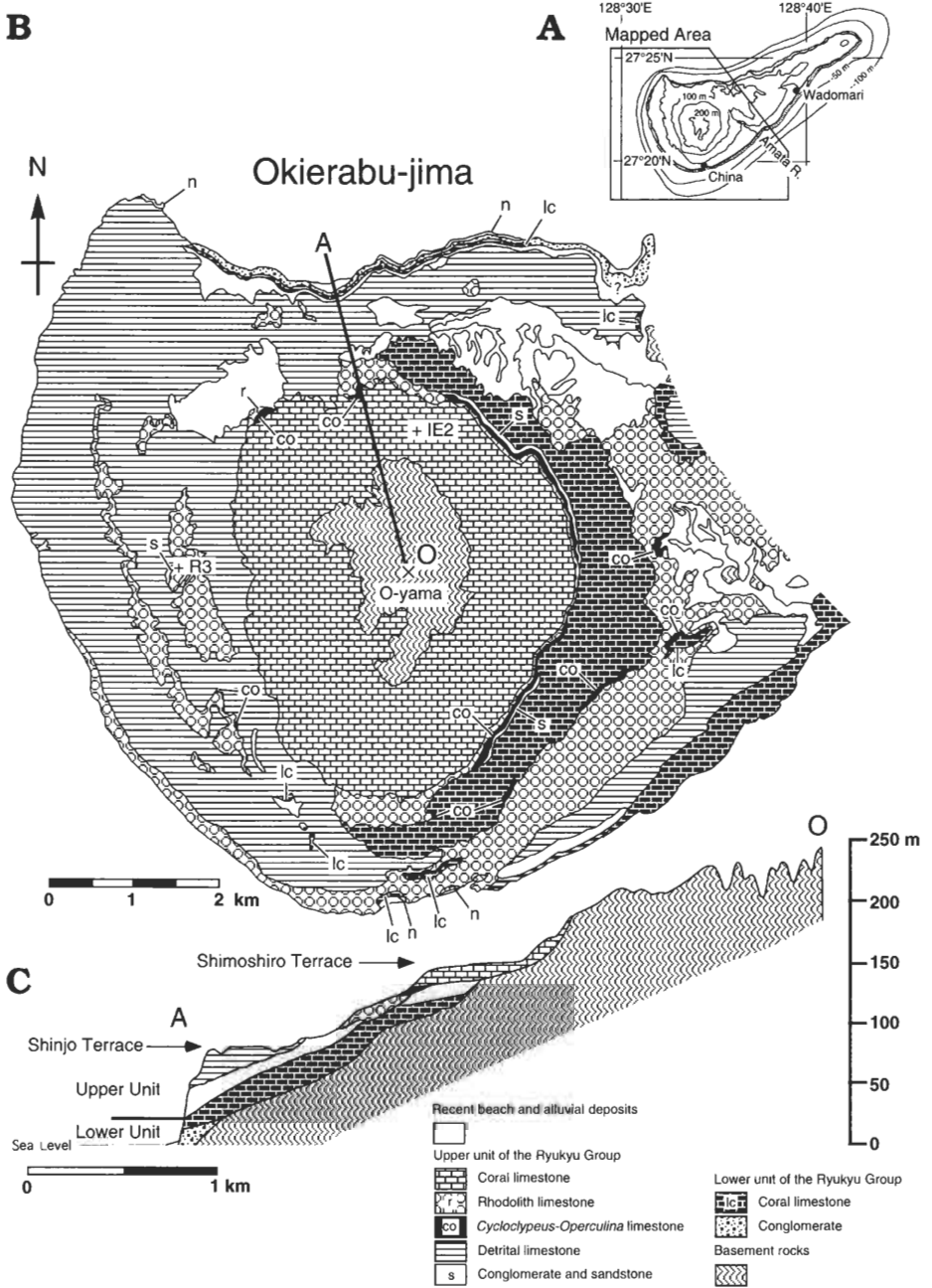


Fig. 1. Topographic (A) and geologic (B) maps of Okierabu-jima. Samples of studied coralline crusts (IE2) and rhodoliths (R3) are indicated on geologic map. C. Cross section along line O-A on B.

1962), more recent observations suggest that internal precipitates of micrite are typically found in high-energy deposits such as reefal limestone and beachrocks (for review see Focke & Gebelein 1978; Reid *et al.* 1990; Webb 1996). The source of internal micrite

cements is still a matter of considerable controversy (for current exchange of opinion see Friedman 1997; Sami & James 1997). Internal micrite may be transported into or may originate within cavities and pores. However, the significance of the former in reefal deposits is small in comparison with apparently *in situ* produced micritic cements.

The process of internal precipitation of micrite growing attached to fixed substrates was interpreted earlier as successive growth of microcrystals on the walls of cavities resulting sometimes in occlusion of the pore space (Ginsburg *et al.* 1971; Friedman *et al.* 1974). More recent studies suggest, however, that micrite can also nucleate in cavities in suspension and, subsequently, settle on cavity floor (e.g., James *et al.* 1976; Macintyre 1984). The genesis of modern microcrystalline carbonates that precipitate in cavities is problematic. Traditionally, such deposits are referred to as internal chemical sediments (Macintyre 1984). Although attempts have been recently made to attribute some of these deposits to biotic factors, such as mediation by unidentified microbes (Zankl 1993; Webb 1996; Webb *et al.* 1998) or calcium enriched biofilms (Reitner 1993), their nature remains largely unsolved.

The specimens examined in this study are housed in the Institute of Geology and Paleontology, Tohoku University, Sendai (abbreviated IGPS).

Setting

Okierabu-jima is an island (Fig. 1A) located about 60 km north-east of Okinawa-jima. Coralline algal crusts and rhodoliths were collected from the Ryukyu Group (Iryu 1997; Iryu *et al.* 1998), a complex of Pleistocene reef deposits interfingering with terrestrial sediments (Fig. 1B, C). The carbonate deposits of the Ryukyu Group consist primarily of coral limestone, rhodolith limestone (Fig. 1B), *Cycloclypeus-Operculina* limestone, and detrital limestone (Fig. 1B, C). Rhodoliths and coralline-algal crusts are abundant components of the Ryukyu Group (Minoura & Nakamori 1982; Iryu 1992). The distribution of modern rhodoliths off Okinawa-jima suggests that the Pleistocene red algal deposits of Okierabu-jima accumulated in deep fore-reef and shelf areas within the depth range of 50–150 m (Iryu *et al.* 1995).

The Ryukyu Group on Okierabu-jima is divided into two units (Fig. 1C): the lower unit consists of conglomerate with intercalated beds of sandstone, and coral limestone up to 90 m thick. It is unconformably covered with the upper unit, which is 50 m thick, composed at the base of marine conglomerate and/or sandstone overlain by coral limestone that may also rest directly on the basement rocks. The rhodolith limestone is up to 10 m thick and, as a rule, encircles the coral limestone (Fig. 1B). The upper unit forms two terraces: a higher one ranging from 150–200 m above sea level, built of coral limestone, and a lower one, reaching from 30 to 100 m above sea level, composed of rhodolith limestone and poorly sorted detrital limestones.

Rhodoliths and coralline algal crusts

The diameters of rhodoliths occurring in the rhodolith limestone range from 1 to 8 cm. They are composed of nongeniculate coralline algae alternating with the foraminifers

Acervularia inhaerens and, much less commonly, *Homotrema rubrum*. The concentration of rhodoliths is high, often exceeding 20% of rock volume. Among numerous species of coralline algae found in the rhodoliths, *Hydrolithon* sp., *Lithoporella melobesioides*, *Lithophyllum* sp., *Mesophyllum* sp., *Lithothamnion australe*, and *Lithothamnion* spp. are particularly common. Peyssonneliacean algae, dominated by *Cruoriella*(?) sp. or *Cruoriopsis*(?) sp., have also been observed. The coralline algae and foraminifers overgrew each other rather tightly leaving only a few open spaces in the rhodolith structure. Specks of yellow-brownish microcrystalline (micrite) cement are visible in spaces beneath overarching thalli. Larger cavities in the rhodoliths are generally lined with microspar and filled by blocky spar. The rhodoliths were bioeroded to various degrees by multicyclic borings of sponges and bivalves. In some, multicyclic borings of sponges and pelecypods are so extensive that the internal framework structures are almost entirely destroyed. Borings are open to fully infilled with poorly- to well-indurated micrite/bioclast mixture. Bioclasts are coarse-grained sand-sized or finer, comprising skeletal fragments of benthic foraminifers, mollusks, coralline algae, echinoids, and less abundant bryozoans and *Halimeda*.

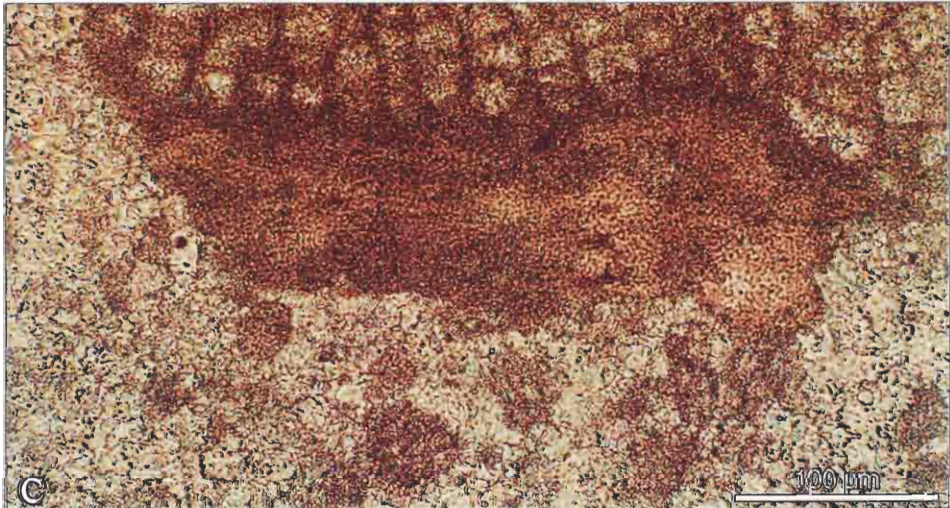
The coralline algal crusts, in turn, are mostly associated with the coral limestone. They encrust hermatypic corals (both *in situ* and rubble), other coralline algae, and, occasionally, mollusks. *Neogoniolithon fosliei* and *Mastophora pacifica* are common species (Fig. 3). Their sheet-like thalli commonly form a series of overlapping, small canopies, leaving much open space between them. Some of the larger spaces are partly or entirely filled by microspar and/or blocky spar, others with various admixture of skeletal detritus and micrite. A characteristic feature of the coralline algal crusts is the presence, in many open spaces, of yellow-brownish microcrystalline (micrite) cement identical with that observed in the rhodoliths.

Microcrystalline cements

The bulk of the yellow-brownish microcrystalline cement forms fringes or festoons attached to ventral surfaces of the dorsiventral thalli of *Neogoniolithon fosliei*. The fringes are, on average, 80–120 μm thick; the festoons are typically thicker (up to 250 μm) and bulbous in shape (Fig. 2A, B). The cements are almost perfectly homogeneous, rarely irregularly speckled. Some are indistinctly striped with the stripes arranged more or less perpendicularly to the ventral surfaces of *N. fosliei* thalli.

Identical yellow-brownish microcrystalline cements also occur as coatings of uniform thickness (8–12 μm) on dorsal and ventral surfaces of *Mastophora pacifica* thalli (Fig. 3B). Those coatings are common on loosely growing thalli of *M. pacifica*. In rare cases, however, only the ventral surfaces of *M. pacifica* thalli are coated with the microcrystalline carbonate (Fig. 3A). The coatings are absent on those thalli of *M. pacifica* that adhere to each other tightly. In contrast to the rather irregular and discon-

Fig. 2. **A, B.** Microcrystalline Mg-calcite fringes (arrow) precipitated by films of coccoid cyanobacteria growing attached to ventral surfaces of *Neogoniolithon fosliei* thalli (Ne). **C.** Magnified section of a microcrystalline fringe to show the dense 'microcellular' texture typical for pseudoparenchymatous coccoid cyanobacteria (compare Fig. 3F). All transmitted light photomicrographs of vertical sections (in **A** taken with blue filter); loc. IE2; **A** – thin section IGPS 103714; **B, C** – thin section IGPS 103710.



tinuous hypobasal fringes and festoons on *N. fosliei*, the microcrystalline coatings on *M. pacifica* are as a rule continuous structures covering whole thalli more or less uniformly, although variably extending protuberances and larger outgrowths occur in places (Fig. 3B).

The microcrystalline cements may also occur as almost equidimensional encrustations, 10–12 μm thick, distributed around branched tubules representing thalli of noncalcifying epiphytic and/or chasmolitic green algae (*Gomontia* or *Ostreobium*) which occurred as prostrate mono- or multilayers in spaces between the coralline algal thalli (Figs 3C, D, 5D).

Energy-dispersive X-ray analyses (EDS) have shown that the microcrystalline cements are composed of Mg-calcite with an almost constant amount of magnesium of about 6–8 Wt %. According to Folk's (1959) limestone classification, the 2–3 μm average size of the cement grains allows classification of the cements as almost perfect micrite. Scanning electron microscope (SEM) images of polished and EDTA-etched samples revealed that the cement consists of typical anhedral grains. Larger (4–7 μm), rhombohedral calcite crystals have been observed only in patches of porous kerogenous material etched occasionally from the EDTA-treated polished cement surfaces (Figs 4B, 5B).

Cyanobacterial nature of the cements

SEM images of polished and EDTA-etched sections of the cements have revealed, within their almost homogenous texture (Figs 4A, 5A, D), subglobular structures, 15–30 μm in diameter (Fig. 4B), typically occurring in groups (Fig. 5B, E). They are typically visible as densely packed pits surrounded by elevated porous walls. The walls are common for neighbouring pits. The subangular pores in the walls represent apparently spaces left after etching of anhedral grains of CaCO_3 comparable to those forming the bulk of the cement (Fig. 5B). The pits are strikingly similar in morphology to capsular units characterizing mats of benthic pleurocapsalean and entophysalidacean cyanobacteria (compare Fig. 5B, C and E, F). The capsular organization of the mats results from the fact that the outer gelatinous sheaths enveloping groups of cells are usually thicker than the sheaths surrounding individual cells. Additionally, it is known that during the calcium carbonate permineralization of coccoid mats, the outer sheaths are the main site of CaCO_3 precipitation (Horodyski & Vonder Haar 1975). Capsule sheaths are also particularly resistant to degradation processes and commonly are the only organic remains of coccoid cyanobacteria in subfossil and fossil microbial mats (e.g., Horodyski & Vonder Haar 1975; Kaźmierczak & Krumbein 1983; Krumbein & Swart 1983; Kempe & Kaźmierczak 1993; Kaźmierczak *et al.* 1996). Although in transmitted light microscopy, the remnants of outer sheaths surrounding groups of coccoid cells are not well visible, the 'microcellular' texture of the cements leaves no doubt as to their similarity, if not identity, with microscopic images of living noncalcified coccoid cyanobacteria (compare Figs 2C and 3E with 3F). The sameness of the microgranular calcareous material from the remnants of sheaths with the surrounding micrite indicates their common origin. This feature together with the yellow-brownish colour and the homogenous fine-grained texture of the fringes and festoons

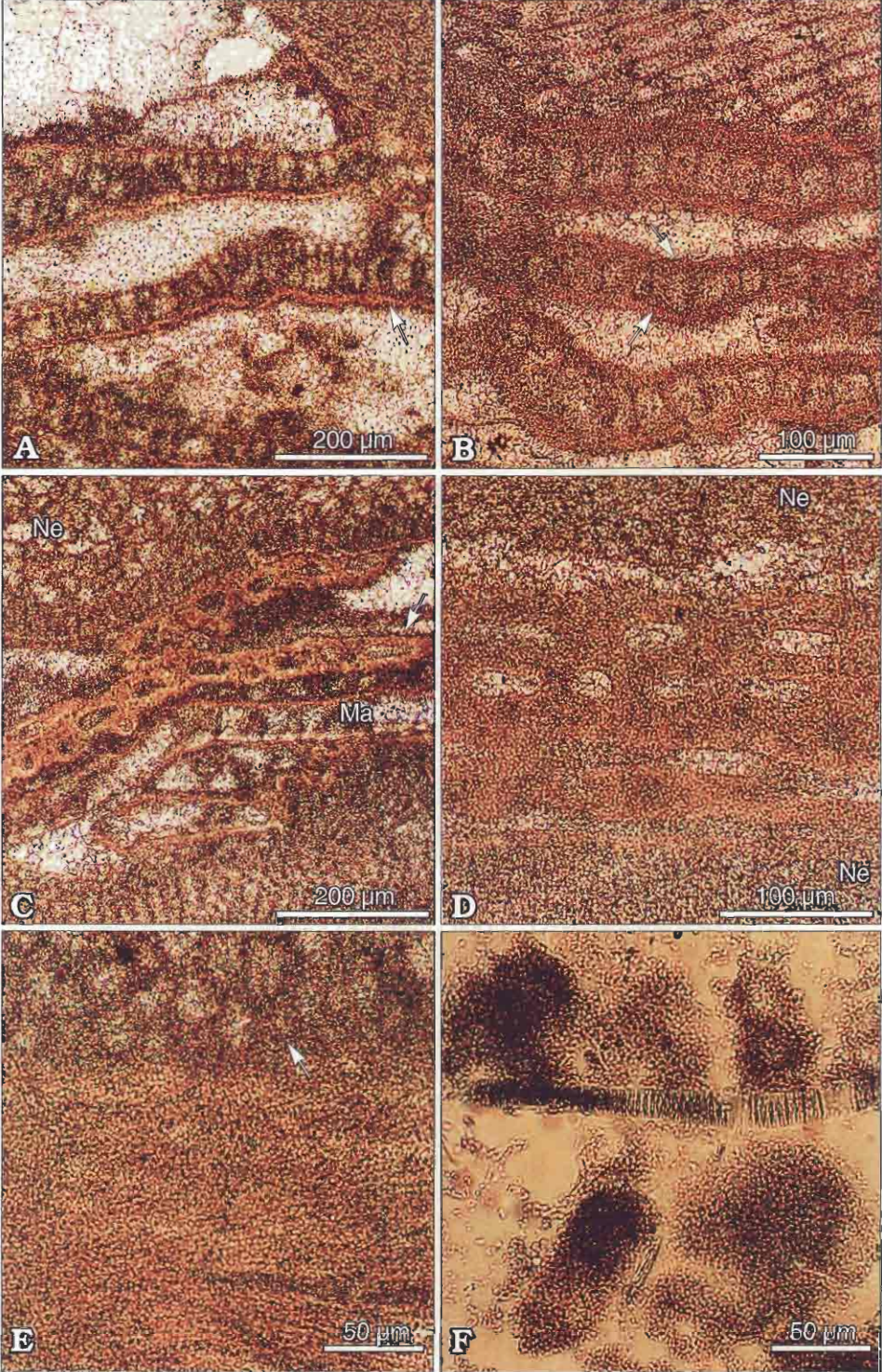
on *N. fosliei*, the coatings on *M. pacifica*, and the encrustations around the filamentous green alga permit to ascribe the origin of all these cements to most probably *in vivo* calcified coccoid cyanobacteria.

A particularly strong support to such an interpretation is offered by the modern *in vivo* calcified mats of pleurocapsalean cyanobacteria associated with calcareous red algae described from the quasi-marine Motitai Crater Lake on Satonda Island, Indonesia (Kempe & Kaźmierczak 1993). The cyanobacteria grow there attached to the basal surfaces of peyssonneliacean red algae (*Peyssonnelia*) or intergrow with the very thin thalli of the coralline alga *Lithoporella* (Fig. 5C, F). *In vivo* calcification of the cyanobacteria produces aragonitic and/or Mg-calcitic micritic fringes and festoons originally interpreted as a product of the metabolic activity of the algae alone (Kempe & Kaźmierczak 1993). Similar subcrustal aragonite botryoids have been described earlier from living, dead and fossil corallines (Alexandersson 1974; Massieux *et al.* 1983; Bosence 1985, 1991). Although they have been usually interpreted as early diagenetic cements, Walker & Moss (1984) considered them as extracellular products of the algae. Identical aragonitic encrustations on lower surfaces of peyssonneliacean red algae from the Holocene reefs of the Caribbean area (Belize) have also been described as rhizoid-associated hypobasal calcification of the algae (James *et al.* 1988). SEM examination of the Indonesian cements has revealed, however, that they are products of pleurocapsalean cyanobacteria. The shape and size of their outer mucilage sheaths (capsules) correspond exactly to the remnants of the cyanobacterial capsular sheaths preserved in the Okierabu-jima cements (compare Fig. 5B, E).

Discussion and conclusions

The discovery of microcrystalline (micritic) cements produced by *in vivo* calcified films of coccoid cyanobacteria in deep water rhodoliths and coralline crusts from a fore-reef slope (for depositional environment of loc. IE2 see Iryu 1992) is unexpected. Although biofilms composed of benthic cyanobacteria, with pleurocapsaleans and entophysalidaceans inclusively, occur commonly on rocky marine shores, particularly in the intertidal and splash zones (e.g., Humm & Wicks 1980; Kaehler & Williams 1996; Nagarkar & Williams 1997), their *in vivo* calcium carbonate permineralization in seawater has not been documented so far. Hydrochemical data from various settings sustaining *in vivo* calcification of cyanobacterial mats indicate that the process is initiated only at high ambient calcium carbonate supersaturations (for example with calcite saturation indices $SI_{\text{calcite}} > 0.8$ comparing with the $SI_{\text{calcite}} \sim 0.5$ of average seawater, see Kempe & Kaźmierczak 1990). Therefore, it may be assumed that the cyanobacterial cements in the Pleistocene coralline algal frameworks were generated in hydrochemical conditions deviating from those associated with average seawater.

The spatial distribution of the cyanobacterial cements indicates that the coccoid cyanobacteria settled and calcified in open spaces within the coralline algal framework. The close association of the cements with the algal thalli and their apparent absence in association with skeletons of bryozoans or foraminifers both suggest that the calcification process in the cyanobacteria was dependent on some physiological activity of the algae. Photosynthetic CO_2 uptake by the red and green algae may have been



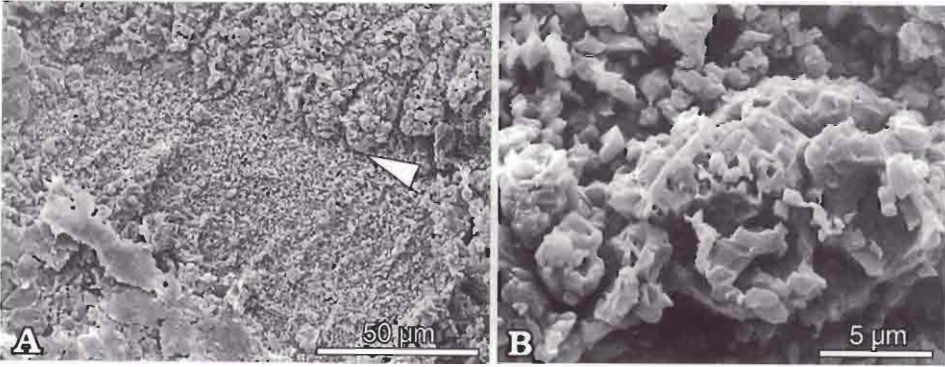


Fig. 4. **A.** SEM image of polished and EDTA-etched vertical section through thallus of *N. fosliei* with a fringe of microcrystalline cyanobacterial Mg-calcite attached to its ventral surface (arrow). The micritic material is indistinctly striped with thin ridges running perpendicularly to the ventral surface of *N. fosliei*. **B.** Highly magnified fragment of the same etched fringe showing micrite grains and subglobular bodies representing remnant of capsular aggregates of coccoid cells comprising cyanobacterial biofilms generating the microcrystalline cements. Loc. IE2, sample IGPS 103714.

a critical factor here because it increases ion activity product of the alkaline earth ions (Ca^{2+} or Mg^{2+}) and, consequently, produces the high supersaturation levels with respect to carbonate minerals in the proximity of the cyanobacterial films necessary for the precipitation of Mg-calcite microcrystals on and within the cyanobacterial mucilage sheaths (Pentecost & Bauld 1988; Kempe & Kaźmierczak 1990; Merz 1992; Merz & Zankl 1993). Increased calcium carbonate saturation in the semiclosed and closed spaces occupied by the cyanobacteria could also result from increased alkalinity associated with internal decay processes (e.g., sulfate reduction) in the coralline algal framework. Excess alkalinity production in interstitial waters during anaerobic decomposition of organic matter is a well-known phenomenon in modern, Pleistocene, and Eocene marine carbonate reefal structures (Pigott & Land 1986; Sansone *et al.* 1990). Alkalinity build-up is a powerful factor increasing carbonate supersaturation and promoting CaCO_3 precipitation in seawater (for review see Kempe & Kaźmierczak 1990). Thus both processes – photosynthesis and decomposition – may have been instrumental in the syngenetic formation of the cyanobacterial micritic cements in the Pleistocene coralline frameworks of Okierabu-jima. Interestingly, the poor light con-

Fig. 3. **A, B.** Coatings of microcrystalline cyanobacterial Mg-calcite (arrows) on ventral and dorsal thallus surfaces of *Mastophora pacifica*; loc. IE2, thin section IGPS 103714. **C, D.** Tubular thalli of green algae encrusted by cyanobacterial microcrystalline Mg-calcite (arrow) filling spaces between thalli of *N. fosliei* (Ne) and *M. pacifica* (Ma); loc. IE2, thin section IGPS 103714. **E.** Magnified portion of a microcrystalline Mg-calcite fringe attached to ventral surface of *N. fosliei* thallus (arrow). The dense 'microcellular' texture of the calcareous material reflects the pseudoparenchymatous organization of coccoid cyanobacterial films generating the fringes (compare with Fig. 3F); loc. IE2, thin section IGPS 103710. All transmitted light photomicrographs in vertical thin sections. **F.** Smear slide of living colonies of noncalcified marine coccoid cyanobacterium *Microcystis litoralis* (with a filament of oscillatiorian cyanobacterium). Note the striking similarity of *M. litoralis* to the calcified cyanobacterial colonies which produced the Okierabu-jima cements (compare Figs 2C and 3E); lower part of the intertidal zone at Wilhelmshaven Harbour, North Sea.

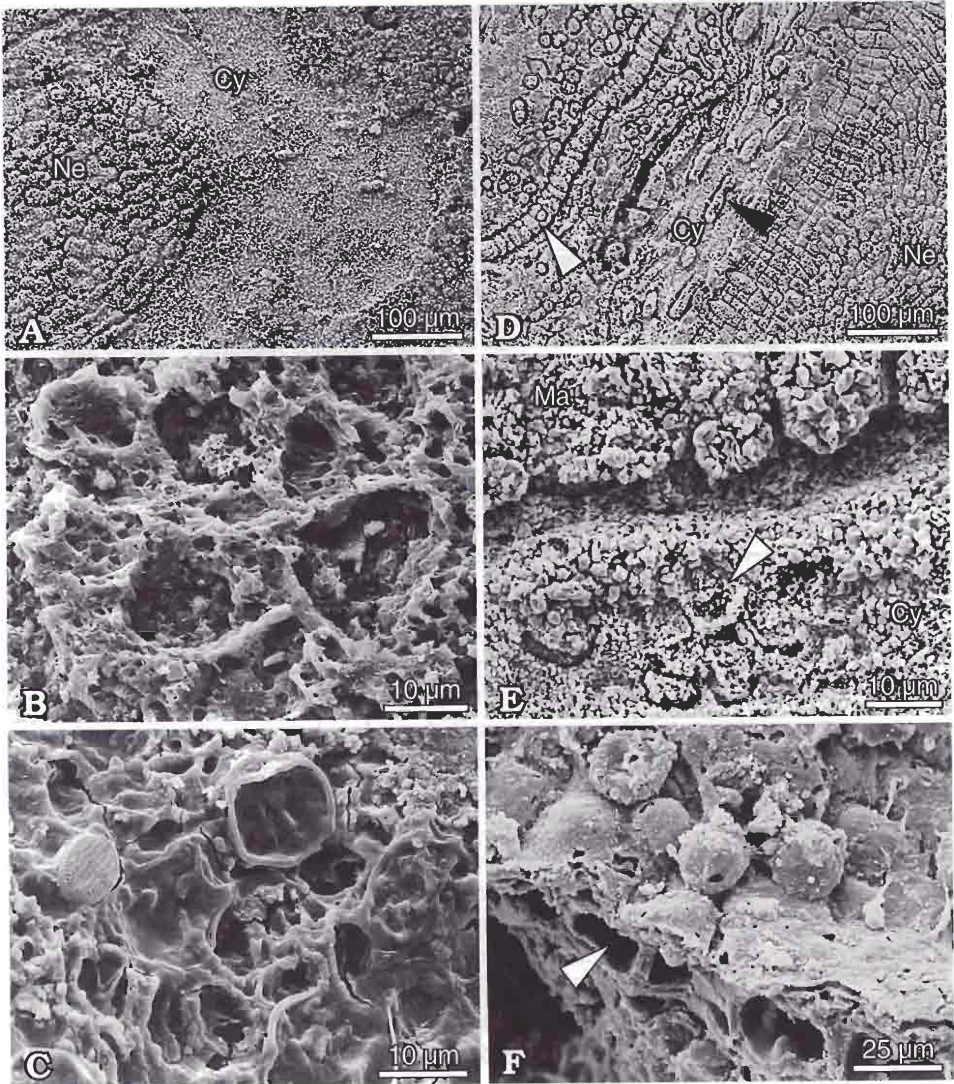


Fig. 5. **A.** SEM image of polished and EDTA-etched cross section through thallus of *N. fosliei* (Ne) with fringe of microcrystalline cyanobacterial Mg-calcite (Cy); loc. IE2, sample IGPS 103714. **B.** Fragment of cyanobacterial Mg-calcite from fringe shown above revealing remnants of capsular sheaths surrounding originally groups of coccoid cells forming cyanobacterial mat. **C.** SEM image of living *in vivo* calcified benthic coccoid cyanobacteria from quasi-marine crater lake on Satonda Island (Indonesia) to show identical as above capsular organization of mat. **D.** SEM image of polished and EDTA-etched cross-section through coralline crust composed of *N. fosliei* (Ne) and *M. pacifica* (white arrow) with tubular thalli of chasmolitic green algae (black arrow) encrusted with cyanobacterially precipitated microcrystalline Mg-calcite (Cy) filling space in coralline framework; loc. IE2, sample IGPS 103714. **E.** SEM image (EDTA-etched) of ventral thallus surface of *M. pacifica* (Ma) coated with microcrystalline Mg-calcite (Cy) in which remnants of capsular sheaths typical for pleurocapsalean cyanobacteria can be distinguished (arrow); loc. R3, sample IGPS 103719. **F.** Surface and side view of capsules of modern *in vivo* calcified mat of pleurocapsalean cyanobacteria intergrowing with coralline alga *Lithoporella* sp. (arrow); Satonda Island, Indonesia.

ditions, which must have characterized the relatively deep-water cryptic microenvironments occupied by the cyanobacteria, apparently had no adverse influence on their growth. This is not surprising, however, considering that many cyanobacterial strains are capable of thriving in very poorly illuminated environments or even in darkness (for review see Van Liere & Walsby 1982; Stal 1995; Stal & Moezellar 1997).

Was the formation of the cyanobacterial micritic cements a phenomenon unique for the Okierabu-jima coralline frameworks, or may our finding be a potential key to the origin of microcrystalline (micritic) cements known from other modern and ancient carbonate reefal deposits? The numerous modern and fossil reefal micritic cements interpreted recently as products of the calcification of unidentified microbes (e.g., Brachert & Dullo 1991; Riding *et al.* 1991; Pedley 1992; Zankl 1993; Camoin & Montaggioni 1994; Laurenti & Montaggioni 1995; Braga *et al.* 1996; Webb 1996; Steneck *et al.* 1997; Webb *et al.* 1998) may represent products of similar *in vivo* calcified films of coccoid cyanobacteria. A search for remnants of coccoid cyanobacterial sheaths on polished and carefully etched surfaces of such cements in SEM images would be strongly recommended.

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Cyjanobakteryjna geneza mikrytowych cementów z plejstoczeńskich rodolitów i naskorupień krasnorostowych Okierabu-shimy, Japonia

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Streszczenie

Geneza mikrytowych (synonimy: mikrokrystalicznych, kryptokrystalicznych, pelitowych, drobnoziarnistych) cementów w dzisiejszych i kopalnych strukturach rafowych jest jednym z bardziej kontrowersyjnych zagadnień współczesnej sedymentologii węglanowej. Sporna jest zarówno kwestia organicznego czy nieorganicznego pochodzenia takich cementów, jak i problem syngenetycznego bądź wczesnodiaogenetycznego charakteru ich genezy. Praca przedstawia wyniki badań nad mikrytowymi cementami wypełniającymi w różnym stopniu pory w rodolitach i naskorupieniach krasnorostowych z powierzchniowych odsłoneń plejstoczeńskich utworów

rafowych na wyspie Okierabu-shima (Wyspy Riukiu, Japonia). Zespół krasnorostów i towarzyszących im organizmów szkieletowych występujący w tych utworach wskazuje, że powstały one w głębszej strefie skłonu rafy, na głębokości 50–150 m. Analiza cementów wykazała, że zostały one utworzone w wyniku wytrącenia bardzo drobnych, bo liczących zaledwie 2–3 μm średnicy, ziaren magnezowego kalcytu przez maty kokkoidalnych cyjanobakterii (sinic) rosnących w porach i kawernach rodolitów i naskorupień krasnorostowych. Cementy te występują w postaci guzowatych narośli na brzusznych powierzchniach *Neogoniolithon fosliei* oraz jako powłoki na brzusznych i grzbietowych powierzchniach *Mastophora pacifica* i nitkowatych plechach epifitycznych i chasmolitycznych zielenic (*Ostreobium*, *Gomontia*). *In situ* – i najprawdopodobniej *in vivo* – kalcyfikacja mat cyjanobakteryjnych zasiedlających przestrzenie wewnątrz rafowych struktur krasnorostowych była przypuszczalnie wywołana lokalnie podwyższonym, w porównaniu ze średnią wodą morską, poziomem przesycenia środowiska węglanem wapnia w stosunku do teoretycznego iloczynu rozpuszczalności kalcytu. Spowodowane było to intensywnym pobieraniem z wody CO_2 , zarówno przez same cyjanobakterie, jak i fotoasymilujące krasnorosty i zielenice, a także podwyższonym poziomem alkaliczności związanym z procesami rozkładu wewnątrz rafowych struktur krasnorostowych. Uzyskane wyniki dają podstawę do przypuszczeń, że wiele mikrytowych cementów opisanych z innych dzisiejszych i kopalnych struktur rafowych jest również wytworem mat kokkoidalnych cyjanobakterii.