

Mat-forming coccoid cyanobacteria from early Silurian marine deposits of Sudetes, Poland

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Mass occurrence of mats comprised of benthic coccoid cyanobacteria is reported from early Silurian black radiolarian cherts exposed at Żdanów village (Bardzkie Mountains, Sudetes, southwestern Poland). The cherts contain laminated organic matter representing degraded benthic coccoid cyanobacterial mats. The remains of cyanobacteria occur as laminated agglomerations of variously preserved subglobular colonies composed of spherical cells of variable size and numbers. The morphology of remnants of cells and their mucilaginous envelopes, structure of colonies, and particularly the presence of small granular structures resembling reproductive cells known in extant coccoid cyanobacteria as baeocytes, permit to compare the Silurian microbiota with modern cyanobacteria assigned to the genera *Staniera* or *Chroococciopsis*.

Key words: Coccoid cyanobacteria, microbial mats, cherts, Silurian, Poland.

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Introduction

Cyanobacteria (Cyanoprokaryota, Cyanophyta), one of the main primary producers in modern marine environments, have a worldwide distribution and occur in wide variety of habitats. They are the largest and most morphologically diverse group of photosynthetic prokaryotes (e.g., Whitton 1992). The contribution of cyanobacteria in marine primary production today and in the past is unquestioned. Some play an important role in nitrogen fixation in marine environments (e.g., Stal 1995; Paerl 2000). Many cyanobacteria, due to their adaptive capabilities, tolerate a great range of environmental conditions and can be found in almost all biotopes, including extreme environments (habitats of various salinity, pH and temperature). Cyanobacteria are commonly regarded as biofilm- and mat-forming microorganisms (for recent reviews see: Van Gernerden 1993; Stal 2000; Paerl et al. 2000), which can produce laminated biosedimentary structures called stromatolites. However, the vast geological literature linking the genesis of fossil marine microbialites with the activity of cyanobacteria encloses only few examples of satisfactorily documented mass occurrences of cyanobacterial microbiota as mats or biofilms builders (for review see: Ginsburg 1991; Grotzinger and Knoll 1999; Riding 2000; Kaźmierczak et al. 2004). The cyanobacteria have one of the longest geological record. The fossil record indicate that they appeared already in Archean (Hayes 1996; Mojzisz et al. 1996) and probably have played an important role in production of some Precambrian carbonates (e.g., Schopf 1993; Ueno et al. 2001; Kaźmierczak and Altermann 2002a; Altermann and Kaźmierczak 2003; Kaźmierczak et al. 2004). The earliest microfossils resembling morphologically cyanobac-

teria were reported from Australia, from the 3.49 Ga old Dresser Formation (Ueno et al. 2001) and from the 3.46 Ga old Apex Chert (Schopf 1993). The interpretation of Ueno et al. (2001) and Schopf (1993) are controversial (for review see Knoll 2003). The fossil record of these earliest cyanobacteria-like forms is meager. Due to their fragmentary preservation the early Archaean microfossils are extremely difficult to identify. Better preserved remnants of cyanobacteria-like microbiota are described from Proterozoic rocks. They derive mostly from stromatolites, silicified dolomites and black laminated cherts (e.g., Hofmann 1975; Knoll et al. 1975; Oehler 1978; Knoll and Golubic 1979; Knoll et al. 1989; Sergeev et al. 1997). Sedimentary structures ascribed to cyanobacterial mats have been also described from siliclastic deposits (e.g., Noffke et al. 2002). The Phanerozoic record of microbialite-forming marine cyanobacteria is extremely poor and practically only few clear-cut examples are known. The rock-building potential of Phanerozoic marine cyanobacteria is thus far documented by *Gloeocapsa*-like coccoid cyanobacteria forming Ordovician organics-rich deposit known as kukersite (e.g., Foster et al. 1990) and by benthic mats of coccoid cyanobacteria-like microbiota controlling the genesis of some late Jurassic fine grained and peloidal limestones (Kaźmierczak et al. 1996; Tribovillard 1998). The majority of well-preserved fossil cyanobacteria is, as a rule, patchily distributed in the embedding mineral matrix and gives little or no clues for their microbialite- or rock-building potential.

The purpose of the present paper is to describe morphologically well-preserved (Kremer 2003) mat-forming cyanobacteria from early Silurian black radiolarian cherts and siliceous shales of the Bardzkie Mountains (Sudetes, southwest-

ern Poland). Contrary to thus far described fossil cyanobacterial mats located in shallow-water environments, the lithological context, associated biota, and palaeogeographical position of the studied early Silurian mats indicate deeper and weakly illuminated environment comparing with that known from modern counterparts (Kremer and Kaźmierczak 2005). Mass occurrence of benthic cyanobacterial mats in early Silurian cherts permits their detailed study. Their mode of preservation allows recognition of almost full spectrum of morphological features, like cell morphology, colony organization and type of cell division, necessary for taxonomic identification. Because of varying degree of post-variscan thermal changes of the mat-bearing siliceous sediment enclosing cellulary preserved cyanobacteria, the mats represent also an interesting comparative material (Kaźmierczak and Kremer 2002) for interpreting similarly thermally changed Earth's oldest traces of life, as the hotly recently debated (Brasier et al. 2002; Schopf 1993) alleged Apex chert "microbiota".

Material and methods

Petrographic thin sections of radiolarian cherts enclosing remnants of cyanobacterial mats were analysed by traditional and advanced optical microscopic methods (Nomarski illumination). The cyanobacterial structure were studied with a Philips XL20 scanning electron microscope (SEM) using polished plates etched with 40% HF. The elemental analysis was made with an EDAX dual-window (UTW/Open) microprobe supplied with an ECON detector.

The material described herein is housed in the Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, within a collection ZPAL Cy.1.

In this paper the rules and conventions of the International Code of Botanical Nomenclature are followed.

Institutional abbreviation.—ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—GBŻ, Góry Bardzkie Żdanów.

Study location

The study focus on black laminated cherts from early Silurian deposits cropping out near the Żdanów village (Fig. 1) in the Bardzkie Mountains, (Sudetes Mountains, southwestern Poland). The Palaeozoic succession in the Bardzkie Mountains has been assigned to the Saxothuringian zone of the European Variscides (Franke et al. 1993). The road-cut near Żdanów village (Fig. 1) comprises the most complete sequence of Lower Palaeozoic rocks in the Bardzkie Mountains. The sequence comprise Upper Ordovician, Silurian, and Devonian deposits divided into five lithostratigraphic units: Jodłownik Beds (Upper Ordovician), Lower Graptolitic

Shales (Llandoveryan–Lower Ludlovian), Grey-greenish Shales (Upper Ludlowian–Pridolian), Upper Graptolitic Shales (Uppermost Pridolian–Middle Pragian), and the Żdanów Series (Middle Pragian–?). These Lower Palaeozoic rocks enclose numerous graptolites (e.g., *Monograptus turriculatus*, *M. spiralis*, *Cyrtograptus murchisoni*, *C. lundgreni*) documenting stratigraphic position of these strata (Porębska 1982; Wyzga 1987; Porębska and Sawłowicz 1997).

The present study focus on Lower Graptolitic Shales lower part of which consists of black radiolarian cherts (lydites) with intercalations of black siliceous shales. The stratigraphic position of the Lower Graptolitic Shales as belonging to the graptolite zones from *Parakidograptus acuminatus* up to *Lobograptus scanicus* have been shown by Porębska and Sawłowicz (1997). The black cherts are massive and generally thick bedded (average thickness of beds about 10 cm), although thin bedded cherts also occur, with distinct lamination visible on weathered surfaces. This type of rock is composed of microcrystalline or cryptocrystalline quartz and chalcedony. The fossil assemblage consists of colonial coccoid cyanobacteria, radiolaria, acritarchs, graptolites, and rare conodonts. Radiolaria content is variable, usually between 20–30% (and more) of the rock volume. The radiolarian skeletons are usually dissolved but in some cases are replaced by chalcedony or pyrite. The upper part of this unit consists mainly of siliceous shales and clayey shales with few intercalations of massive radiolarian cherts. Dispersed grains of detritic minerals, mainly quartz, and phosphatic nodules occur in the chert.

Observations

As visible in vertical thin section (Fig. 2), cherts and siliceous shales are composed of more or less continuous, organised and amorphous organic-rich layers, several to 30 µm thick, oriented parallel to bedding planes. The organic layers range in color from yellowish-brown to dark reddish-brown. In most cases the lamination is clearly visible and detail elements of its morphology are easily recognisable. Organic-rich laminae are composed of densely packed remnants of coccoid cyanobacteria. The coherence of the organic laminae vary. There are some places where lamination is not well recognisable and the organic matter is scattered. Due to compaction, details of laminae morphology are usually not visible in vertical thin sections (Fig. 2D). In less degraded laminae more or less spherical aggregates and groups of cells are sporadically preserved (Fig. 2E, F). Spherical or oblong individual bodies (usually several micrometers in size), or groups of bodies are visible within such laminae. The details of laminae morphology are best visible in horizontal thin sections (Fig. 3). Some aggregates are oval, other elongate or even irregular. Aggregates range from 40 to 120 µm in diameter and contain from 8 to 40 (and more) cells. Cell-like units are more or less spherical and have a variable diameter, from 4–6 µm to 20 µm (Fig. 4). Most frequent are cells between 5 and 10 µm. Besides this

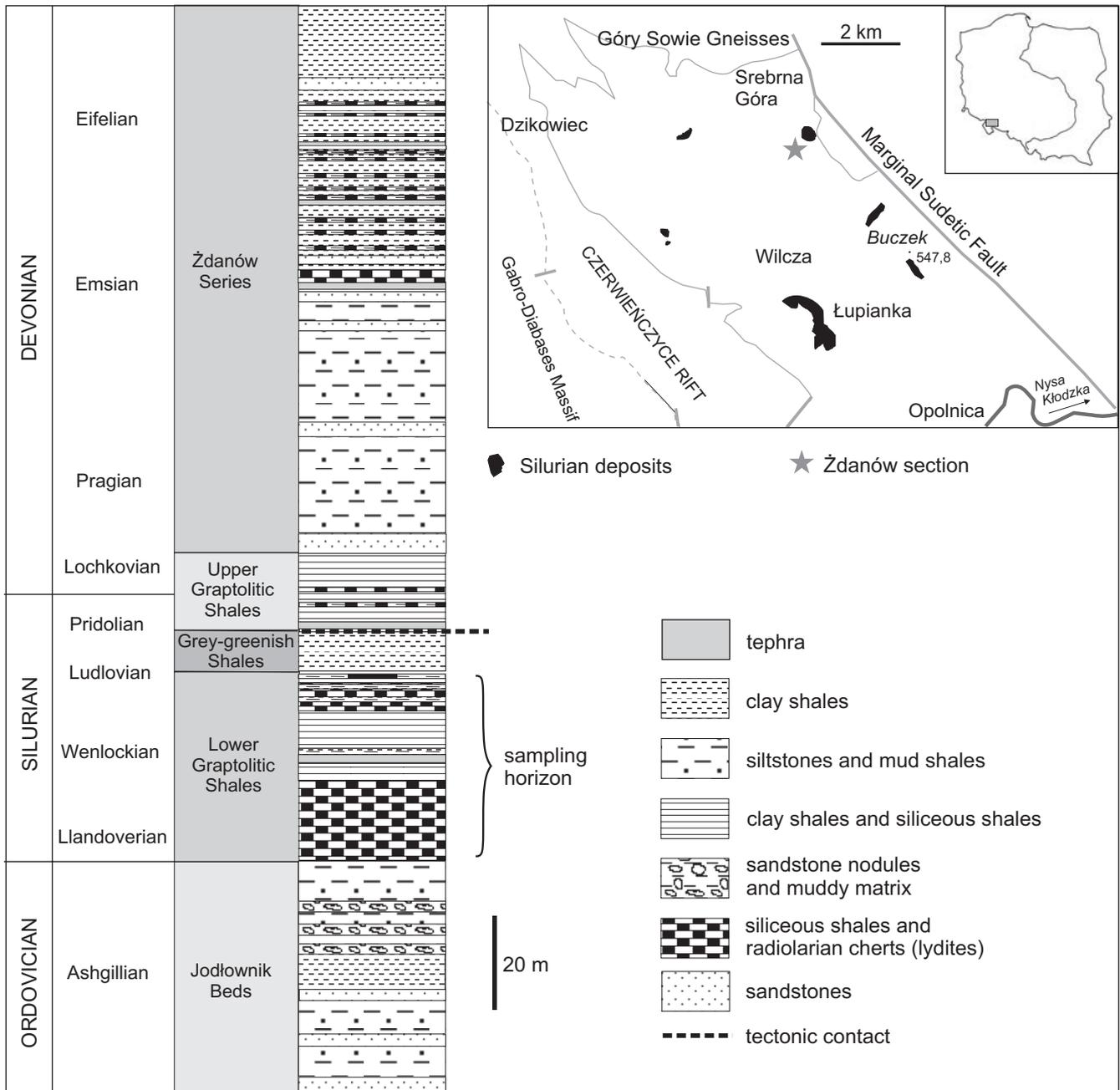


Fig. 1. Geological map of the northern part of the Bardzkie Mountains (Sudetes, southwestern Poland) and stratigraphic section of the Early Palaeozoic deposits at the Żdanów road-cut (after Porębska 1982, and Wyzga 1987; modified).

very small coccoids forms 1.5–3 μm in diameter occur. Usually one aggregate contains several large (10–14 μm), several medium (~6 μm) and several small (1.5–3 μm) cells (Fig. 3B–D). Some of the large spheres contain granular material, some are empty and only the outer sheaths are preserved (Fig. 3). Aggregates are distributed in close proximity to each other forming often differently degraded groups. Some cell-like units are irregularly dispersed forming groups embedded in amorphous organic matter. In case of densely packed cells, their walls form a kind of a spider web-like structure. The webs grade often into well preserved cells grouped in distinct

aggregates. There is a complete gradation of morphologies between well preserved cyanobacterial cells or aggregates and the degraded organic matter. In SEM images of HF-etched platelets remains of kerogenized cell walls or envelopes and silicified common mucilage sheaths (glycocalyx) surrounding originally individual cells and group of cells are well visible (Fig. 5). The cell wall material is often degraded leaving pits separated from each other by 1–3 μm thick walls. The energy-dispersive X-ray spectrum (EDS) of cells wall remains shows high content of carbon. The microprobe elemental analyses of common mucilage sheaths (glycocalyx) surrounding

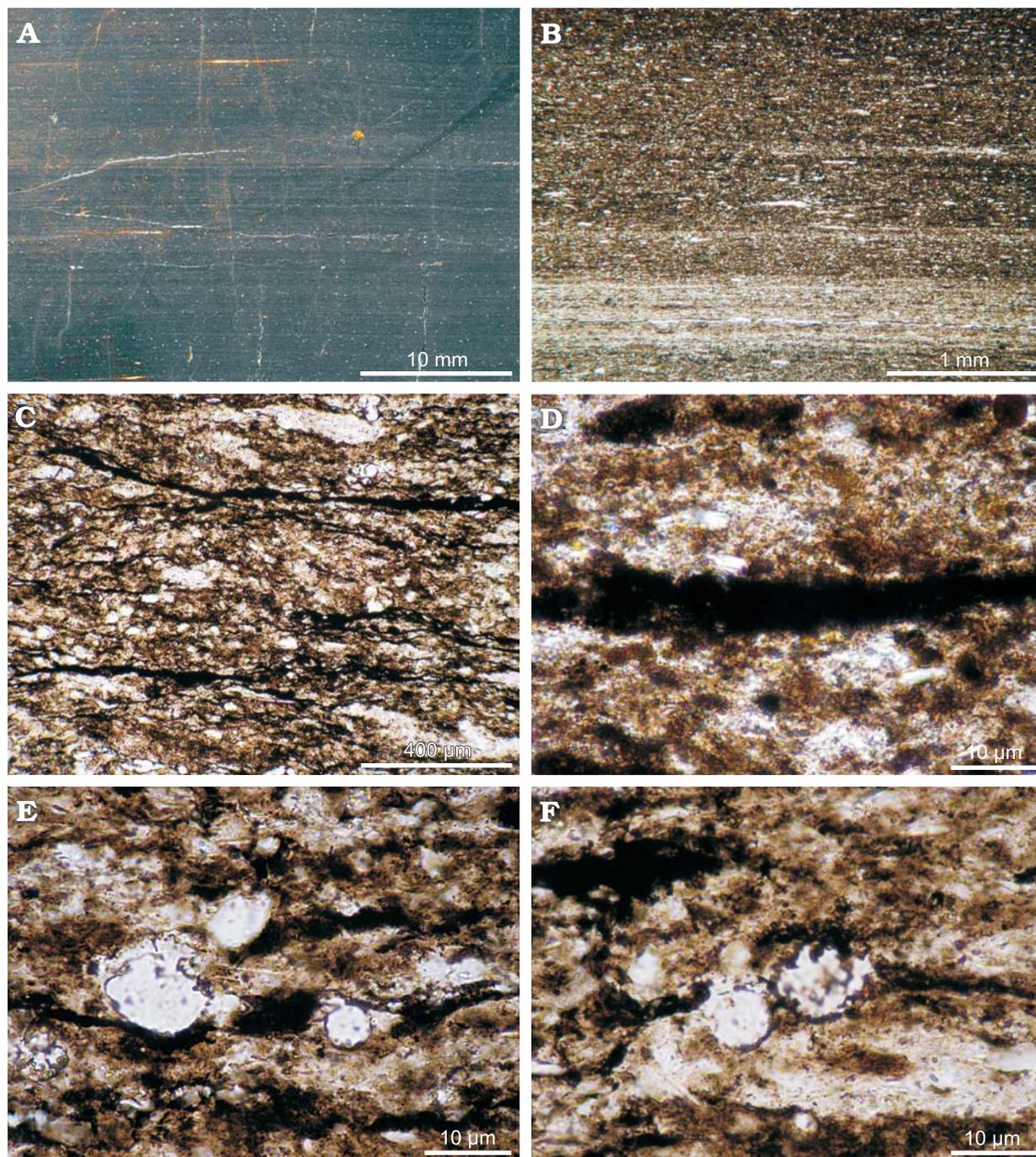


Fig. 2. Optical micrographs of Early Silurian radiolarian cherts from Żdanów in vertical thin sections. A–C. Sections of black radiolarian chert in different magnifications showing well-defined laminae of organic matter composed of coccooid cyanobacterial biomass. D. A fragment of dense organic lamina, in which no details are visible. E, F. Magnified fragment of organic laminae composed of partly degraded and compacted aggregates of coccooid cyanobacteria, some capsule-like remnants of mucilage sheaths remained uncompact. A–C, ZPAL Cy.1 GBŻ 49/1–4; D, ZPAL Cy.1 GBŻ 16/2; E, F, ZPAL Cy.1 GBŻ 23/1.

originally cells and groups of cells forming the spider web-like structures, show the presence of Si, Al, C, Ba, Mg minerals, indicative for silicates. The EDS analyses of cells infilling show beside silica organic (kerogenous) material. Pyrite microcrystals are in places embedded in the mineralised remains of the mucilage sheaths. The rocks contain from 0.73% to 1.73% of TOC, part of which is kerogenous (III and IV kerogen type).

Comparison and discussion

In terms of colony organisation, i.e., aggregates composed of different size of cells and thicker outer walls of larger cells, the Silurian forms resemble modern colonial coccooid cyanobacteria such as representatives of *Stanieria*, *Chroococciopsis*, *Xenococcus*, and *Entophysalis* assigned by some au-

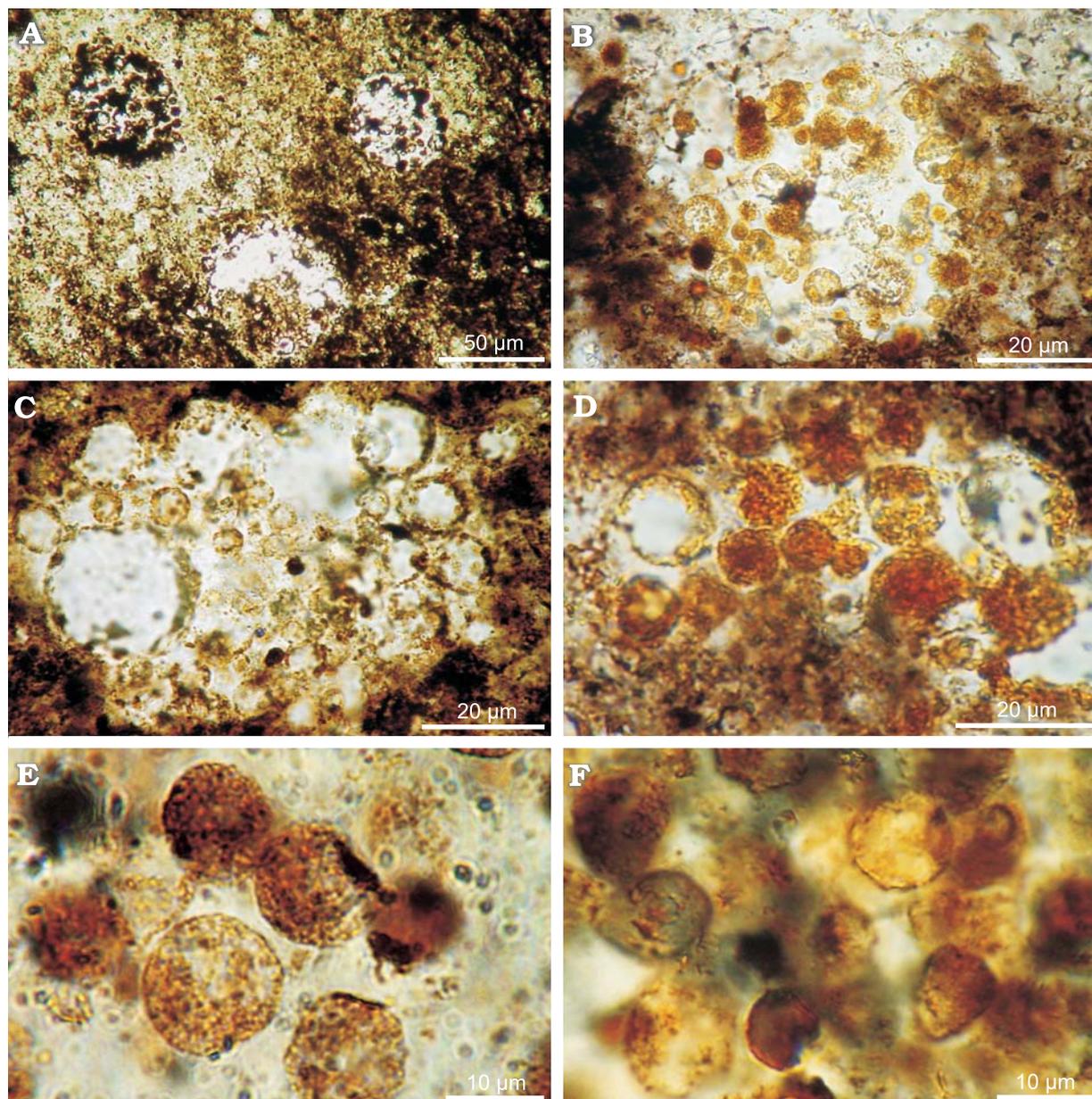


Fig. 3. Optical micrographs of early Silurian radiolarian cherts from Żdanów in horizontal thin sections. **A.** Three globular aggregates of coccoid cyanobacteria forming mats visible in amorphous organic background. **B–D.** Magnified aggregates of variously degraded coccoid cyanobacteria showing different size of cells and mucilage sheaths. Some cells are filled with granular material resembling reproductive cells (baecytes) of modern coccoid cyanobacteria. **E, F.** Magnified fragment of cyanobacterial colony (aggregate), partly degraded, showing individual cells. **F.** Optical micrographs with Nomarski illumination. All ZPAL Cy.1 GBŻ 49/1-4.

thors to the group Chroococcales (unicellular coccoid cyanobacteria; Komárek and Anagnostidis 1998).

Modern Chroococcales, *sensu* Komárek and Anagnostidis (1998), embrace unicellular and colonial forms that do not form filaments (coccoid cyanobacteria; e.g., *Pleurocapsa*, *Entophysalis*, *Chroococciopsis*, *Stanieria*). Their cells are spherical, oval, regular or irregular. The form of cells is rather stable in all known chroococcacean genera. The mucilaginous envelopes around cell walls are variable but their character is usually specific for given taxa, and they can be useful for taxonomic classification (Komárek and Anagnostidis 1998). How-

ever, some factors such as photon flux density, age of culture or temperature can alter thickness and lamellation of the mucilaginous sheaths (Silva and Pienaar 2000). The cell division occur in numerous modification used for classification purposes. There are two main types of cell divisions occurring in chroococcacean cyanobacteria. The first is the binary fission dividing the mother cell into two parts (daughter cells), which grow to approximately the original size before the next division. The second, multiple fission (baecyte division) is characterised by the simultaneous or successive division of a mother cell into numerous daughter cells (Fig. 6A–F). In the

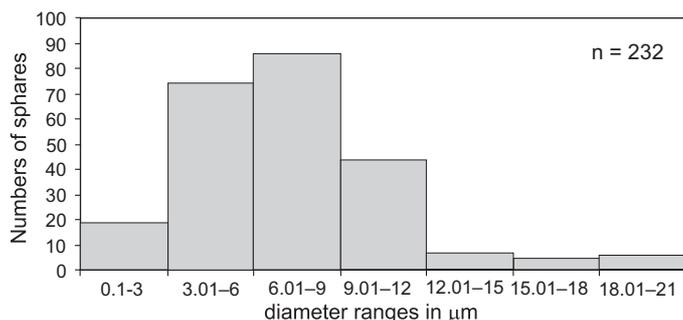


Fig. 4. Size-frequency histogram of cells from the early Silurian mats.

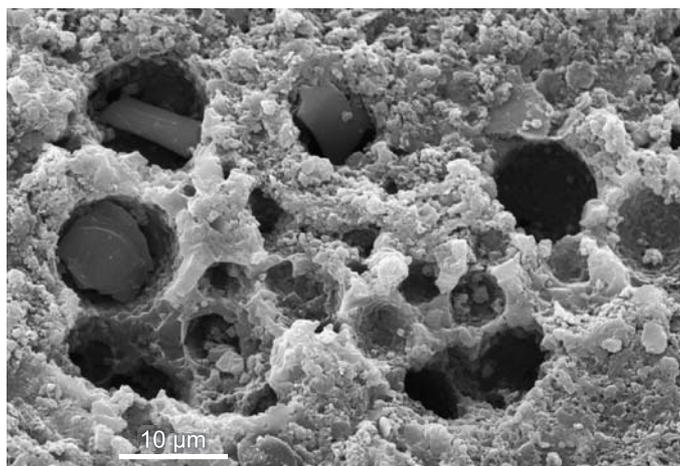


Fig. 5. Scanning electron microscope (SEM) image of early Silurian sub-spherical aggregate of benthic coccoid cyanobacteria from Żdanów in horizontal thin section (sample IV–VI 49), showing HF-etched pattern with extending parts representing silicified common mucilage sheaths (glycocalyx) and pits representing decomposed cells.

chroococcacean cyanobacteria cells embedded in gelatinous sheaths aggregate often into colonies. The colony structure results from the reproduction type (the type of cell division) and the slime production (mucilaginous envelopes). Beside mode of reproduction, also the structure of mucilage sheaths (lamellation, stratification, thickness and morphology) is a diagnostic feature of different genera (Komárek and Anagnostidis 1998).

According to new taxonomic system supported by phylogenetic relationships of 16S rRNA sequences (Bergey's Manual of Systematic Bacteriology; Boone and Castenholz 2001) the Chroococcales group (coccoid cyanobacteria) is divided into two subsections: Subsections I and II. Cyanobacteria assigned to Subsection I reproduce by equal binary fission and by budding (Waterbury and Rippka 1989; Herdman et al. 2001) and those from Subsection II by multiple fission or multiple fission preceded by binary fission (Rippka et al. 2001a).

The best modern counterparts of the Silurian cyanobacteria seem to be forms assigned to the genus *Stanieria* Komárek and Anagnostidis 1986 belonging, according to new taxonomy, to Subsection II (formerly Pleurocapsales

Geitler 1925, emend. Waterbury and Stanier 1978; Rippka et al. 2001a, b) or *Chroococcidiopsis* Geitler 1933, emend. Waterbury and Stanier 1978 (Rippka et al. 2001c) belonging also to Subsection II. *Stanieria* (formerly *Dermocarpa* sensu Waterbury and Stanier 1978) was earlier assigned to the family Dermocarpellaceae Ginsburg-Ardre ex Christensen 1980 (Komárek and Anagnostidis 1998). *Stanieria* has spherical or subspherical cells arranged in more or less spherical groups or aggregates, fixed to the substratum (Figs. 6A–E, 7B, D, F). Cells in a colony are of variable size attaining generally 5–10 μm in diameter, although the mature spherical vegetative cells or cells just before fission may vary in diameter from 20 to 30 μm . Cells are enveloped by firm, homogeneous sheaths. *Stanieria* reproduces by multiple fission producing numerous spherical baeocytes, which varies greatly from 16 to 128 per cell or even >1000, depending on the mother cell size prior to division. Baeocytes are 1.5–4 μm in diameter and are liberated by rupture of a sheath or gelatinization of sheaths. *Chroococcidiopsis* (Fig. 6F) has a spherical, hemispherical or irregular-rounded cells enveloped by sheaths and arrange in groups forming colonies. Cells divide by binary or irregularly fission, but binary fission plays a dominant role in this genus. Binary fission is always followed by cell growth. The mother cells divide often into daughter cells of different shape and size. Some cells in a colony later change into spherical baeocytes, which enlarges symmetrically. Cells grow usually to 10 μm (during differentiation up to 20 μm) in diameter. Baeocytes numerous, attain 0.5 (or smaller) to 4 μm in diameter, usually spherical. The size and shape of the cells and the thickness of the mucilaginous sheaths is not strictly defined for this genus. The variability of this features depends on environmental conditions such as photon flux density, salinity, season, temperature etc. (Silva and Pienaar 2000).

Both *Stanieria* and *Chroococcidiopsis* occur in marine and freshwater environment (Anagnostidis and Pantazidou 1991; Komárek and Anagnostidis 1998). They are exclusively benthic, also epilithic or epiphytic forms attached to the substrate by any side (not polarised cells); none are known to be planktonic (Komárek and Anagnostidis 1998; Rippka et al. 2001a).

The here described early Silurian cyanobacteria seem to form similar colonies consisting of cells of different age, forming as their modern counterparts aggregates (Fig. 7). A comparison of the early Silurian with modern cyanobacteria shows that the shape and size of the Silurian cells is similar. The varying size of cells (3–4 to 20 μm) inside the aggregates reflect the different stage of cell growth and multiple fission (Fig. 6G). Multiple fission in modern cyanobacteria occur when a vegetative cell has reached a certain size (usually greater than 9 μm) and environmental factors are favourable (Kunkel 1984). The baeocytes develop into mature vegetative cells (Fig. 5). Similarly in Silurian aggregates the large cells, containing the granular material inside (Fig. 6), might be the mother cells with small daughter cells inside (baeocytes). The medium size cells are the vegetative cells

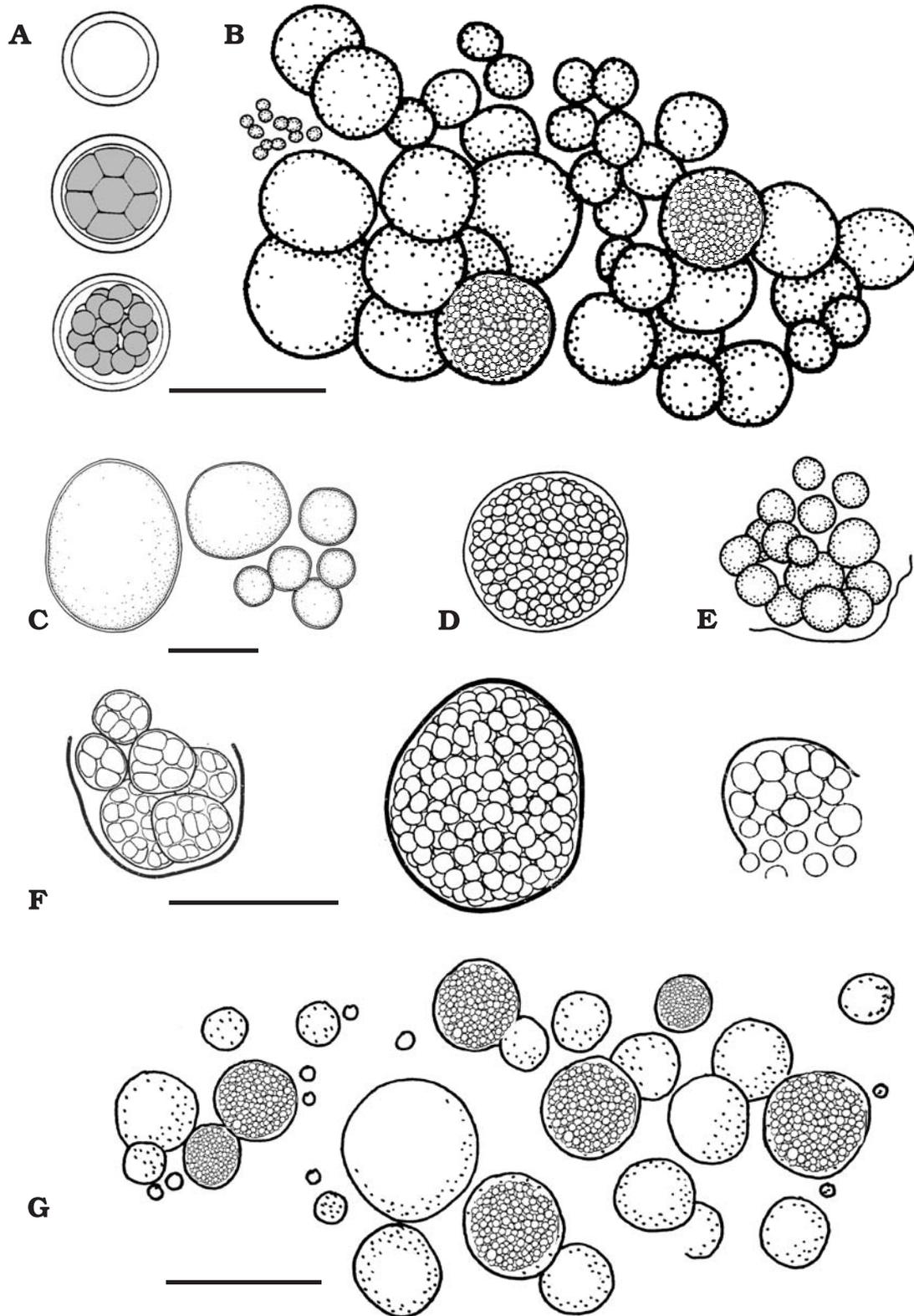


Fig. 6. Schematic drawing showing examples of vegetative cells of different age and baeocytes formation in modern colonial coccoid cyanobacteria. **A.** *Stanieria sphaerica* (Setchell and Gardner) Komárek and Anagnostidis 1986, scheme of baeocytes formation (after Komárek and Anagnostidis 1998). **B–E.** *Stanieria cf. cyanosphaera* (Komárek and Hindák) Komárek and Anagnostidis 1986, modern coccoid cyanobacteria grown in culture under irradiance level $20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ at 22 (~ 0.5) $^{\circ}\text{C}$. **B.** Cells of different age. **C.** Vegetative cells of different age. **D.** Baeocytes differentiation. **E.** Baeocytes liberation. After Komárek and Hindák from Silva and Pienaar 2000, modified. **F.** *Chroococcidiopsis kashayi* Friedmann 1961, various stage of baeocytic cell division (multiple fission), after Komárek and Anagnostidis 1998 modified. **G.** Fragment of early Silurian coccoid cyanobacterial mat. ZPAL Cy.1 GBŻ 49/1-4. Scale bars $20 \mu\text{m}$.

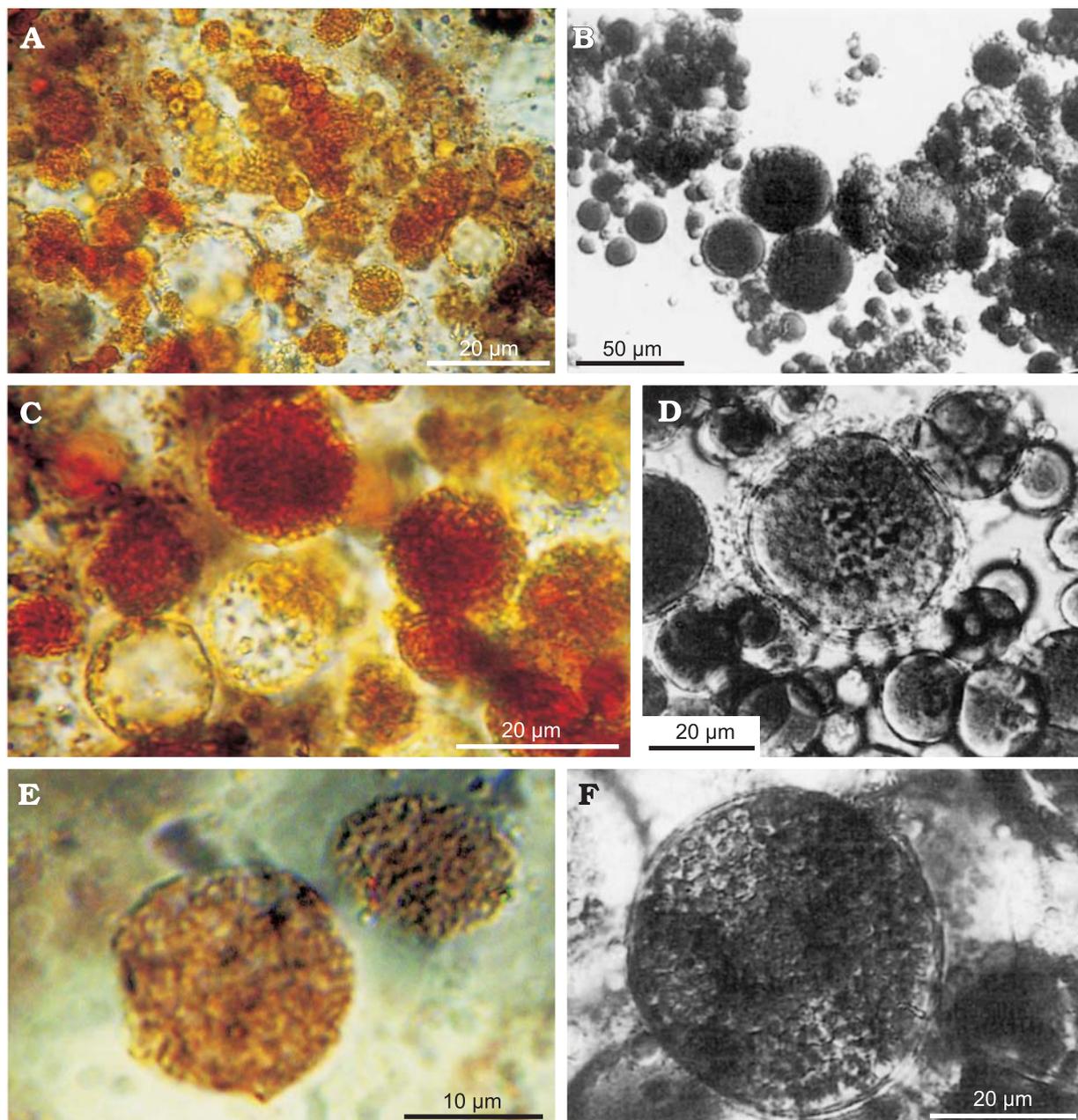


Fig. 7. Comparison of early Silurian coccoid cyanobacteria (left) from radiolarian cherts exposed at the Żdanów road-cut (Bardzkie Mountains) and modern coccoid cyanobacteria (right), all optical micrographs. **A, C, E.** Examples of cells of early Silurian *Stanieria*-like cyanobacteria at different stage of cell fission filled with minute reproductive cells (baeocytes). **E.** Optical micrographs with Nomarski illumination. **A, C, E,** ZPAL Cy.1 GBŻ 49/1-4. **B, D, F.** Mass culture of *Stanieria* cf. *cyanosphaera* (Komárek and Hindák) Komárek and Anagnostidis 1986, grown under irradiance level $20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ at 22 (~ 0.5) $^{\circ}\text{C}$, revealing spherical cells of varying size; some cells are filled with baeocytes (from Silva and Pienaar 2000, with publisher permission <http://www.schweizerbart.de>).

and the smaller can be the baeocytes liberated from the mother cells. The Silurian cells and aggregates are in some cases more irregular than its modern counterpart probably due to post-mortem alterations and later diagenetic processes. Dead cells of cyanobacteria may rapidly collapse and shrink forming polyhedral, irregular granules, or disappear completely (Knoll et al. 1975). Generally the contents of cyanobacterial cells decompose rapidly leaving usually the sheath material preserved. The thickness of the sheaths seem

to be related to the size of cells, thus, the thicker and larger in diameter sheaths are frequently better preserved (Horodyski and Vonder Haar 1975). As mentioned above, compactional deformation of the studied early Silurian cyanobacterial mats makes the recognition of their biotic components in vertical thin sections almost impossible. In horizontal thin sections, in turn, the morphology of the compacted mat-forming cyanobacteria is often quite well visible. The diagram in Fig. 8 is explaining this phenomenon.

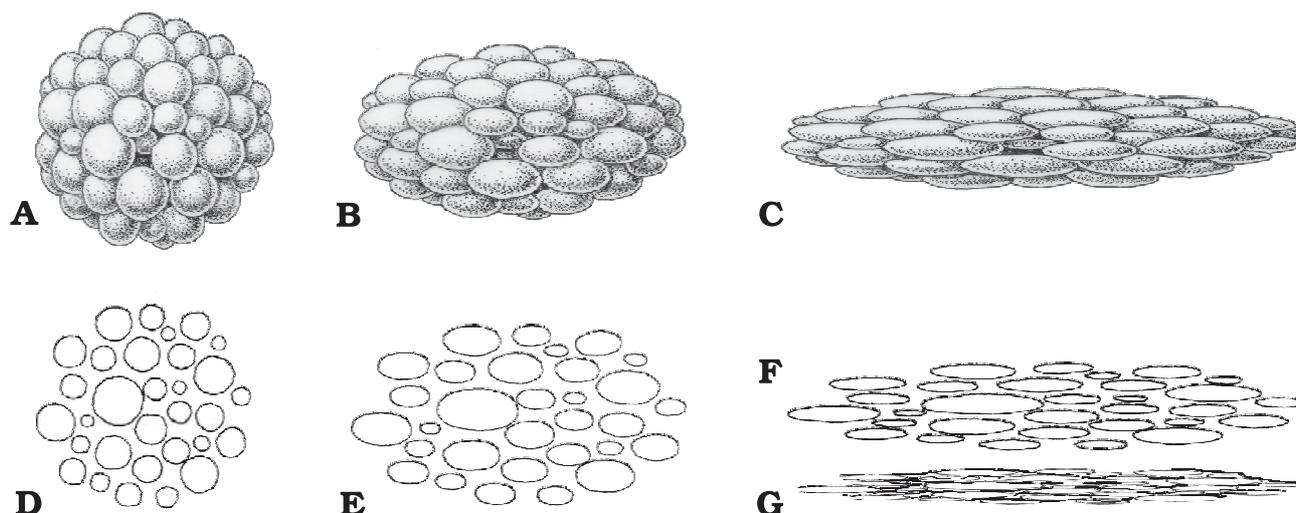


Fig. 8. Diagram showing effect of compaction of a coccoid cyanobacterial aggregate. **A–C.** 3D aggregate without compaction (**A**) and under different degree of compaction. **D–G.** Axial vertical section of the same aggregate without compaction (**D**) and under different degree of compaction; note that in **G** outlines of cells and/or capsules are no more identifiable. Not to scale.

The basic question arising here concerns the benthic character of the examined cyanobacterial mats. Benthic mat-forming cyanobacteria have, as a rule, thick common mucilage sheaths (glycocalyx) or capsules enveloping cells and group of cells (Stal 2000). Such thick and cohesive mucilage sheaths are more resistant to degradation and can easier mineralise. Such mineralised glycocalyx is visible, both in SEM (Fig. 5) and optical images, in the studied Silurian mats as system of walls forming spider-web-like structures. In contradistinction to benthic cyanobacteria, planktonic coccoid cyanobacteria do not form thick and cohesive sheaths and capsules, but excrete loose mucilage substances (e.g., *Microcystis*), which easily decompose after death (Zohary and Pais Madeira 1990). The post-bloom cyanobacterial and algal biomass undergo in the water column rapid degradation caused by bacterial activity or grazing and have no chance to reach the sea bottom in morphologically recognisable form (Paerl 1996; Simon et al. 2002). Bacteria are capable of complete degradation of cyanobacterial biomass (Doemel and Brock 1977). The degradation and permineralisation of the Silurian mats must have therefore occurred in situ during early diagenesis. The morphological (cellular) preservation of the early Silurian coccoid cyanobacterial mats can be an argument for their benthic character. Mass occurrence of cyanobacterial mats on the early Silurian sea bottom suggests that the water-mat interface must have been located within the photic zone (or close to limit of light penetration) and, due to oxygen production by the mat, might have been characterised by oxic to dysoxic conditions (Kremer and Kaźmierczak 2005). The common mucilaginous sheaths of the early Silurian cyanobacterial colony are mineralised by silica and silicate minerals (mostly Al-Fe silicates). Similar aluminium silicate mineralisation were noticed by Kaźmierczak and Altermann (2002b) from glycocalyx of Neoproterozoic benthic coccoid cyanobacteria. The same authors have shown that authigenic minerals, with silicate minerals inclu-

sively, nucleated and grew within the extracellular matrix. EDS analyses of modern mat-forming coccoid cyanobacteria from the alkaline Lake Van in Turkey (Kaźmierczak and Altermann 2002b; Kaźmierczak et al. 2004), have shown presence of authigenic carbonate and silicate minerals within their mineralised common mucilage sheaths, almost identical with those occurring in the Neoproterozoic and the Silurian mats described herein.

Coccoid colonial cyanobacteria are widely known from Proterozoic cherts. Their mode of preservation is quite similar to those from the early Silurian mats, although the Proterozoic forms are usually preserved in isolated groups. Similarly preserved coccoid microfossils were detected in Middle Proterozoic cherts of Dismal Lakes Group in Canada (Horodyski and Donaldson 1983). For instance, spheroid microfossils comparable with representatives of modern *Entophysalis* Kützing 1843 have been described by Schopf (1968) as *Sphaerophysycus parvum* Schopf 1968, by Horodyski and Donaldson (1983) as *Myxococcoides grandis* Horodyski and Donaldson 1980 and as *Eoentophysalis dismallakesensis* Horodyski and Donaldson 1980. Their spherical and ellipsoidal cells, isolated or grouped in aggregates, attain diameters from 2.4 to 8 μm .

Stromatolite-forming cyanobacteria were described from mid-Precambrian Belcher Supergroup in Hudson Bay (Hofmann 1976; Golubic and Hofmann 1976). The colonies of *Eoentophysalis belcherensis* Hofmann 1976 preserved in ~2 billion years old black stromatolitic chert seem to be highly analogous to modern *Entophysalis*. The mats are preserved as colonial cellular aggregates, where the interior outlines of cell-like structures vary from 2 to 6 μm , while the outer envelopes reach a diameter of 10 μm . These colonies show similarity to the early Silurian and modern cyanobacterial colonies in several morphological characters: (i) the structure of the colony, (ii) cell division, (iii) arrangement of cellular envelopes. According to Golubic and Hofmann (1976) the cell size reduction in these fossil cyanobacteria is

comparable with early diagenetic changes observed in degraded modern analogues.

From Palaeozoic deposits well-preserved chroococcacean colonial cyanobacteria *Eomerismopedia maureeniae* Foster, Wicander, and Playford 2002 have been described from the Lower Ordovician Coolibah Formation, Georgina Basin, Australia (Foster et al. 2002). Similarly as the early Silurian cyanobacteria they form irregular colonies with tightly packed spherical to oblong cells, measured 7–21 μm in diameter, but they differ from the early Silurian forms in cell division pattern. Their division plane changes regularly in two perpendicular directions producing tabular colonies. Often the cells are packed in groups of four.

Modes of preservation of cyanobacterial mats make sometime recognition of reproductive structures and way of cell divisions impossible. Also, as in the members of modern *Gloeocapsa* Kützing 1843 one species could be represented by multiple morphotypes, which can be modified by genetics and environment (Padmaja 1972). *Gloeocapsomorpha prisca* Zalesky 1917, the principal organic component of Middle Ordovician marine oil shales- kukersites, is an enigmatic form, which biological affiliation is still uncertain (Wicander et al. 1996). On morphological and geochemical evidences *Gloeocapsomorpha* Zalesky 1917 from kukersites has been assigned to cyanobacteria (ancient form of modern *Gloeocapsa*; see Zalesky 1917; Foster et al. 1989, 1990), to green algae (Fowler and Douglas 1984; Douglas et al. 1991), also to alga closely related to *Botryococcus* Kützing 1849 (Guy-Ohlson 1992; Derenne et al. 1994) or to mat-forming non-photosynthetic prokaryotes (Reed et al. 1986).

Great similarity of fossil and modern cyanobacteria indicates that cyanobacteria change little or not at all since they appear on Earth billions of years ago. This evidences of their low rate of evolution. A special term “hypobradytely” has been proposed by Schopf (1987) to refer to the exceptionally low rate of evolutionary changes exhibited by cyanobacterial taxa. The fossil taxa show little or no evident morphological changes over hundreds of millions of years. This “morphological evolutionary conservatism” (Schopf 1992) is especially well documented for both coccoid and filamentous form by numerous workers (for review see Schopf 1992). Comparison of more than 600 species of modern living cyanobacteria with Precambrian microfossils shows that almost all of the fossils can be placed in present-day genera. Most of colony forms known in the modern groups are present among the fossils (Schopf 1992). Excellent examples of *status quo* evolution in cyanobacteria is the 2,100-Ma-old genus *Eoentophysalis* Hofmann 1976, which is identical to modern *Entophysalis* in cell shape, colony structure, type of cells division and growth and even the stromatolitic structures they build (Golubic and Hofmann 1976; Schopf 1992). Similarly microfossils known as *Eopleurocapsa* Liu 1982 and *Paleopleurocapsa* Knoll, Barghoorn, and Golubic 1975 are indistinguishable from species of the modern genus *Pleurocapsa* (Schopf 1992).

Conclusions

Coccoid cyanobacteria were common in early Silurian seas. They formed extensive mats, which played important role in the benthic ecosystem. Comparative studies shown that the described early Silurian coccoid cyanobacteria are, by their cell size and morphology, colony organisation and cell division, well comparable with representatives of modern coccoid cyanobacteria assigned to genera *Stanieria* Komárek and *Anagnostidis* 1986 and *Chroococciopsis* Geitler 1933. Similarly as they modern counterparts, the early Silurian cyanobacteria were benthic forms with a high mat-forming potential.

The mode of preservation of cyanobacterial mats observed in early Silurian cherts reflects post-mortem degradation processes, time of silicification and degree of sediment compaction.

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