PERIODICUM BIOLOGORUM
VOL. 112, No 3, 227–238, 2010

UDC 57:61
CODEN PDBIAD
ISSN 0031-5362

Spiridion Brusina lecture

Encounters with greater bacteria

STJEPKO GOLUBIĆ

5 Cummington Street
Boston, MA 02215-2406, USA
E-mail: golubic@bu.edu

Received August 8, 2010.

PRELUDE

Croatia is today proud of its National Parks, which cover about 7.5 % of its territory. They are today superb tourist attractions and economic assets. That development was not always understood or appreciated. Within the economic recovery following World War 2 in what was then Yugoslavia, the options to preserve carbonate depositing waterfall of the river Krka in Dalmatia (today a National Park), or use them for energy generation, were seriously and vigorously debated and – the conservationists lost. It was then clear how little was known about the processes of carbonate dissolution and precipitation in the karstic region, or globally as a part of the carbon cycle. A modest research program was subsequently organized by Vale Vouk, professor at the University of Zagreb and member of the Yugoslav Academy of Sciences and Arts, to study this unique phenomenon and, as students, we had a chance to participate. The project to elevate the travertine barrier at Skradinski Buk and increase the capacity of the reservoir lake behind it for hydroelectric exploitation was later abandoned, probably after realization about the hidden hazards because of the porous and cavernous nature of the travertine deposit.

The organisms that most prominently contributed and modified carbonate deposition, which made the Krka River famous were the aquatic mosses as it has been documented earlier for the Plitvice lakes and waterfalls (also a National Park and a UNESCO-registered World Heritage site of Croatia) *(1)*. However, the detailed work has been performed by microorganisms associated with mosses but invisible to the plain eye. Each of the aquatic mosses, *Cratoneuron (Palustriella) commutatum, Didymodon tophaceus, Cynclidotus aquaticus* was covered by cyanobacteria *(2)* and microscopic algae, especially stalked diatoms and an unusual desmid *Oocardium stratum (3, 4)*. Many of these microorganisms contributed to the process of carbonate deposition in specific ways and left imprints on the precipitate that has formed *(5)*. However, under the most severe environmental conditions, in places under the impact of falling water, on sites of maximum carbonate precipitation or in the shade of the surrounding caves, the dominant microorganisms were always cyanobacteria (then called blue-green algae, cyanophyceae, myxophyceae or schizophyceae). This was my first encounter with blue-green algae that were not really algae and often not blue-green either. They were then considered a primitive group of phototrophic microorganisms marginal to cryptogamic botanists and completely ignored by bacteriologists, although their kinship to bacteria has been noticed brilliantly by Ferdinand Cohn more than hundred years earlier *(6, 7)*.

The search for the identity of greater bacteria

Blue-green algae or cyanobacteria, a group known generally as a nuisance causing waterblooms in eutrophic lakes, attracted early the attention of limnologists, but were also known to a few specialists as inhabitants of interesting littoral, terrestrial and marine habitats, especially by their prevalence in environments that are considered ecologically extreme. These organisms were known to dominate in thermal springs, in hypersaline environments, on tidal flats, sporadically wetted cliffs and desert soils. Although less conspicuous, they occur regularly in »normal« freshwater and marine environments engaged in a variety of ecological roles including formation and consolidation of sediments, in destruction of rocks in the process of bioerosion and, through these activities, in cycling of nutrients: carbon, nitrogen, phosphorus and trace elements (Figure 1). As prokaryotes, many of them are able to reduce atmospheric nitrogen, thus tapping the biologically least accessible pool of this often limiting nutrient. The distribution of natural populations of these phototrophs, their identity and ecological role, and conversely, their value as environmental indicators was the concern of those researchers. As primary producers of the organic matter, able to fix carbon as well as nitrogen, cyanobacteria support entire microbial communities and are in that sense indeed the greater bacteria (Figure 2).

In 1959 at the 14th International Limnology Congress (SIL, Societas Internationalis Limnologiae) was hosted in Austria by Professor Franz Ruttner. During the post-congress excursion on the lake Traunsee, the Austrian phycologist Edith Kann organized a separate boattrip. On a raft constructed of two traditional dug-out boats, equipped with outboard motors, she invited a group of limnologists interested in the study of blue-green algae, to visit the cliffs on the opposite shore of Traunsee she studied at that time.

Amidst of a lively discussion that has developed on board of the raft, about the difficulties in determining the identities within that group of microscopic phototrophs, and about the need for coordinated effort in dealing with the ecology and taxonomy of the group, Professor Otto Jaag of the EAWAG/ETH Institute in Zurich, Switzerland invited the group to meet the following year at the then newly constructed Hydrobiological Laboratory in Kastanienbaum on the lake Luzern to participants at an »Arbeitssymposium« or Workshop-Symposium. Thus started the tradition of the IAC (International Association

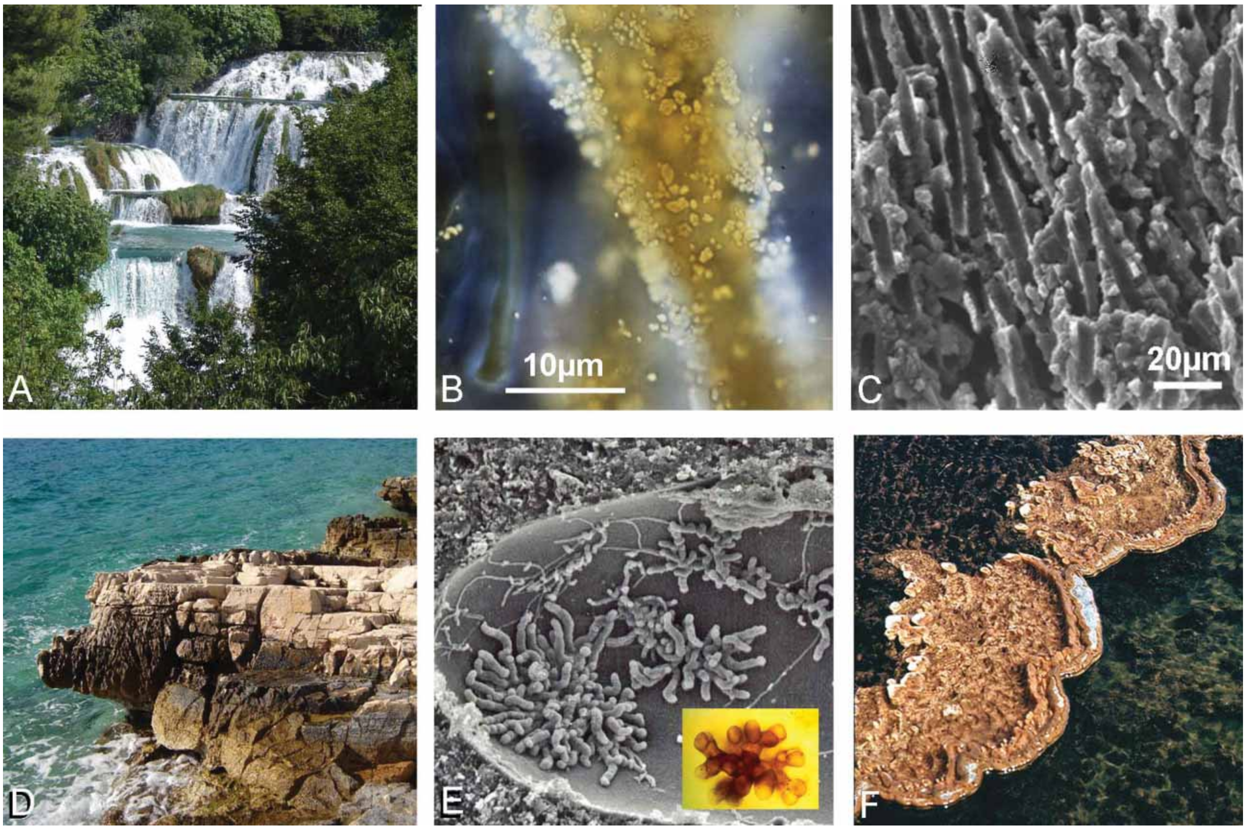

Figure 1. *Environments formed and modified by cyanobacteria. A – Cascades of calcareous tufa, river Krka, Croatia. B – Crystalls of calcium carbonate precipitating on the sheath of the cyanobacterium* Scytonema. *C – Imprint of the filaments of the cyanobacterium* Phormidium incrustatum *in carbonate precipitated around them. D – Coastal limestone colonized by zonally distributed microboring cyanobacteria. E – The insight view of a carbonate sand grain with microborings of the cyanobacterium* Hyella. *Insert: The fossil, Neoproterozoic* Eohyella, *preserved in chert. F – Silica – encrusted microbial reefs in thermal water pools of the Yellowstone National Park, USA. Each color and shape is build by a different population of cyanobacteria (conophytons are marked by arrow). The picture covers ca* $1m^2$ *area.*

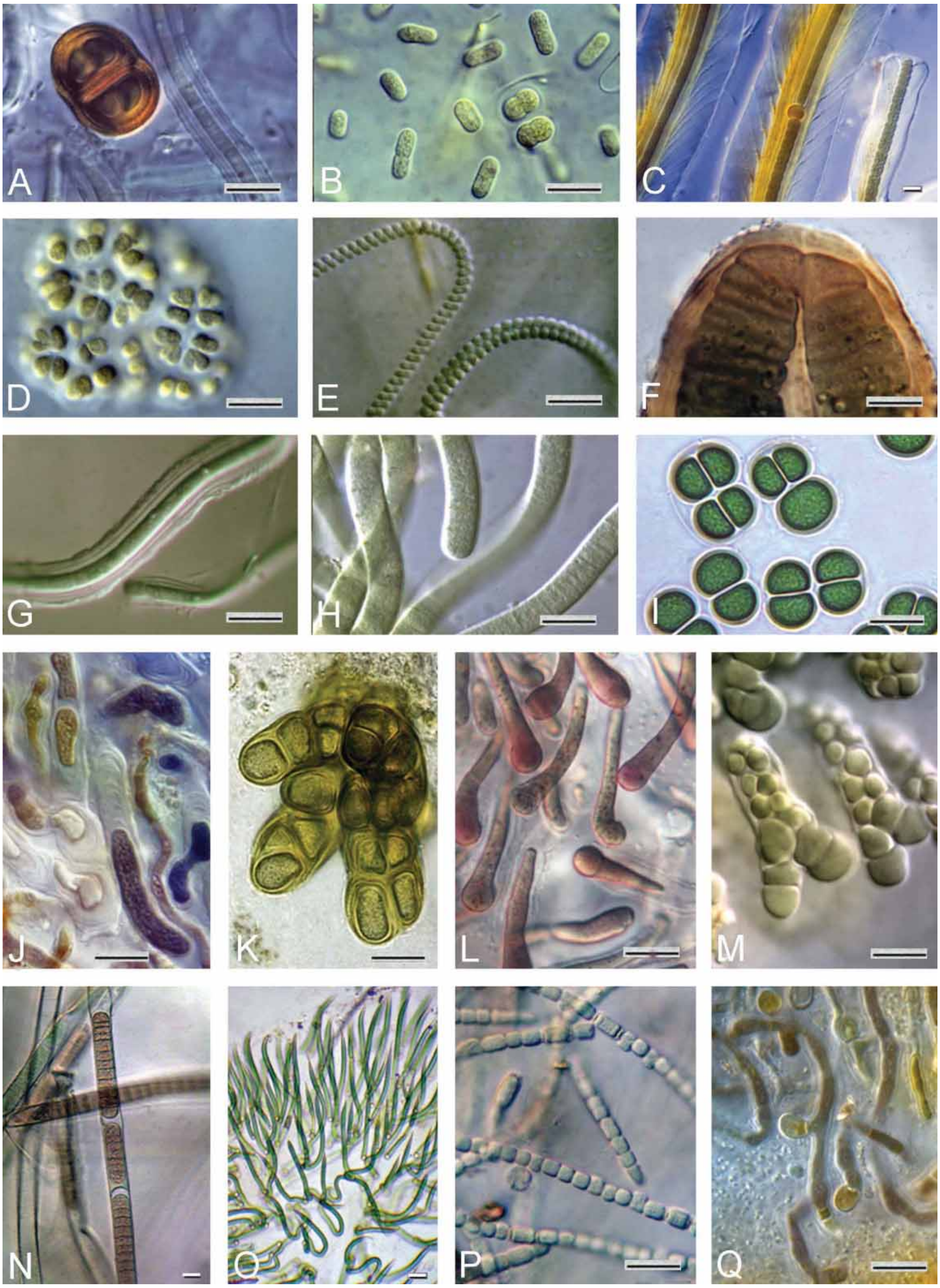

Figure 2. *Light micrographs of cyanobacterial morphotypes from various habitats. Scale bars are 10ìm long. A – Chroococcus and* Schizothrix*, Intertidal mats of Abu Dhabi UAE, B –* Aphanocapsa*, solar ponds, Eiat, Israel. C –* Petalonema alatum*, Skocjan cave, Slovenia. D –* Gomphospheria aponina*, Salt marsh, Woods Hole MA, USA. E –* Spirulina subsalsa *and* S. labyrinthiformis*, Adriatic Sea. F –* Scytonema *sp., Bermuda. G –* Schizothrix splendid*, microbial mats Abu Dhabi, UAE. H –* Oscillatoria bonnemaisonii*,coral reef, La Reunion, Indian Ocean. I –* Chroococcus submarines*, Rangiroa, French Polynesia. J –* Solentia achromatica*, Euendolith in coastal limestone, Dalmatia, Croatia. K –* Hyella balani*, wave spray zone, Adriatic, Croatia. L –* Solentia foveolarum*, marine coastal pools, Mediterranean at Marseille. M –* Hyella *sp. boring in ooid sandgrains, Bahamas. N –* Symploca hydnoides*, coral reef, New Caledonia. O –* Rivularia polyotis*, lower intertidal zone, Adriatic, Croatia. P – Marine benthic* Anabaena *sp. coral reef, Mayotte, Indian Ocean. Q –* Mastigocoleus testarum*, penetrating shells in shallow marine waters, Safaga, Egypt.*

for Cyanophyte Research) symposia, which since meet in late July or August every three years, hosted by Institutions in different countries.

The first six symposia took place in the Kastanienbaum, Switzerland with a spectacular view of the Mount Pilatus (1–1960; 2–1961; 3–1963; 4–1966; 5–1969; 6–1972); then in the castle of Lednice, Czechoslovakia (7–1976); again in Kastanienbaum (8–1979, 9–1983); then in Athens, Greece (10–1986), Plön, Germany (11–1989), Sweden (12–1992); Rome, Italy (13–1995), Lammi, Finnland (14–1998), Barcelona, Spain (15–2001), Luxembourg (16–2004) and Merida, Mexico (17–2007). The 18th IAC Symposium takes place Aug. 16–20, 2010 in České Budìjovice, Czech Republic.

The orientation of the IAC-meetings was predominantly ecological, dealing with recognition of cyanobacterial populations in aquatic and terrestrial environments. The history of the first 25 years of IAC, including brief retrospect of the first 9 symposia with bibliography was summarized by Kann and Golubic *(8)*. The proceedings of IAC-symposia with peer-reviewed contributions were published initially in the journal Schweizerische Zeitschrift für Hydrologie (Aquatic Sciences, Basel) and later in Algological Studies, Supplementa of Archive of Hydrobiology, (E. Schweizerbart Science Publishers, Stuttgart).

A different approach to deal with difficulties in separating various kinds of blue-greens was taken in the United States by Francis Drouet *(9)*. It was based on observations that many bluegreens change their appearance in response to ecological influences or pathology and lead to conclusion that only very few properties of these microorganisms are genetically stable and thus taxonomically useful while the differences in their appearance are largely caused by their pliable ways to adjust to environmental conditions forming »ecophenes«. Drouet followed botanical traditions by using strict rules of priority in naming, but drastically reduced the number of taxa, from 140 to 24 genera and from about 2000 to merely 62 species, thus creating long lists of synonymes *(10)*. A desire to reduce complex problems to simple, thus manageable levels is not new. More than a century earlier Ferdinand Cohn *(7)* described his problems of recognizing, documenting and describing distinct bacteria against the assumption of the physician Theodor Billroth who placed all bacteria into a single species, an almost mythical omnipotent germ capable of infinite transformations and causing all sorts of different diseases.

Cyanobacteria or Blue-green Algae

At its 6th Symposium in 1972, IAC welcomed Roger Stanier with his team of the Institute Pasteur, Paris, who brought the interest and expertise for the study of axenic cyanobacterial strains in culture collections. Both approaches were accepted as useful and desirable, but not mutually exclusive. Both groups accepted Geitler *(11)* but not Drouet *(9, 12)*, as a reasonable point of departure in revising the system for identifying blue-greens. It was about at that time that the term cyanobacteria, Stanier preferred, entered the common use, which persisted since then, because it so clearly expressed the prokaryotic nature of the group. Stanier's proposal, however, to submit blue-greens to the jurisdiction of the Bacteriological rather than Botanical Code of Nomenclature *(13)*, was met with resistance by researchers who favored the traditional treatment *(14, 15)*, and pointed to misunderstandings concerning the interpretations of the two approaches *(16)*. The objections included the concern that the requirement of axenic cultures for naming of cyanobacteria would discourage or exclude the study of their diversity in nature, although such cultures represented only a miniscule proportion of the total diversity of the group *(17)*. An ad hoc meeting was organized by Wolfgang Krumbein to discuss the acceptance of different approaches and possible future developments in dealing with cyanobacterial diversity *(18)* in which, among other topics, the applications of the numerical taxonomy and the Hutchinsonian niche concept in cyanobacterial taxonomy were discussed *(19, 20)*.

The problem that surfaced at that time referred to the fact that all classifications were based on phenotypic expression of genetic properties of organisms, which were not expressed the same way in axenic cultures as in the wild. Identification of cyanobacteria in cultures used different criteria for characterizing taxa, potentially leading to an emergence of a yet another system using the same names to describe different organisms. This has been largely avoided by the restrain in the use species names in designation of cultured strains, or even using some joint designations of genera, e.g. the LPP for *Lyngbya-Phormidium-Plectonema* complex *(21)*.

The common effort of different approaches was to recognize genetically stable distinctions between taxa that resulted from their evolution and thus were of phylogenetic significance from variants caused by environmental influences within the accommodation capacity of a given genome. However genotypic properties could only be seen through the veil of their phenotypic expressions. All these concerns proved exaggerated and unjustified in view of the enormous progress that has occurred since in the application of methods of molecular biology to analyze directly the genetic basis of microbial diversity, which by extension opened new avenues for the developments in microbial ecology.

Cyanobacteria, the Architects of sedimentary structures

The most conspicuous property of biogenic mineral deposits is their porosity. Early mineralization of these deposits provides for instant preservation of the rock often preserving the traces of microbial behavior of organisms that participated in its formation *(22)*. Due to its porous nature, relatively small amounts of mineral matter, when guided by organisms, produce voluminous but firm deposits, which are able to divert the river flow, build travertine barriers with lakes forming behind them *(23)*. This light but strong rock material has been long recognized and used in architecture through centuries for building the vaults of churches and cloisters. Biogenic sedimentary structures known as stromatolites fossilized and persisted through billions of years and are still forming today (Figure 1).

In calcareous tufa deposits (ambient temperature travertine), it is the rheophile nature of the aquatic mosses and their ability to anchor themselves preferentially in the rapids that causes an ecological re-arrangement of the sediment deposition *(24, 25)*. Sediment particles, including insipient carbonate precipitates become deposited in flowing water, rather than being deposited in calm portions of the river flow. Consequently, the flow is divided and the water distributed evenly across the river bed accompanied by the deposition and consolidation of carbonate. The upward accumulation of the deposit builds a series of dams with pools forming behind, ranging from cm-size in thermal overflows to large barriers across the river valleys to transform the river into a series of lakes and waterfalls. In karstic rivers such as Krka, Mrežnica and Korana with the famous Plitvice lakes and waterfalls, the porosity of the barrier is enhanced by encrusting of parabolic arches of falling water building curtains, which enclose caves of different dimensions *(1)*. Instead of physical deposition in lentic portion of the river flow, most carbonate is deposited around the organisms in the rapids in form of calcareous tufa or cold water travertine *(26)*.

Ecologically significant consequence of this process is in the formation of new habitats, each with its own set of ecological niches, introducing new biological opportunities which are not part of an average river: Lakes with planktonic, benthic and littoral communities, thermal stratification and light transparency; caves with various light and water supply regimes; waterfalls and rapids with different chemical conditions, saturation levels and dynamics (Figure 1AC).

There is a surprising effect along a relatively short distance of water passage through the travertine system: The water improves significantly in transparence, its color shifts from green to blue: The system acts like a natural water purification plant. The lakes collect the sediments like in the primary water treatment; the rapids and waterfalls provide aeration, stimulating respiration like in a secondary treatment and phosphorus co-precipitates with calcium carbonate, thus removing the critical limiting factor for algal growth.

In Carbonate depositing thermal springs, the mineral deposition and the resulting forms of deposits are smaller, the porosity is and the cyanobacteria are the main and exclusive guides of deposition. Cyanobacteria escape the burial in the precipitate by their gliding motility while leaving their gelatinous exopolymer sheaths behind, acting like structural re-enforcements of the resultant structure. In that sense, they are stressed by the product or their activity, but also adapted to the process which selectively excludes most of their competitors *(27)*.

The most important constructive role of cyanobacteria is in stabilization and consolidation of loose sediments, which goes a long way in preventing or reducing the erosion of soil and beaches. Cyanobacteria are the principal primary producers of coastal microbial mats which are able to tolerate a wide range of hypo- to hypersaline conditions across the intertidal ranges of coasts with different climates *(28, 29)*. At different stages of sediment consolidation, these mats are subject to stratification against a steep red-ox gradient in which the anoxic sediment acts as an electron resource whereas the cyanobacteria produce a layer of oxygen supersaturation above. Their action converts the sediment-water interface into a charged battery with energy used by various chemo-lithotrophs, phototrophs and organotrophs alike. In addition, there is a strong interaction in marine microbial mats between carbon and sulfur cycles, so that the lower strata in the mat are occupied by other mostly purple sulfur unoxygenic phototrophs, and sulfate-reducing bacteria, forming a multicolor banded layered mud (»Farbstreifensandwatt«). There are enormous potential energies in the construction of microbial mats, in support of microbial communities, which, in turn accelerate the degradation of organic products and promote recycling of nutrients. With the evolution of invertebrates, especially worms and crustaceans, this microbial system was first exploited and then destroyed via bioturbation, an action Dolf Seilacher termed the first »agricultural revolution« *(30)*.

Changes of the Earth's climate, especially in distribution of arid-humid seasons and regions often affected salinity and mineral solubility while the mats that adjust to these changes fossilized and preserved the historic record. More recent changes in microbial mats measured in sediment cores on central Pacific islands Kiritibati and Teraina documented a historic shift of the Intertropical Convergence Zone, which governs the distribution of tropical rains. That change did have a global impact coinciding with the »little ice age« periods in Europe between 15th and mid 19th centuries *(31)*.

Desert crust is a microbial community comprised of filamentous cyanobacteria, *Microcoleus vaginatus* that forms filaments of bundled cellular trichomes interspersed between soil particles, supported by the nitrogen-fixing heterocystous *Scytonema* species and a number of lichens. The crust is brittle when dry and easily crushed by feet of vehicle tires, but when wet it turns instantly into a coherent and elastic coating which protect the soil beneath it. In the Canyonlands National Park Utah, USA, the desert crust is pioneer vegetation covering bare sandstone surfaces where it traps the wind-blown dust and forms shallow soil patches. The seeds of grasses and gradually shrubs and bushes are added to the crust, starting a succession and expanding the vegetation cover. The textbooks state that continents were occupied by plants in the Silurian, maybe even earlier during Ordovician *(32)*, but they do not mention that they were welcomed by long established cyanobacteria-dominated desert crust, which was responsible for the existence of mature Proterozoic soils *(33)*.

Microbial films coating the periodically wetted cliffs are made of another ancient community based on cyanobacteria. In the Alps this epilithic coating follows the snow-melting seeps and rain drainage with dark »Ink-streaks« (»Tintenstriche«) *(34)*. Coccoid cyanobacteria, mostly species of the genus *Gloeocapsa* encapsulated in multiple gelatinous envelopes and filamentous *Scytonema* and *Tolypothrix* are protected from UV by extracellular pigments Gloeocapsin and Scytonemin *(35)*; their envelops retard the water loss while the cells switch to the latent state during dry periods between rains. Croatian oceanographer Ante Ercegović has started his scientific career analyzing microbial world on the rocks: The lithophytic vegetation *(36)*. He distinguished between microorganisms coating the rock surface from those that penetrated in the interior of the rock. Later Ercegović extended the study to the cliffs of the Adriatic limestone coast and described numerous previously unknown endolithic genera and species of cyanobacteria *(37)*.

Life in a grain of sand

Not all cyanobacteria are constructors and sculptors of structures like biofilms, mats, stromatolite reefs and travertin mounds. Some are equally active carvers that excavate the rock to live inside it as endoliths. Discovery of endolithic organisms in Dry Valleys of the Antarctica were made famous by Imre Friedmann *(38, 39)*, while pursuing the survival of microorganisms in the harshest conditions within the interest of NASA in exploration of life on other planet. These microbes, again mostly cyanobacteria of the genus *Chroococcopsis* were hiding in the intergranular spaces of sandstone in cold Dry Valleys as well as in the hot desert of Negev. These community are now called cryptoendoliths (cryptos = hidden), those which colonize preexisting fissure in rocks are called chasmoendoliths so to distinguish these passive dwellers from those Ercegović described as actively penetrating the rock, or euendoliths *(40)* (Figure 1D). Thus very different microbial communities live inside the hard carbonate substrates. The work of Jürgen Schneider and his students added an important component to our understanding of bioerosion. They evaluated the impact of snails, numerous tiny grazers equipped with magnetite-enforced radulas (»iron teeth«), which pursued the euendolithic cyanobacteria for food and removed fine layers of the rock in the process. As they did so, the light penetrated deeper into the rock and the bioerosion continued, which would have otherwise stopped as soon as the phototrophic cyanobacteria penetrated into the dark interior of the rock. The combined action explained also the origin of biokarst, the rugged razor-sharp coastal stretch every swimmer on the Adriatic has to pass. The dark rim over the white limestone along the coast is an internal biofilm, wall-to-wall comprised of cyanobacteria that are wrapped into their sunglass-stained envelopes (Figure 1D). Schneider and Torunski could follow the meals of gastropods beyond their grazing action, finding neatly perforated fragments as contributions to fine grain sediment fraction, after it has passed through snails *(41)*. Similar interactions between cyanobacteria and animals was intensified in tropical coral reefs where the much larger grazers among sea urchins and parrot fish have joined the action. Later research documented fine zonation of euendoliths matched by similar zonation of grazers across the gradient of tides, wave action and water supply in the formation of coastal notch *(42)* a feature that many years earlier Conrad Neumann used to determine past sea-level changes *(43)*.

Euendoliths penetrate various carbonate substrates from rocky limestone coasts (e.g. Croatian side of the Adriatic, Mediterranean at Marseille); they are in shells scattered on the seafloor, down to single grains of sand along the shoaling ooid sands of the Bahamas and the Arabian Gulf. Entire assemblages of cyanobacteria have been encountered in grains half a mm across, and many more species could be described in the shallow, illuminated waters of tropical seas *(44, 45)* (Figure 1E). In their study of ancient Neoproterozoic oolite rocks in Spitsbergen and Greenland, Andy Knoll and coworkers observed well preserved fossil endoliths that penetrated ooid grains 800 Ma ago and remained preserved in translucent amber-like chert *(46)* (Fig. 1E, insert). Geological impact of microboring cyanobacteria is treated as a part of bioerosion *(47)*.

Decifering the past: is the Present a key for the Past?

Paleontologists have often invoked the metaphore for the historic sedimentary record to be a book in which history is written layer by layer. There are few places in the world where the pages of this book were not scrambled by the past tectonic movement in the process of rearrangement of continents. However, long before the technology of radio-dating of rocks, the geologists have made an amazingly accurate reconstruction of the sequence of events over the past 550 millions of years. Five sixth of the Earth's history laid below that time mark usually referred to as the Precambrian. The sediments of that very old age were preserved on the margins of continental shields often featuring laminated structures assumed to be lithified microbial mats or stromatolites *(48)*. Stromatolites were the only structures of biological origin in sediments of that age and such structures, also called microbialites *(49)* were sought in modern environment as models on which to learn the processes that were operating in distant past *(50)*. The modern stromatolites in Shark Bay, West Australia became among the first testing grounds, which brought almost instantly two opposing interpretations of ancient stromatolites: (a) that they were an intertidal phenomenon *(51)*, which might provide a measure of ancient tidal ranges or (b) that they grew submerged and became stranded after local lowering of the sea level *(52)*. When the microbiota were studied a few years later, the model of Shark Bay actually supported both conclusions: Different microorganisms built the structures in the subtidal ranges down to 4 m depth and different ones dominated intertidal stromatolites *(53)*. Further models to explain the Proterozoic stromatolites have been located in different parts of the world and some of them were especially exciting.

Geysers in the Yellowstone National Park deposit silica in and around microbial mats, which grow lithified barriers around terraced pools of hot water, not unlike miniature Plitvice lake systems, only that these become encrusted with silica rather than carbonate. In some of these pools, the microbial mats grow small, 5 to 10 cm tall cones, which become hardened by the mineral. Among the variety of laminated sedimentary structures deposited during the vast Precambrian times, conical stromatolites called conophytons attracted special attention, because these could not be explained by any non-biological process. Conophytons did not extend into the Phanerozoic, and finding modern conophytons was of particular interest. Malcolm Walter, a leading expert in ancient stromatolite from Australia and Tom Brock the foremost American microbial ecologist described jointly the microbial roles and the construction of the cones relevant to understanding of their ancient counterparts *(27)*. They disagreed about how to name what they found, because both used the Linnean binary nomenclature to name the organisms, thermophilic cyanobacteria and the structures which they have produced. But their most valuable contribution for the interpretation of the ancient structures was that there is a genetic basis to the microbial ability to build them. The little structures changed their conical shape when they reached the surface of the pool; they widened and grew smooth rings around a tiny depression, a miniature atoll, 1–2 cm in diameter. Microscopic analysis revealed, however, a change in microbial composition at the point the morphology of the stromatolite changed. Each microorganism was a specialist, one in building the cones, the other in growing atolls. The entire setting was no more than 2 m wide, and the similarity with a coral reef was not accidental, although the work was performed by different architects (Figure 1F).

Stromatolites of Shark Bay live in a hypersaline basin, those in the Yellowstone geysers live in hot water so it was concluded that these ancient stock cyanobacteria are today able to grow mats and stromatolites only under so extreme conditions that would keep animals from gazing them away or churning their ground; that may have been the reason why stromatolites declined as the animals evolved *(54)*. Research has continued in other hypersaline settings with elevated temperatures such as the intertidal mats of Baja California and in environments with unusual chemistry, like the Pososs of the Quatro Cienegas basin, Mexico and elsewhere.

The next exciting discovery was when Bob Dill and Eugene shinn found modern stromatolites in perfectly normal sea water of the Bahamas *(55)*. Again were the cyanobacteria the responsible agents for the accretion of the sand as building material, and in promotion of stromatolite consolidation. The binding of ooid sand grains and forming the early micritic crust was carried out by a cyanobacterium, a new species described as *Schizothrix gebeleinii* in honor of Conrad Gebelein,who studied microbial mats and stromatolites especially on and around Andros Island, Bahamas *(56)*. However, the modern members of the tropical marine ecosystems interacted in the formation of these organosedimentary structures modifying the stromatolites with additional constructive and destructive elements that called thrombolytic structures *(57)*. The action of microboring cyanobacteria has also been recognized in the process of cementing stromatolitic laminae by alternating the dissolution and reprecipitation of carbonate *(58, 59)*. Cyanobacteria have apparently an edge over benthic algae, corals and other settlers in these environments even under normal salinity due to rapid sediment accretion and cementation in stromatolites, just as in other marine and freshwater carbonate-depositing settings.

Ancient Microbes »frozen« in glass

Stromatolites were ample witnesses of enormous microbial activity for most of the Earth's geological past, but they retained hardly any remains of the organisms that build them. Grains were sometimes organized and oriented and layers of sediment folded and curled so as to reflect a coherent arrangement of ancient mats. But the details showed that the actual microorganisms were obliterated by recrystallizations during diagenesis of the rocks. The inferences about them depended on studies in modern environments, which were supposed to fill the gaps in our understanding. This was in contrast to the rich information that has been extracted from calcareous and siliceous skeleton-bearing protists in the course of the Phanerozoic. This situation has changed dramatically with the discovery of microbial fossils preserved in transparent subcrystalline cherts, frozen in glass like the insects in Tertiary amber.

There were reports about the existence of microbial fossils including bacteria in Precambrian rocks e.g. by Charles D. Walcott *(60, 61)*, which were not taken seriously and studied further because, apparently, it was generally accepted that the Precambrian rocks are not fossiliferous. This view has been invalidated with the discovery of the microbiota of the 2000 My old Gunflint Iron Formation in Southern Canada by Stanley A. Tyler, who published a short note with Elso Barghoorn of Harvard University in 1954, but the acceptance of the significance of this information was still sluggish until ten years later when a well documented and illustrated contribution was about to be published by Barghoorn and Tyler *(62)* and practically at the same time by his main competitor in the search for the ancient life, Preston Cloud of the UCLA, a story very personally told by Barghoorn's former student E. William (Bill) Schopf *(63)* in the context of by then exploding international interest for Precambrian microbiata.

Major contributions in the subsequent intensified exploration of early life would need a separate review. It involved the search of the earliest microbial fossils in 3500 Ma old deposits in Western Australia, South Africa and

Greenland, early history of the Earth received sufficient attention to divide the Precambrian time slot into Hadaean, Archaean and Proterozoic, with subdivisions. The Oparin-Halden theory of the origin of life received an experimental booster by Urey-Miller experiments and the geochemical evidence supported the theories that early Earth's atmosphere must have been without free oxygen *(64)*. It was known from comparisons with the neighboring terrestrial planets and theoretical considerations that inorganic water photolysis could not possibly account for the oxygen content of Earth's atmosphere. The evidence was also present in form of ancient rocks considering mineral solubilities under anoxic vs. oxidized conditions. These combined interdisciplinary research assessments brought the inevitable conclusion that the free oxygen in the Earth's atmosphere has been a byproduct of cyanobacterial oxygenic photosynthesis.

Cyanobacteria, like later algae and plants employed a combination of two photosystems to tap the water as an almost unexhaustible supply of electrons. Phototrophy using single photosystems must have evolved earlier in different bacterial phyla. Anoxygenic phototrophs employed an ingenious principle of recycling of electrons, but the invention of using water as an abundant electron source afforded the creation of wastes, in this case, the release of oxygen into the atmosphere. For the microbial world evolved in an oxygen-free environment of the early Earth, that event must have been a devastating blow. The surviving anaerobes retreated into remaining anoxic environmental shelters and/or developed mechanisms to detoxify oxygen. Evolution of aerobic bacteria ensued with a lag, leaving an excess of buried organic matter in the sediments and increasing oxygen content in the atmosphere.

Radiometric dating of historic occurrences of Banded Iron Formations helped to determine the time span when soluble ferrous iron resided in voluminous water bodies, from where it precipitated together with silica following pulses of oxygen release. After 2000 Ma the transport of Iron in the surface waters was mainly as insoluble oxidixed particles and Fe was added to the list of limiting nutrients.

On reading the past in retrospect

In 1965 Emil Zuckerkandl and Linus Pauling *(65)* discussed the possibilities to use the molecules as archives of evolutionary history. They stated that the cumulative mutations over the evolutionary time change the genomes of two related groups of organisms differently. This record could be read to estimate the time when they separated from a common ancestor as well as the distance to which they have departed. With other words, the evolutionary history could be read in retrospect and the phylogenetic relations reconstructed from analyzing the genes of extant representatives of the groups compared. The ability to read the sequences of nucleotides has become available soon thereafter, but the selection of the appropriate genes took a little longer. The molecular sequences to be selected for phylogenetic reconstruction needed to be universal, conservative, i.e. not too variable and functionally unconstrained. It was the work of Carl Woese *(66)* and Norman Pace *(67),* who introduced 16S ribosomal RNA as such a molecule and published the first microbial phylogenetic reconstructions. The method was instantly tested by comparing known phenotypic properties of microorganisms which were now correlated with their positioning on the 16S rRNA tree *(68)*. In addition, the methodology introduced was equally suitable for analyzing axenic cultures as well as natural populations of microorganisms, which opened new avenue in the study of microbial ecology *(69)*.

Several major surprises were soon to derive from the introduction of microbial phylogenetics: (1) The deepest distinctions revealed by the 16S rRNA gene sequences separated the living world into three domains, in which the positioning of the Domain Archaea in many respects moved closer to the Eukarya than the rest of the prokaryotes, which were first called Eubacteria, and then simply Bacteria *(66)*. As a consequence, the concept of the Bacterium as formulated by Stanier and van Niel *(70)* as synonymous to Prokaryote, has obtained a narrower meaning in the system as one of the two domains of microorganisms with prokaryotic cellular organization. (2) The Darwinian Tree of Life, introduced for the first time with the backing of genetic information, revealed several points of adaptive radiation that constituted bursts of diversity, especially among bacteria and protists and appended the three of the former five kingdoms, i.e. plants, animals and fungi, at the tips of fairly recent branches. (3) Most eukaryotic organisms, including us turned out to be chimeras, composite functional entities comprised of integrated eukarian and bacterial components. Most fascinating, the engines that generate the energy for protists, plants and animals are of bacterial origin: the plastids in plants and phototrophic protists and mitochondria in almost all eukaryotic organisms. (4) The comparisons of obtained ribosomal gene sequences showed how surprisingly rich and diverse is the world around us. Within the last 15 years, the number of recognized bacterial (divisions) grew from 12 that were known for about a century, all represented in cultures to over 80 phyla, many of them known only by their genetic signatures thus earning the status of phylum candidates until the sources of those signatures are found and studied *(71)*. One of the bacterial phyla remained unique and was now acknowledged as the sole monophyletic origin of oxygenic photosynthesis: The Cyanobacteria *(72, 73)*.

Principle of Cooperation

The early microscopists paid detailed attention to cellular structures before the methods for chemical analyses, isotope fractionation, molecular sequencing and other quantitative measures were available. Ferdinand Cohn *(7)* formally proposed that the phototrophic blue-greens (Schizophyceae) and heterotrophic bacteria (Schizomycetes) belong together as representative of prokaryotic cellular organization, which he recognized by observing their mode of cell division by fission, instead by the process of mitosis, which characterized all known eukaryotic cells. This basic property of bacteria must have been known much earlier, because the name Schizomycetes was proposed first by Carl Wilhelm von Nägeli already in 1857 *(74)*. By 1883 Andreas F.W. Schimper *(75)* noticed that the chloroplasts in plant cells divide independent from the division of the cell and wondered about the nature of their independence.

Between 1905 and 1910 Constantin Sergeevich Merezhkowsky *(76, 77)* developed a comprehensive theory of symbiogenesis in which he proposed that the eukaryotic cell originated by symbiosis of independent (prokaryotic) organisms, which must have sounded incredible and bizarre as it has not been seriously considered until the very recent times. The organelles proposed to be derived from once independent microorganisms included chloroplasts and mitochondria, which in eukaryotic cells perform energy-generating functions: chloroplast using solar energy in production of organic matter by oxygenic photosynthesis, and mitochondria engaged in the release of chemical energy from the organic matter as a part of the oxidative respiration.

Lynn Margulis *(78)* was one of the few contemporary researchers, who accepted the idea of endosymbiosis as a major principle in evolution and systematically collected the evidences as these emerged in the published record. Chloroplasts just as mytochondria not only divided independent of the cells they inhabit, they were surrounded by double (and later found also triple) membrane, one possibly belonging to the endosymbiont and the other to the host. Phagocytosis has been known since early day as the mean cells engulf food particles including bacteria, and that same behavior in white blood cells has been known as a part of our defense system against bacterial invaders. It may have been the likely mechanism for endosymbiotic relations. Both, chloroplasts and mitochondria contained smaller ribosome, like those of bacteria and some DNA of their own. The fact, that a lot of the genetic information has been transferred to the nucleus as »central government« was a part of a tendency practiced by many parasites that enjoyed the products of the host's metabolism instead of producing them themselves. Different degrees of interdependence between hosts and parasites have long been known. Even distinction between the concepts of parasitism vs. symbiosis has been semantically difficult, because the latter implied moral judgment in establishing the benefit. Other examples came from intermediate stages of integration in mutual interdependence, from Glaucophytes, protists that contained almost intact cyanobacteria inside their cells, to ectosymbioses with cyanobacteria and algae in lichens, in aquatic fern *Salvinia,* in the Gymnosperm *Cycas,* to foraminifera and corals with their zooxantellae, and mollusks that delay the digestion of consumed algal chloroplasts and continue to exploit their photosynthesis.

When the sequences of the 16S rRNA gene were compared, the chloroplasts clustered together with their ancenstral relatives, the cyanobacteria. The endosymbiotic origin of eukaryotic energy generating organelles was confirmed, as was the principle of the progress in the course of evolution by cooperative combining of properties, while the often misunderstood concept of »struggle for survival« moved in the background. In analyzing protists, the most diverse group of eukaryotes, several events of endosymbiosis could now be documented: from the original incorporation(s) of an ancient proteobacterium that started the line of mitochondria, which are now maternally inherited intracellular organelles, followed later by various events of incorporation(s) of cyanobacteria, which continued their destiny as chloroplasts. Green and red algae obtained their plastids from cyanobacteria directly; other phototrophic protists, e.g euglenoids and dinoflagellates contain chloroplasts that have been incorporated repeatedly into another and yet another eukaryan host *(79)*.

Long standing dilemmas, for example, whether to classify euglenoids or dinoflagellates as algae or as protozoa, because they featured both phototrophic and organotrophic members, found a simple explanation: they had at least two lines of heritage with separate phylogenies and each was legitimate to support a »natural system«, based, as required, on evolutionary history and phylogeny. The other old dilemma around the question whether the blue-greens are algae or bacteria *(7, 70)* has experienced an inversion: It is now clear that algae as well as all green plants are by their principle function, in fact, cyanobacteria. Even the use of the term »Prokaryote« has recently been questioned *(80)*. The new and revised treatment of Prokaryote-Eukaryote relation and the meaning of the word bacterium was recently summarized by Sapp *(81)*.

Sex in greater bacteria

Like sexual reproduction, the endosymbiosis constitutes a lateral transfer of genetic information; unlike sexual reproduction, it is not intraspecific, i.e. limited to closely related organisms, in fact, in most known examples it involves evolutionary very distant partners. The free bacteria have sex, i.e. the lateral transfer of genetic information through the known mechanisms of transformation, viral transduction and conjugation has an intermediate position regarding the inter-relatedness of the partners. A similar picture is expected to occur in cyanobacteria, where most of the evidence is in support of likely transduction by viruses, which in large numbers accompany cyanobacterial blooms, some of these viruses carrying fragments of genes used in cyanobacterial photosynthesis *(82)*.

The existence of lateral transfer of genetic information places new question marks on our hopes to construct natural systems, based by definition on the tree of life that transferred that information along ever diverging forks. Inconsistencies in using the 16S rRNA yardstick to reconstruct phylogenies do continue. In the case of cyanobacteria there is evidence of speciation into finer and specialized niches that this molecule does not see *(83)*. It looks more like the life flowed more like a braded stream, never quite deciding whether to diverge or fuse, and as Doolittle stated, we could at best follow the lineages of genes which may have visited and then departed from many organisms thus contributed to the interrelatedness of organisms beyond the contribution of their ancestral inheritance *(84, 85)*.

CONCLUSIONS

In a lecture presented in 2006, explaining why we need 16S rRNA gene sequences (and other genetic tools) Roberto Kolter at Harvard University illustrated Darwin's finches with their varied beaks, that signified the speciation of the group as fostered by of natural selection, favoring specialized food exploitation. In contrast, he stated, the bacteria do not have beaks and thus require genetic markers to distinguish among them. This may be true for simple sphere16 and rod-shaped bacteria, but there is sufficient phenotypic distinction in cyanobacteria to approach them polyphasically, i.e including their phenotypic, morphological gene expression (Figure 2). True, cyanobacteria do not have beaks, but their shapes, pigments, exopolymers and their behavior are all evident, more like plumage rather than beaks of finches. These expressions of their genetic information, wherever the latter came from, whether transferred vertically or horizontally, are the warrant for their continued existence. These are the properties that matter for the selective pressures to act on, and that action takes place in nature. We are now waiting for more information of a myriad of transfers at the stages of genomics, transcriptomics and proteomics to learn about the secrets of their success. In the meantime it is rewarding to approach them the other way around, starting from the niches they successfully occupy and answer to the environmental challenges. So far the greater bacteria have done surprisingly well and are likely here to stay some of them to our chagrin and discomfort, others to earn our appreciation while we consume the product of their invention and breathe the oxygen, they first have learned to sequester, and last not least, to enjoy them esthetically. It is amazing what cyanobacteria have accomplished by joining the world of Eukaria. They made corals grow like plants, jellyfish to turn upside down, and every shrub and tree to behave as candle holders with innumerable variations of design – just to achieve the most satisfactory position for their now domesticated cyanobacteria harvesting sunlight.

Acknowledgements: *With thanks and appreciation to Croatian Society of Natural History and the honor of the Spiridion Brusina Award of 2009, and with fond memories of learning from nature with friends and colleagues in Croatia and abroad. The works were supported by the International Programs of the National Science Foundation of the USA, the Alexander-von-Humboldt Foundation, Bad Godesberg and Hanse Wissenschaftskolleg, Delmenhorst, Germany. Specialthanks are due to Dr. Gudrun Radtke, Wiesbaden, Germany for discussions, suggestions and help in writing.*

REFERENCES

1. PEVALEK I 1935 Der Travertin und die Plitvice Seen. *Verhand Intern Ver Theor Angew Limnol 7*: 165-81
2. GOLUBIC S 1957 Die Algenvegetation des Flusses Krka in Dalmatien (Croatian w. Summary in German). *Rad Jugosl Acad Sci Arts Zagreb 312*:208-259
3. GOLUBIC S, MARCENKO E 1958 Zur Kenntnis der Morphologie und Taxonomie der Gattung *Oocardium*. *Schweiz Z Hydrol 20*: 177-185
4. MATONICKIN I, PAVLETIC Z 1961 Epibiontische Verhältnisse auf den Kalktuffwasserfällen des Flusses Krka in Dalmatien. *Hydrobiologia 18*: 219-224
5. EMEIS K-C, RICHNOW H-H, KEMPE S 1987 Travertine formation in Plitvice National Park, Yugoslavia: chemical versus biological control. *Sedimentology 34*:595-609
6. COHN F 1853 Untersuchungen über die Entwickelungsgeschichte mikroskopischer Algen und Pilze. *Nov Act Acad Leop Carol 24*: 103-256
7. COHN F 1872 Untersuchungen über Bakterien. *Beiträge zur Biologie der Pflanzen 1 (Heft 1)*: 127-224
8. KANN E, GOLUBIC S 1985 Twenty five years of the International Association for Cyanophyte Research (IAC). *Algological Studies 38/39*: 3-14
9. DROUET F, DAILY W A 1956 A revision of coccoid Myxophyceae. Butler Univ. *Bot. Studies 12*:1-218
10. FRIEDMANN EI, BOROWITZKA LJ 1982 The symposium on taxonomic concepts in Bluegreen algae: towards a compromise with the Bacteriological Code? *Taxon 31(4):* 673-683
11. GEITLER L 1932 Cyanophyceae. *In*: Rabenhorst L (*ed*) Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, 14, Akad. Verlagsges., Leipzig, p 1196
12. DROUET F 1981 Revision of the Stigonemataceae: with summary of the classification of the blue-green algae. J Cramer, Vaduz, Sand WD, p 221
13. STANIER R Y, SISTROM W R, HANSEN T A, WHITTON B A, CASTENHOLZ R W, PFENNIG N, GORLENKO W N, KONDRATIEVA E N, EIMHJELLEN K E, WHITTENBURY R, GHERNA R L, TRÜPER H G 1978 Proposal to place the nomenclature of the cyanobacteria (bluegreen algae) under the rules of the International Code of Nomenclature of Bacteria. *Int J Syst Bacteriol 28*: 335-336
14. BOURRELLY P 1979 Les Cyanophycés, algues au bactéries? *Rev Algol NS 14*: 5-9
15. GEITLER L 1979 Einige kritische Bemerkungen zu neuen zusammenfassenden Darstellungen der Morphologie und Systematik der Cyanophyceen. *Plant Syst Evol 132*: 153-160
16. LEWIN R A 1979 Formal taxonomic treatment of cyanophytes. *Intern J Syst Bact 29*: 411-412
17. GOLUBIC S 1979c Einführung in die Evolution von Ökosystemen am Beispiel der Cyanophyten. I. Warum erforscht man die Blaualgen extremer Standorte? *In*: Krumbein W E (*ed*) Cyanobakterien – Bakterien oder Algen? Littmann-Druck, Oldenburg, p 85-87
18. KRUMBEIN W E 1979 Cyanobakterien: Bakterien oder Algen? Littman-Druck, Oldenburg, p 130
19. GOLUBIC S 1979a Einführung in die Probleme der numerischen Taxonomie bei Cyanophyten (Introduction to numerical taxonomy in cyanophytes). *In*: Krumbein W E *(ed)* Cyanobacterien: Bakterien oder Algen? Littman-Druck, Oldenburg, p 15-32
20. GOLUBIC S 1979b Einführung in die Evolution der Õkosysteme am Beispiel der Cyanophyten (Introduction to evolution of ecosystems exemplified by cyanophytes). *In*: Krumbein W E *(ed)* Cyanobakterien: Bakterien oder Algen? Littman-Druck, Oldenburg, p 85-87
21. RIPPKA R, DERUELLES J, WATERBURY J B, HERDMAN M, STANIER RY 1979 Generic assignments, strain histories and properties of pure cultures of Cyanobacteria. *J Gen Microbiol 111*:1-61
22. GOLUBIC S, SEONG-JOO L, BROWNE K M 2000 Cyanobacteria: architects of sedimentary structures. *In*: Riding R E, Awramik S M *(eds)* Microbial Sediments, Springer-Verlag, Berlin, p 57-67
23. GOLUBIC S 1969 Cyclic and noncyclic mechanisms in the formation of travertine. *Verh Int Verein Limnol 17*: 956-961
24. PEDLEY H M 1990 Classification and environmental models of cool freshwater tufas. *Sediment Geol 68*: 143–154

25. FORD T D, PEDLEY H M 1996 A review of tufa and travertine deposits of the world. *Earth-Science Rev 41*: 117-175

26. GOLUBIC S 1967 Zwei wichtige Merkmale zur Abgrenzung der Blaualgengattungen. *Schweiz Z Hydrol 29*: 175-184

27. WALTER M R, BAULD J, BROCK T D 1976 Microbiology and morphogenesis of columnar stromatolites (*Conophython, Vacerrilla*) from hot springs in Yellowstone National Park. *In*: Walter M R *(ed)* Stromatolites. Elsevier, Amsterdam. *Develop Sedimentol 20*: 273-310

28. PAERL H W, PINCKNEY J L, STEPPE T F 2000 Cyanobacterial-bacterial mat consortia: examining the functional unit of microbial survival and growth in extreme environments. *Internat Soc Microb Ecol 2:* 11-26

29. SECKBACH J, OREN A (*eds*) 2010 Microbial Mats: Modern and Ancient Microorganisms in Stratified Systems. Springer, Berlin, in press

30. SEILACHER A 1986 Evolution of behavior as expressed in Marine Trace Fossils. *In:* Nitecki M H, Kitchell J A (*eds*) Evolution of Animal Behavior. *Paleontological and Field Approaches*. Oxford University Press, New York, p 62-87

31. SACHS J P, SACHSE D, SMITTENBERG R H, ZHANG Z, BATTISTI D S, GOLUBIC S 2009 Southward movement of the intertropical convergence zone AD 1400-1850. *Nature Geoscience 2*: 519-525

32. HECKMAN D S, GEISER D M, EIDELL B R, STAUFFER R L, KARDOS N L, HEDGES S B 2001 Molecular evidence for the early colonization of land by fungi and plants. *Science 293*: 1129-1133

33. CAMPBELL S E 1979 Soil stabilization by a prokaryotic desert crust: implications for Precambrian land biota. *Origins of Life 9*: 335-348

34. JAAG O 1945 Untersuchungen über die Vegetation und Biologie der Algen des nackten Gesteins in den Alpen, im Jura und im schweizerischen Mittelland. *Beiträge zur Kryptogamenflora der Schweiz 9*: 1-560

35. GARCIA-PICHEL F 1998 Solar ultraviolet light and the evolutionary history of cyanobacteria. *Origins Life Evol Biosph 28*: 321-347

36. ERCEGOVIC A 1925 La vegetation des lithophytes sur les calcaires et les dolomites en Croatie. *Acta Bot Inst Bot Univ Zagreb 1*: 64-114

37. ERCEGOVIC A 1932 Études écologiques et sociologiques des Cyanophycées lithophytes de la còte Yougoslave de l' Adriatique. *Bull Internat Acad Youg Sci Arts, Cl Sc Math Nat 26*: 33-56

38. FRIEDMANN E I 1982 Endolithic microorganisms and the Antarctic cold desert. *Science 215*: 1045-1053

39. FRIEDMANN E I, OCAMPO R 1976 Endolithic blue-green algae in the dry valleys: Primary producers in the Antarctic desert ecosystem. *Science 193*:1247-1249

40. GOLUBIC S, FRIEDMANN E I, SCHNEIDER J 1981 The lithobiontic ecological niche, with special reference to microorganisms. *Jour Sed Petrol 51*: 475-478

41. SCHNEIDER J 1976 Biological and inorganic factors in the destruction of limestone coasts. *Contr Sed 6*: 1-112

42. RADTKE G, LE CAMPION-ALSUMARD T, GOLUBIC S 1996 Microbial assemblages of the bioerosional »notch« along tropical limestone coasts. *Algol Stud 83*: 469-482

43. NEUMANN A C 1966 Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*. *Limnol Oceanogr 11*: 92-108

44. AL-THUKAIR AA, GOLUBIC S 1991 Five new *Hyella* species from the Arabian Gulf. *In*: Hickel B, Anagnostidis K, Komárek J (*eds*) Cyanophyta/Cyanobacteria-Morphology, Taxonomy, Ecology. *Algol Stud 64*: 167-197

45. AL-THUKAIR A A, GOLUBIC S, ROSEN G 1994 New euendolithic cyanobacteria from the Bahama Bank and the Arabian Gulf: *Hyella racemus* sp. nov. *J Phycol 30*: 764-769

46. KNOLL A H, GOLUBIC S, GREEN J, SWETT K 1986 Organically preserved microbial endoliths from the Late Proterozoic of East Greenland. *Nature 321: 856-857*

47. GOLUBIC S, RADTKE G, TRIBOLLET A 2010 Bioerosion. *In*: Encyclopedia of Geobiology. Springer, Berlin, in press

48. WALTER M R (*ed*) 1976 Stromatolites. Elsevier, Amsterdam. *Develop Sedimentol 20:* 790

49. BURNE R V, MOORE L S 1987 Microbialites: Organosedimentary deposits of benthic microbial communities. *Palaios 2*: 241-254

50. MONTY C L V 1972 Recent algal stromatolitic deposits, Andros Island, Bahamas, preliminary report. *Geol Rundsch 61*: 742-783

51. LOGAN B W 1961 *Cryptozoon* and associated stromatolites from the Recent of Shark Bay, Western Australia. *J Geol 69*: 517-533

52. PLAYFORD F E, COCKBAIN AE 1976 Modern algal stromatolites at Hamelin Pool, a hypersaline barred basin in Shark Bay, Western Australia. *In*: Walter M R (*ed*) Stromatolites. Elsevier, Amsterdam. *Develop Sedimentol 20*: 389-412

53. GOLUBIC S 1985 Microbial mats and modern stromatolites in Shark Bay, Western Australia. *In:* Caldwell D E, Brierley J A, Brierley C L (*eds*) Planetary Ecology. Van Nostrand Reinhold, New York, p 3-16

54. GARRETT P 1970 Phanerozoic stromatolites: noncompetitive ecological constriction by grazing and burrowing animals. *Science 169:* 171-173

55. DILL R F, SHINN E A, JONES A T, KELLY K, STEINEN R P 1986 Giant subtidal stromatolites forming in normal salinity waters. *Nature 324*: 55–58

56. GOLUBIC S, BROWNE K M 1996 *Schizothrix gebeleinii* sp. nov. builds subtidal stromatolites, Lee Stocking Island, Bahamas. *Algol Stud 83*: 273-290

57. FELDMANN M, MCKENZIE J A 1998 Stromatolite-Thrombolite associations in a modern environment, Lee Stocking Island, Bahamas. *Palaios 13*: 201-212

58. MACINTYRE I G, PRUFERT-BEBOUT L, REID R P 2000 The role of endolithic cyanobacteria in the formation of lithified laminae in Bahamian stromatolites. *Sedimentology 47*: 915-921

59. REID R P, MACINTYRE I G 2000 Microboring versus recrystallization: Further insight into the micritization process. *J Sedim Res 70*: 24-28

60. WALCOTT C D 1914 Pre-Cambrian Algonkian Algal Flora. *Smithsonian Misc Coll 64 (2)*

61. WALCOTT C D 1915 Discovery of Algonkian Bacteria. *Proc Natl Acad Sci USA 1*: 256-257

62. BARGHOORN E S, TYLER S A 1965 Microorganisms in the Gunflint Chert. *Science 147*: 563-575

63. SCHOPF J W 2000 Solution to Darwin's dilemma: Discovery of the missing Precambrian record of life. *Proc Natl Acad Sci USA 97:* 6947-6953

64. BROCKS J J, LOGAN G A, BUICK R, SUMMONS RE 1999 Archean molecular fossils and the early rise of eukaryotes. *Science 289*: 1033-1036

65. ZUCKERKANDL E, PAULING L 1965 Molecules as documents of evolutionary history. *J theor Biol 8*: 357-366

66. WOESE C R 1987 Bacterial evolution. *Microbiol Rev 51: 221-271*

67. PACE N 1997 A molecular view of microbial diversity and the biosphere. *Science 276*: 734-740

68. WOESE C R, KANDLER O, WHEELIS M L1990 Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya. *Proc Natl Acad Sci USA 87*: 4576-4579

69. OLSEN G J, LANE D L, GIOVANNONI S J, PACE N R 1986 Microbial ecology and evolution: a ribosomal RNA approach. *Annu Rev Microbiol 40*: 337-365

70. STANIER R Y, VAN NIEL CB 1962 The concept of a bacterium. *Arch Mikrobiol 42*:17-35

71. RAPPE M S, GIOVANNONI S J 2003 The uncultured microbial majority. *Annu Rev Microbiol 57*: 369-394

72. GIOVANNONI S J, TURNER S, OLSEN G J, BARNS S, LANE D J, PACE N R 1988 Evolutionary relationships among cyanobacteria and green chloroplasts. *J Bacteriol 170*: 3584-3592

73. RUDI K, SKULBERG O M, JAKOBSEN K S 1998 Evolution of Cyanobacteria by exchange of genetic material among phyletically related strains. *J Bacterol 180*: 3453-3461

74. NÄGELI C W 1857 Bericht über die Verhandlungen der bot. Section d. 33. Versammlung deutscher Naturforscher. *Botanische Zeitung 15*: 1-760

75. SCHIMPER A F W 1883 Über die Entwicklung der Chlorophyllkörner und Farbkörper. *Botanische Zeitung 41*: 105–112

76. MEREZHKOWSKY C 1905 Über Natur und Ursprung der Chromatophoren im Pflanzenreiche. *Biologisches Zentralblatt 25*: 593-604

77. MEREZHKOWSKY C 1910 Theorie der zwei Plasmaarten als Grundlage der Symbiogenesis, einer neuen Lehre von Entstehung der Organismen. *Biologisches Zentralblatt 30*: 277-303, 321-347, 353-367

78. MARGULIS L 1968 Evolutionary criteria in thallophytes: A radial alternative. *Science 161*:1020-1022

79. FALKOVSKY PG, KATZ M E, KNOLL A H, QUIGG A, RAVEN J A, SCHOFIELD O, TAYLOR F J 2004 The evolution of modern eukaryotic phytoplankton. *Science 305 (5682)*:354-360

80. PACE N 2008 Problems with »Prokaryote«. *J Bacteriol 191*: 2008-2010

81. SAPP J 2005 Bacterium's place in nature. *In*: Sapp J (*ed*) Microbial Phylogeny and Evolution, Concepts and Controversies. University Press, Oxford, p 3-52

82. ZHAXYBAYEVA O J P, GOGARTEN J P, CHARLEBOIS, R L, DOOLITTLE W F, PAPKE R T 2006 Phylogenetic analyses of cyanobacterial genomes: Quantification of horizontal gene transfer events. *Genome Res 26(9)*: 1099-1108

83. ABED R M M, PALINSKA K A, CAMOIN G, GOLUBIC S 2006 Common evolutionary origin of planktonic and benthic nitrogen--fixing oscillatoriacean cyanobacteria from tropical oceans. *FEMS Microbiol Letters 260*: 171-177

84. DOOLITTLE W F 1999 Lateral Genomics. *Trends Cell Biol 9*: M5-M8

85. GOGARTEN J P, DOOLITTLE W F, LAWRENCE J G 2002 Prokaryotic evolution in light of gene transfer. *Mol Biol Evol 19*: 2226-2238