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Areas of distribution in Cyanobacteria; specificity of the cyanoprokaryotic microflora in the Mediterranean region

Abstract

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Cyanoprokaryotes have had a chance to colonise almost all biotopes over the biosphere during their long existence from early Precambrian till present time, without loss of their vitality and diversity. Their evolution is a continual and rapid process of adaptation to changing environmental conditions, but in the range of the certain cyanobacterial genetic and structural pattern. As a consequence of this process, numerous genotypes and morphotypes (morphospecies) arise, which are strictly ecologically delimited. In principle, they did not have any ubiquitous species within cyanobacteria. The cosmopolitan species exist, but only these ones, which are ecologically connected with corresponding cosmopolitan distributed biotopes (saline coastal swamps, eutrophic freshwater reservoirs, soil biotopes, etc.). And, of course, numerous species exist restricted in specialised and extreme biotopes and endemic in various local biotopes with specific conditions. - Numerous ecological types of cyanobacterial microflora are present in Mediterranean region. Cosmopolitan and wide-spread species occur particularly in plankton of eutrophic reservoirs and in soils. Special cyanobacterial assemblages are present in other habitats (sometimes microhabitats). Marine calcareous coasts (with endolithic types), saline and mineral inland waters (sometimes hypersaline localities), deserts, calcareous subaerophytic and wetted rocks, and volcanic substrates (wetted volcanic rocks, volcanic localities, lava soils, thermal springs) belong to prominent biotopes with communities with high number of ecologically delimited species and often with endemic types in Mediterranean region. Cyanobacterial biodiversity from all these localities contains lot of differently diversified and adapted species, but it is still little known and needs special studies and protection.

Introduction

Cyanobacteria are the oldest oxyphototrophic (plant) organisms over the world. They developed in early Precambrian and survived up to present time without loss of their vitality and diversity. They have had the chance to colonise almost all habitats in the biosphere over hundreds million years, and they were considered as world-wide distributed. However, their evolution is a continual adaptation process to changing conditions in the Earth biosphere according to the schematic principle "variation in the given theme". Their morphology did not change substantially over the long period of their existence, but they

diversified enough, and numerous different morpho- and ecotypes are recognisable. It was proved recently that they are able to diversify and adapt quickly to changed environmental conditions (like other prokaryotic bacterial organisms), and to form stable new ecotypes under drastically changed conditions. From all these facts follows that in various (sometimes very extreme) biotopes a wide spectrum of cyanobacterial types occurs, distinguishable according genetic, biochemical, ecophysiological and phenotypic characters. Cyanobacteria are not ubiquitous and occur in numerous morphotypes with very strictly delimited ecological demands. The distribution of different cyanobacterial types depends therefore on the distribution of corresponding ecological conditions.

The ecological diversity and specificity of cyanobacteria is not commonly known and accepted. The simple morphology of cyanoprokaryotes and the fact, that analogous morphological types existed already from the beginning of cyanobacterial evolution (Schopf 1974; Schopf in Pennisi 1994) led to the conclusion, that only few genotypes can occur (in many modified morphotypes) quite arbitrary under various conditions (Drouet & Daily 1956; Drouet 1968, 1973; Castenholz 1992; etc.). The species ecology is underestimated also in main cyanobacterial monographs of the 20th century (Geitler 1932; Desikachary 1959; etc.), and the ubiquitous and cosmopolitan character of cyanobacteria is commonly accepted. However, the modern molecular and taxonomic data are in contradiction to this concept. The proved genotypes evaluated by 16s rRNA sequencing correspond almost exactly to clusters on the traditional generic level, and inside of these clusters we find many stable morpho- and ecotypes connected with distinct and delimited ecological conditions. The insufficiently evaluated diversity of cyanoprokaryotic microflora, particularly from tropical areas and extreme biotopes, many mistakes (misinterpretations) and diverse concepts of many types in literature are the logical consequence of this situation.

Objectives

Diversification strategy:

One from the most interesting problems of the present cyanobacteriology is the explanation of the diversification and speciation strategies from Precambrian to present time. Such evolution processes have a character of continually changing and adapting populations, which stabilise under changed conditions for period, in which the convenient conditions are preserved. This process, called "static evolution" according to Schopf (Schopf 1974; Schopf & Golubić in Pennisi 1994), is probably the main reason of surviving of cyanoprokaryotes during the long period.

Two strategies were discovered recently explaining the diversification of cyanobacteria. Cyanoprokaryotic organisms are asexual, but the extracellular exchange of genetic material within populations was detected in several planktic genera (Rudi & al. 1998; Barker & al. 2000). This strategy can explain the existence of more genotypes in morphologically and ecologically uniform populations (Waterbury & al. 1986; Hayes & al. 1997) and easier adaptation to changed conditions. Certain molecular affinities, found between morphologically different types from the same extreme conditions and indicating the relationship

of cyanobacterial morphotypes developing in the same habitat (Garcia-Pichel & al. 1998), can be connected also with this strategy.

The second important process in cyanoprokaryotic diversification is the easy and very rapid physiological adaptation to changed environmental conditions, and stabilisation in new conditions. Each ecotype (ecospecies, morphospecies) and each cyanobacterial population is, in principle, composed from numerous individual deviations (Kondrateva 1968; Rippka & al. 1979; Kohl & Nicklisch 1981; Kato & al. 1991; Komárek 2001, etc.). If the principal conditions remain unchanged, or if this type is transferred in similar corresponding locality, the character of a morphotype remains unchanged for a long period. Under changed conditions, which still enable survival near the limiting conditions, the morphology, cytology, all ecophysiological and biochemical characters and finally also the genotype can be changed (Komárek & al. 2002). This process is rapid as in all prokaryotic organisms and yields a lot of separated ecotypes, particularly in specialised microbiotopes. If corresponding conditions are widely present over the biosphere (saline swamps, eutrophic freshwater water bodies, several soil types, etc.), the adapted ecotypes can have cosmopolitan distribution, but only in corresponding conditions. In contrast, endemic species can be developed in isolated and specialised microbiotopes. All the cyanobacterial genotypes and stable morphotypes have therefore their own ecological niches. From all these facts can be summarised the following conclusions:

1. Cyanoprokaryotes have a wide adaptability, which enabled their survival over hundreds millions years without lost of their vitality.
2. They are able to adapt quickly to changed environmental conditions. Changes in both phenotype and genotype characters are dependent on adaptation processes.
3. The present cyanoprokaryotic diversity represent a set of ecologically delimited genotypes and morphotypes.
4. The cyanobacterial genotypes/morphotypes have therefore very delimited ecological limits in nature (numerous examples are available).
5. Ubiquitous types do not exist.
6. Ecology is an integral part of cyanoprokaryotic classification; in different biotopes numerous different cyanobacterial eco- and morphospecies exist.

Examples of species distribution:

The widely distributed species, occurring in "common" habitats were found often with cosmopolitan distribution. But also such types have delimited ecology. Their world-wide distribution is therefore conditioned by the distribution of conditions, convenient for corresponding morpho- and ecotypes. The cosmopolitan species are represented mainly by the types connected with soils, freshwater eutrophic waters, polluted streams, several sub-aerophytic biotopes, etc. Several examples:

- The genus *Microcystis* is distributed in freshwater eutrophic phytoplankton. According to modern investigations, all the morphotypes were found genetically very uniform (see, e.g., GeneBank of NCBI) and several authors consider the whole *Microcystis* as mono-

specific (Otsuka & al. 2000). However, several different and clearly distinguishable morphotypes (traditional species) occur within this genus with different morphology, ecology, life cycles, toxicity and distribution (Tables 1, 2). The commonest water-bloom forming and cosmopolitan is *Microcystis aeruginosa*, which, however, has characteristic life cycle (Reynolds & al. 1981), occurs only in eutrophic water reservoirs of distinct type, and grows only in temperate and tropical zones (it lacks in subpolar and polar regions).

- Similar situation is in the genus *Planktothrix*, also with almost "cosmopolitan" *P. agardhii* and with numerous other morphospecies with diverse ecological requirements and different areas of distribution (Table 3).
- Characteristic are species with cosmopolitan distribution, but occurring only under very specialized ecological conditions. Several examples are selected in Table 4.

More common are species, which have restricted areas of distribution. They are ecotypes, which need specialised habitats. Endemic species can occur particularly in various

Table 1. Part of phylogenetic tree with the genus *Microcystis* (derived from GeneBank of NCBI); the differences between various morphospecies are quite irrelevant. However, different morphospecies have different areas of distribution, sometimes with different ecology.

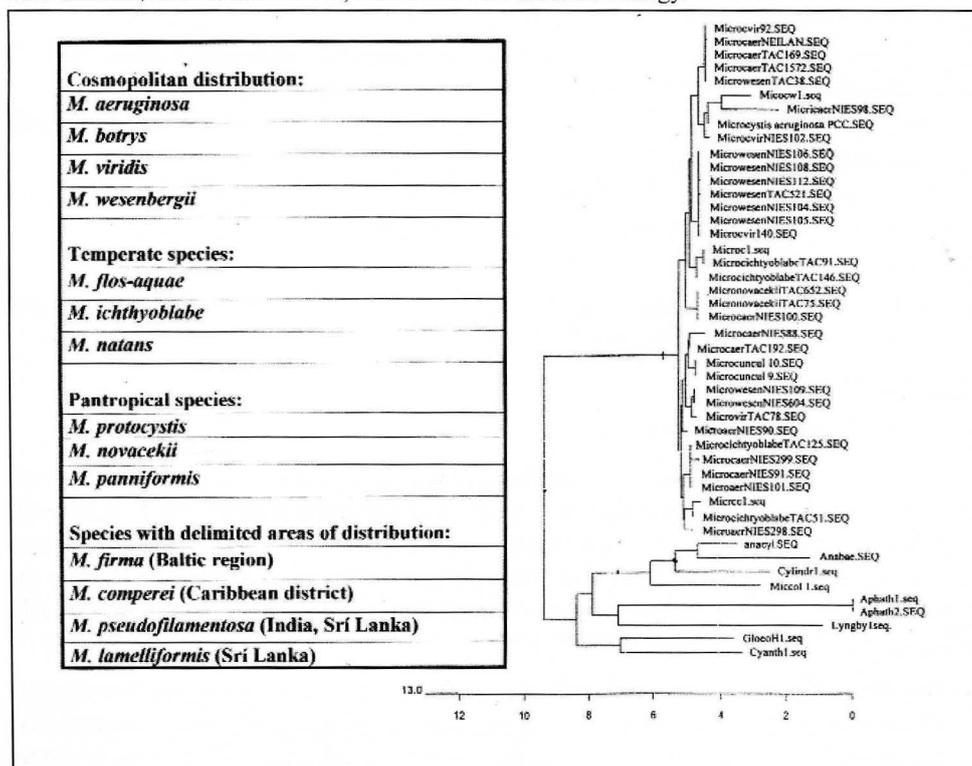
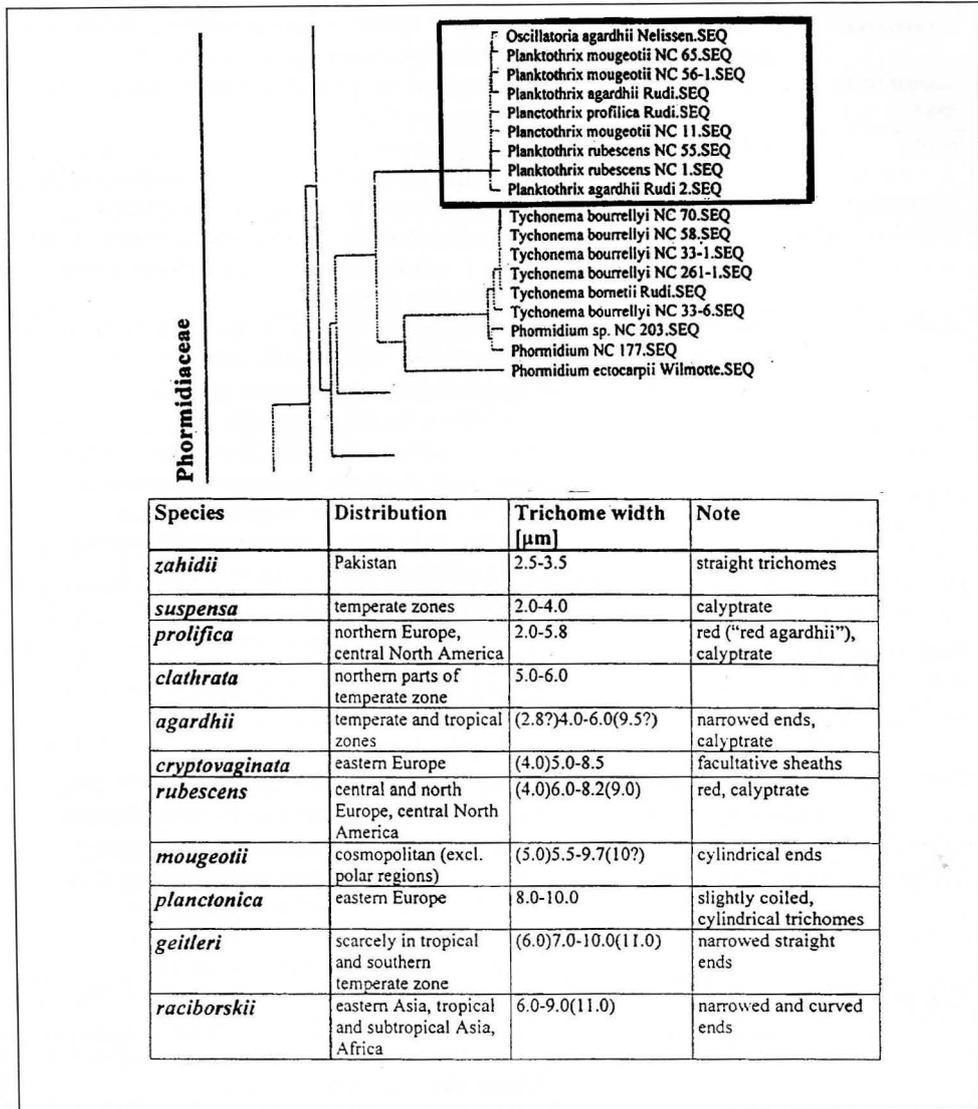


Table 2. Main morphospecies of the genus *Microcystis* occurring in Europe.

Morphospecies	Cell size (μm)	Shape of colonies
<i>aeruginosa</i> (cosmopolitan species)	(3.5)4-6.5(9.4? before division)	Irregular in outline, lobate and with distinct holes (old colonies); cells densely agglomerated; mucilaginous envelopes diffluent, slightly overlapping cell agglomerations.
<i>botrys</i> (cosmopolitan species)	4.9-6(7)	Cells agglomerated in \pm spherical subcolonies, which are often joined irregularly together, without holes; cells densely aggregated, few ("expulsing") in enveloping slime; mucilaginous envelopes wide, distinct, usually radially structured with irregular, not refractive margin.
<i>flos-aquae</i> (temperate zones)	(3)3.5-4.8	Colonies usually solitary, irregularly spheroidal, without holes; cells very densely and homogeneously agglomerated; slime diffuse, not overlapping the margin of cells.
<i>ichthyoblabe</i> (northern regions and temperate zones)	2-3.2(3.8)	Young colonies spheroidal, later irregular, without holes, often flattened, disintegrating in masses of solitary cells, with very irregular outline of colonies; cells agglomerated regularly, \pm densely; slime indistinct, not overlapping cells, diffuse.
<i>novacekii</i> (tropical and facultatively in temperate zone, summer)	2.4-6	Colonies always in outline \pm spherical and slightly flattened, sometimes aggregated together; cells \pm densely concentrated in the centre, few "expulsing" cells in enveloping mucilage; slimy margin wide, delimited, homogeneous or indistinctly concentrically lamellated.
<i>panniformis</i> (tropical species, similar populations in South Europe?)	(2.5)3-4.6(4.8)	Young colonies spherical, later irregular, distinctly flattened up to monolayers with irregular outline and small holes, disintegrating in small groups; cells regularly agglomerated, often in indistinct rows; mucilage not overlapping cells, diffluent.
<i>protocystis</i> (tropical species)	(3)3.5-6.5(7.2)	Colonies irregular in outline, without holes (or very indistinct); cells distributed sparsely (always, in vegetative stage); mucilage overlaps widely the cells, fine, unstructured, diffuse at the margin.
<i>viridis</i> (cosmopolitan species)	(3)4-7.9	Colonies composed from typical packet-like (almost cubic) subcolonies, irregularly agglomerated together; cells arranged irregularly, clearly three-dimensionally, indistinctly in perpendicular rows; mucilage overlaps slightly cells, at the margin wavy and refractive.
<i>wesenbergii</i> (cosmopolitan species)	4-8.5(10)	Young colonies spherical, later irregular, lobate, with holes when old; cells sparsely to densely agglomerated, often near the surface of subcolonies; mucilage overlapping cells, delimited, with smooth, intensely refractive margin.

Table 3. The morphospecies of the genus *Planktothrix* are genetically almost identical (from GeneBank of NCBI). However, the different morphospecies have different distribution and ecology.



extreme conditions. The example is *Geitleria calcarea*, see in Table 4. It is possible to conclude, that (I) areas of distribution of cyanobacteria reflect areas of distribution of ecological situations convenient for corresponding species, and (II) specific and endemic species occur under specific conditions, especially in tropical and extreme habitats (deserts, hyper-saline localities, thermal waters, polar regions, specialised tropical sites, etc.).

Table 4. Examples of cosmopolitan cyanobacterial species with special ecological demands.

<i>Cyanotheca aeruginosa</i>	peaty bogs, cold, stenotherm	mainly temperate, subpolar and polar regions, rarely in highest mountains in tropical areas
<i>Gloeocapsa sanguinea</i>	subaerophytic, granitic wetted rocks, high mountains	high mountains (Alpine zone) over the world
<i>Nodularia harveyana</i>	halophilic, thermotolerant, saline swamps	marine coastal areas and inland salines over the world, incl. Antarctica
<i>Mastigocladus laminosus</i>	hot springs (40-72°C)	Iceland, central Europe, Greece, Israel, Indonesia, Japan, Kamchatka, New Zealand, Antarctica, Yellowstone, etc.
<i>Geitleria calcarea</i>	caves with distinct humidity and temperature, restricted illumination	Cook Islands, Israel, France, Romania, Spain, USA – Florida, ancient Yugoslavia

Examples of cyanobacteria from extremalized biotopes:

The cyanobacterial microflora of different regions is composed from species (morpho- and ecotypes) with different ecological demands and, consequently, with different areas of distribution. Higher number of endemic species (Tables 5, 6) occurs in rare biotopes and in tropical and extreme regions. In many tropical countries is the cyanobacterial microflora very little known and if it is carefully analysed, numerous not yet defined species are found (Table 7).

Unfortunately, the morphological simplicity of cyanobacteria, the lack of good floristic-taxonomic papers from many regions, and the lack of modern identification keys cause the application of traditional European keys in very distant regions for identification. The names of similar taxa are applied usually arbitrary, and the ecology is terribly neglected. From many examples is mentioned the genus *Chlorogloea* (Komárek & Montejano 1994;

Table 5. Review of cyanoprokaryotic species studied from selected habitats in state São Paulo, Brazil, in years 1997-1999 (in%).

	cosmopolitan (identified)	tropical (identified)	unidentified
Soils	42%	39%	19%
Planktic species	38%	44%	18%
Streams	13%	15%	72%
Subaerophytic (wet rocks)	23%	8%	69%
Subaerophytic (tropic. forests) "Mata atlantica"	—	9%	91%
"Restingas"	—	—	100%
Mangroves	—	35%	65%

Table 6. Review of cyanoprokaryotic species from Antarctic King George Island (South Shetland Islands, maritime Antarctica); number of species and %.

Number of registered species	68	
Antarctic (endemic) species	16	23%
Cosmopolitan species (widely distributed)	13	19%
Evidently new species	10	15%
Not identified	29	43%

Table 7. Number of endemic cyanoprokaryotic species (in %) from tropical and extreme biotopes (examples).

Region and biotope	Identified species („cosmopolitan“)	Identified, ± endemic species	Unidentifiable species
Volcanic lakes in Mexico (Puebla state)	21.4%	15.1%	63.5%
Tolantongo hot springs (central Mexico)	7.2%	3.0%	89.8%
Freshwater biotopes in central Mexico	26.2%		73.8%
Freshwater species in São Paulo State, Brazil	24.0%	20.0%	56.0%
Tropical lakes, planktic species (H. FERNANDO's coll.)	20.0%	± 45.0%	± 35.0%
Freshwater <i>Anabaena</i> -species, Cuba	5.9%	70.6%	23.5%
Okavango swamps, S. Africa (G. CRONBERG's coll.)	12.2%	30.6%	57.2%
S. Shetland islands, Antarctica	19.0%	38.0%	43.0%

Komárek 2001). In Geitler's (1932) monograph are only two freshwater species, from which *C. purpurea* has very unique phenotype characters (red cells, colonial morphology) and very specialised ecology. The second species, *C. microcystoides* from cold limestone Alpine streams, seems to be more variable. Therefore, many authors, who found later similar morphotypes in very different habitats and very distant regions, used this name for designation of their populations without proof of their identity, and often also morphologically diverse. It is impossible to suppose, that morphologically similar, but different populations, which occur in Alpine streams, hot springs, saline biotopes, on stems of palms, and in glacial pools in Antarctica can belong to one and the same genotype (Table 8).

Table 8. Review of localities of *Chlorogloea microcystoides*, derived from various authors. The very diverse ecology is improbable.

<p>GEITLER 1932: <i>Chlorogloea microcystoides</i> - alpine streams, periphyton on limestone <i>Chlorogloea purpurea</i> - alpine lakes, benthic, limestone</p>
<p>Examples from literary data (<i>Ch. microcystoides</i>): BISWAS 1936 - epilithic in streams in Assam, India SAMPAIO 1941 - brackish waters, Portugal GONZALEZ GUERRERO 1946 - subaerophytic on trunks of palms, S. Spain SKUJA 1949 - epiphytic in swamps, Burma COMPÈRE 1970 - small pools in Ennedi, Chad KOGAN 1973 - thermal springs, Tourkmenistan BOURRELLY 1984 - epilithic in streams, New Caledonia CHU & al. 1991 - thermal springs, China VINO CUR & PIZARRO 1995 - glacial pools, Antarctica</p>
<p>Our samples - morphologically different types:</p> <ul style="list-style-type: none"> ■ Austria, Alps, calc. streams, 2 localities - typical <i>Ch. microcystoides</i> ■ Himalayas, cold streams above 4-5000 m a.s.l. - 1 unident. species ■ Mexico, alkaline swamps - 1 unident. species ■ Czech Republic, subaerophytic, travertines - 1 unident. species ■ Egypt, epipsammic in hypersaline lakes - 1 unident. species. ■ Mexico, warm streams in limestone areas - 2 unident. species

It is possible to summarise, that in extremalized biotopes increases the number of specialised types. If similar conditions are more distributed in the biosphere, corresponding species can be distributed in such localities. However, numerous endemic or subendemic species can be common in distinctly specialised biotopes.

Distribution of cyanoprokaryotes in Mediterranean region

Mediterranean region has a transitional character from the point of view of distribution of freshwater algae. The countries are situated between numerous seas, the freshwater biotopes are not common and the existence of vast, very arid regions separates the freshwater biotopes of this area from the diverse tropical microflora, which could be a source of expanding species. While nordic regions and central-European water bodies have several common cyanoprokaryotic assemblages and characteristic set of dominant species, the composition of cyanobacterial phytoplankton in reservoirs of the Mediterranean countries is difficult to characterise yet. Of course, the diaspores of cyanobacteria are easily transferable and various thermophilic or thermotolerant types can occur here in mass development, but the uniform character of freshwater phytoplanktic communities is not

definable. In spite of it, numerous very special biotopes occur in Mediterranean region, with well developed cyanobacterial communities.

Several examples of important cyanobacterial habitats.

1. *Freshwater planktic types:*

Distribution of common and widely distributed planktic species is dependent in certain degree on the easy transport of diaspores, and invasions of various species. Especially thermophilic (tropical) species, invading to temperate zone, appeared in last decades in warm areas of Europe. The phenomenon of global climatic changes with eutrophication of the biosphere play evidently substantial role in distribution of several species and Mediterranean region is important for transport of such species.

The natural freshwater stagnant waters are not too common in Mediterranean countries. The artificial reservoirs are of similar character as lakes, but the algal phytoplanktic communities seem to be here less developed and less stable. The lakes (Spain, Italy, Greece) are intensely studied recently, and it is interesting, that the phytoplanktic communities from eastern and western Mediterranean seem to be more rich and more diverse, than the cyanobacterial assemblages from the central part (Sicily, Apennin peninsula). This state is probably connected with migration ways of water birds, which prevail in marginal eastern and western parts of Mediterranean area (Fig. 1).

The phytoplanktic cyanobacteria in freshwater heliothermal (and sometimes periodically drying) stagnant waters in Mediterranean countries belong usually among common species (*Microcystis aeruginosa*, *Planktothrix agardhii*), or invasive types transported in last years mainly from tropical regions appear (e.g., *Arthrospira maxima*, or toxic *Microcystis panniformis*, *Cylindrospermopsis raciborskii*, etc.). The study of phytoplankton diversity and seasonality is highly recommendable in all Mediterranean countries.

2. *Subaerophytic communities:*

The subaerophytic cyanoprokaryotic assemblages develop mainly on wet rocks. They have a rich diversity in limestone areas, which are common in Mediterranean region. Numerous communities with several specificities in different regions occur here. However, the specificity of this microflora in Mediterranean region is not well known. They exist only few articles concerning natural biotopes of this type (Abdelahad & Bazzichelli 1991), and misinterpretations in identification complicate the orientation in species diversity. It seems, that aside of cosmopolitan or widely distributed species (from the genera *Gloeocapsa*, *Cyanosarcina*, *Leptolyngbya*, etc.) also endemic (thermotolerant) species occur (*Homoeothrix balearica* in original concept, *Chroococciopsis fissurarum*, and others).

To this category belong also the cyanobacterial assemblages from walls of historical monuments and buildings, where they play very negative role in destruction of their substrate. This microflora is more known in respect to their importance (examples of several papers: Anagnostidis & Roussomoustakaki 1983 from Greece; Albertano 1993 from Italy; Noguerol-Seoane & Rifon-Lastra 1996 from Spain), but the whole diversity is still little known. Another interesting sites with special aerophytic cyanobacterial microflora are caves, in which several specialised species were found. Several Mediterranean regions seem to be rich on this microflora (Hernández-Mariné & Canals 1994; Hernández-Mariné & al. 1999; etc.).

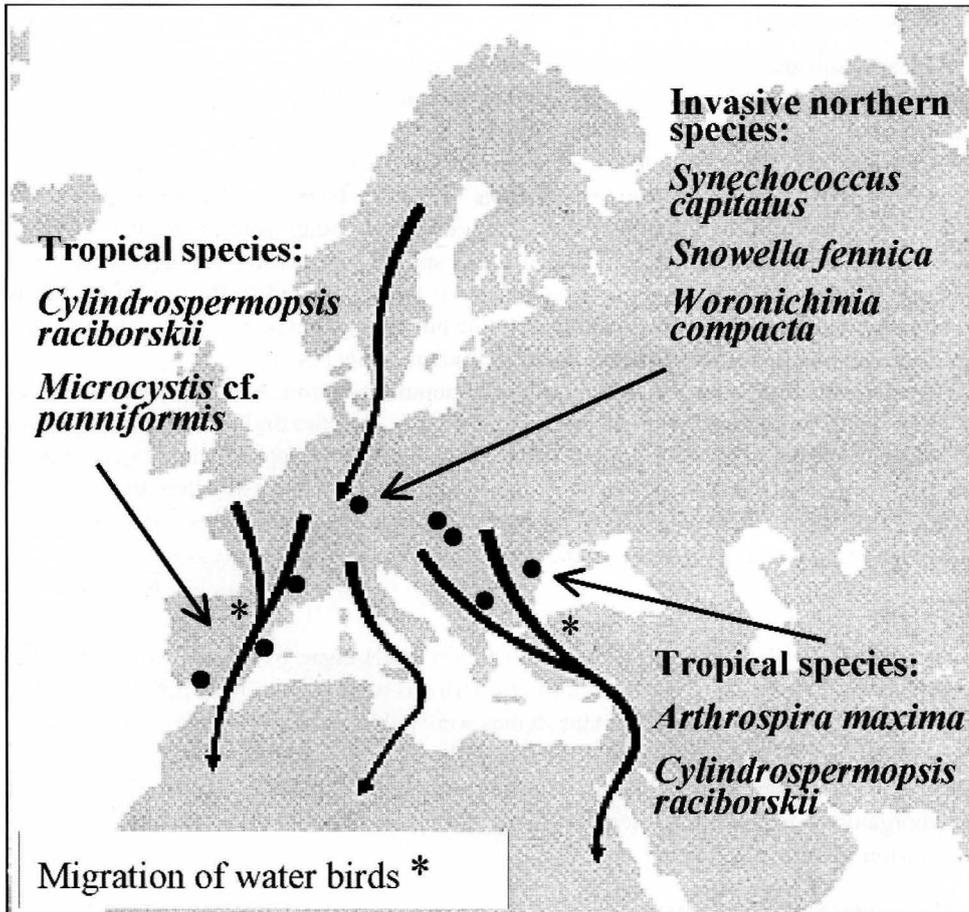


Fig.1. Main migration ways of European water birds with main localities of few tropical invading cyanobacterial species. (The map according to Cloudsley-Thompson 1978).

3. Calcareous coasts:

The endolithic, epilithic and epiphytic marine cyanoprokaryotic microflora contain quite specialised geno- and morphotypes with interesting life cycles and seasonality. It was discovered at first by the Croatian phycologist Ercegović in Dalmatia (1925, 1929, 1932, etc.), and later in almost all littoral zones over the world with a pretty wide diversity of species, particularly in warm zones. These types occur commonly in all rocky shores in Mediterranean seas, but they were studied sporadically by later authors. Most important are papers of LeCampion-Alsumard (1969, 1979) from France and Pantazidou (1991) from Greece. However, the whole diversity and ecology of these communities has still many white places. Various species with cosmopolitan, or geographically restricted, or endemic distribution can occur in these habitats, as it follows from up to date published results.

4. *Volcanic habitats:*

Volcanic substrates represent little known biotopes over the world, where cyanobacterial assemblages quickly develop and contain very interesting types. Mediterranean volcanic regions (e.g., islands of southern Italy, NE Sicily, Santorini Island in Greece) belong to "classical" localities of volcanic cyanoprokaryotes, and several morphospecies were described from there many years ago (studies of Borzi). However, it does not exist any modern revision of these localities (with exception of one study from Santorini). Volcanic biotopes (rocks, soils, solfataras, cold and hot springs) represent very specialised and extreme habitats, and the study of cyanobacterial types, adapted to this environment, is extremely important. The exception are only the hot springs in Greece, the cyanoprokaryotic flora of which was described in detail by Anagnostidis (1961).

The diversity and relations of cyanobacterial populations from Mediterranean localities of other volcanic regions is little known. Interesting is, e.g., the find of *Eucapsis terrestris* in Santorini Island, described originally from volcanic soils in Japan. Among cyanobacteria from volcanic habitats is probably the same situation, like in other extremalized biotopes: the both widely distributed species as well as endemic species can there occur. However, corresponding detailed studies are still lacking.

5. *Deserts:*

The relatively rich literature exist about desert (soil) algae over the world, including cyanobacteria. However, the whole northern Africa is almost unknown from this point of view. Several prominent and important studies were published from Israel (especially from Negev), but other Mediterranean localities are almost untouched from phycological point of view. The desert cyanobacteria represent again ecologically interesting group of microorganisms adapted to water deficiency and desiccation stresses, and important for succession in arid soils.

6. *Saline and mineral waters:*

The long coastal line of Mediterranean sea is rich on different types of saline swamps, lakes and mires. Only few localities were studied more intensely (Solar Lake in southern part of Sinai Peninsula, several papers concern hypersaline localities in Greece and NE Africa), and yielded lot of remarkable results concerning cyanobacterial microvegetation. From heliothermal salines were described numerous species, from which several are widely distributed (e.g., *Myxosarcina salinum* and *Limnothrix hypersalina*, both described from Solar Lake), or can be endemic. Examples are, e.g., *Chlorogloea pharaonis* from desert lakes in Wádí Natrun in Egypt, *Cyanothece halobia* from coastal saline swamps in Greece, *Cyanothece shiloi* from Solar Lake, or *Arthronema africanum* known only from inland, seasonal saline lakes of oasis Waw en-Namus in Libya and from Kuwait. Also this vegetation needs urgently further studies, as the whole algal microvegetation in Mediterranean region.

References

(Note: The following citations do not represent bibliography of Mediterranean cyanobacteria. The few important examples are only included).

- Abdelahad, N. & Bazzichelli, G. 1991: The genus *Gloeocapsa* Kütz. (*Cyanophyta*) on calcareous rock surfaces in the upper Valley of the river Anine (Latium, Italy). — *Crypt. Bot.* **2/3**: 155-160.
- Albertano, P. 1993: Epilithic algal communities in hypogean environment. — *Giorn. Bot. Ital.* **127**: 386-392.
- Anagnostidis, K. 1961: Untersuchungen über die Cyanophyceen einiger Thermen in Griechenland. — *Inst. Syst. Bot. Pflanzengeogr.*: 322. — Thessaloniki.
- & Roussomoustakaki M. 1983: Epilithic and chasmolithic microflora (*Cyanophyta*, *Bacillariophyta*) from marbles of the Parthenon (Acropolis-Athens, Greece). — *Nova Hedwigia* **38**: 227-287.
- Barker, G. L. A., Handley, B. A., Vacharapiyasophon, P., Stevens, J. R. & Hayes, P. K. 2000: Allele-specific PCR shows that genetic exchange occurs among genetically diverse *Nodularia* (*Cyanobacteria*) filaments in the Baltic Sea. — *Microbiology* **146**: 2865-75.
- Castenholz, R.W. 1992: Species usage, concept and evolution in the *Cyanobacteria* (Blue-green algae). — *J. Phycol.* **28**: 737-745.
- Desikachary, T. V. 1959: *Cyanophyta*. — Pp. 686 in: I.C.A.R. Monographs on *Algae*. — New Delhi.
- Drouet, F. 1968: Revision of the classification of the *Oscillatoriaceae*. — *Acad. Nat. Sci. Philadelphia, Monogr.* **15**: 370. — Philadelphia.
- 1973: Revision of the *Nostocaceae* with cylindrical trichomes. — Hafner Press, New York — London, 292 pp.
- 1977: Revision of the *Nostocaceae* with constricted trichomes. — Pp. 258 in: *Beih. Nova Hedwigia* **57** — J. Cramer, Vaduz.
- & Daily, W. A. 1956: Revision of the coccoid *Myxophyceae*. — *Butler Univ. Bot. Studies* **12**, Ann Arbor-Michigan: 222.
- Ercegović, A. 1925: Litofitska vegetacija vapnenaca i dolomita u Hrvatskoj. [La végétation des lithophytes sur les calcaires et les dolomites en Croatie]. — *Acta Bot. Univ. Zagreb* **1**: 64-114.
- 1929: Sur quelques nouveaux types des Cyanophycées lithophytes de la côte adriatique. — *Arch. Protistenk.* **66**: 164-174.
- 1932: Études écologiques et sociologiques des Cyanophycées lithophytes de la côte Yougoslave de l'Adriatique. — *Bull. internat. Acad. Yougosl. Sci. Arts, Cl. mat.-nat.* **26**: 33-56.
- Garcia-Pichel, F., Nübel, U. & Muyzer, G. 1998: The phylogeny of unicellular, extremely halotolerant cyanobacteria. — *Arch. Microbiol.* **169**: 469-482.
- Geitler L. 1932: *Cyanophyceae*. — Pp. 1196 in: Rabenhorst's *Kryptog.-Fl.* **14**. — Leipzig.
- Hayes, P. K., Barker, G. L. A. & Walsby, A. E. 1997: The genetic structure of *Nodularia* populations. — IXth Internat. Symp. Phototroph. Prokaryotes — Abstracts, Vienna (Austria): 187, Abstract to poster.
- Hernández-Mariné, M. & Canals, T. 1994: *Herpyzonema pulverulentum* (*Mastigocladaceae*), a new cavernicolous atmophyte and lime-incrusted cyanophyte. — *Arch. Hydrobiol./Algolog. Stud.*, Stuttgart **75**: 123-136.
- , Asencio, A. D., Canals, A., Ariño, X., Aboal, M. & Hoffmann, L. 1999: Discovery of populations of the lime-incrusting genus *Loriella* (*Stigonematales*) in Spanish caves. — *Arch. Hydrobiol., Algolog. Stud./ Stuttgart* **94**: 121-138.
- Kato, T., Watanabe, M. F. & Watanabe, M. 1991: Allozyme divergence in *Microcystis* (*Cyanophyceae*) and its taxonomic interference. — *Arch. Hydrobiol./Algolog. Stud.*, Stuttgart **64**: 129-140.
- Kohl, J. G. & Nicklisch, A. 1981: Chromatic adaptation of the planktonic blue-green algae *Oscillatoria redekei* Van Goor and its ecological significance. — *Internat. Revue ges. Hydrobiol.* **66**: 83-94.

- Komárek, J. 2001: Problems in cyanobacterial taxonomy — October 2000; implication for most common toxin producing species. — Pp. 6-43 in: Melchiorre, S. & al. (ed.), Proceedings from the Workshop "Le Fioriture di Alghe Tossiche nelle Acque Dolci". — Roma 17.10.2000.
- , Kaštovský, J., Kopecký, J., Lederer, F. & Sulek, J. 2002: Long-term adaptation of thermophilic cyanobacterial strain of *Synechococcus bigranulatus* to lower temperature. — Internat. J. Syst. Evol. Microbiol. (in prep.).
- & Montejano, G. 1994: Taxonomic evaluation of several *Chlorogloea* species (*Cyanoprocarvota*) from inland biotopes. — Arch. Hydrobiol./Algolog. Studies, Stuttgart **74**: 1-26.
- Kondrateva, N. V. 1968: Voprosy morfologii i sistematiki *Microcystis aeruginosa* Kuetz. emend. Elenk. i blizkich k nemu vidov. [Problem of morphology and systematics of *Microcystis aeruginosa* Kuetz. emend. Elenk. and related species.] — Pp.13-42 in: Cvetenie vody. — Kiev.
- Le Campion-Alsumard, T. 1969: Contribution a l'étude des cyanophycées lithophytes des étages supralittoral et médiolittoral (Region de Marseille). — Tethys **1**: 119-172.
- 1979: Les Cyanophycées endolithes marines: systématique, ultrastructure, ecologie et biodestruction. — Thèse état, Univ. Aix-Marseille, 198 pp.
- Noguerol-Seoane, A. N. & Rifon-Lastra, A. B. 1996: Aportación al conocimiento de la ficoflora epilithica en monumentos del noroeste de España. Estudio del monasterio de Samos (Lugo). — Anales Jard. Bot. Madrid **54**: 37-42.
- Otsuka, S., Suda, S., Li, R., Matsumoto, S. & Watanabe, M. M. 2000: Morphological variability of colonies of *Microcystis* morphospecies in culture. — J. Gen. Appl. Microbiol. **46**: 39-50.
- Pantazidou, A. 1991: Studies on euendolithic cyanophytes from marine coastal carbonate substrates of Greece. — Doctor Thesis, Univ. Athens, 298 pp.
- Pennisi, E. 1994: Static evolution. — Science News **145** (11): 168-169.
- Reynolds, C. S., Jaworski, G. H. M., Cmiech, H. A. & Leedale, G. F. 1981: On the annual cycle of the blue-green alga *Microcystis aeruginosa* Kütz. emend. Elenkin. — Phil. Trans. R. Soc. Lond. B. **293**: 419-477.
- Rippka, R., Deruelles, J., Waterbury, J. B., Herdmann, M. & Stanier, R. Y. 1979: Generic assignments, strain histories and properties of pure cultures of cyanobacteria. — J. gen. Microbiol. **111**: 1-61.
- Rudi, K., Skulberg, O. M. & Jakobsen, K. S. 1998: Evolution of cyanobacteria by exchange of genetic material among phyletically related strains. — J. Bacteriol. **180**: 3453-3461.
- Schopf, J. W. 1974: The development and diversification of Precambrian life. — Origins of Life **5**: 119-135.
- Waterbury, J. B., Watson, S. W., Valois, F. V. & Franks, D. G. 1986: Biological and ecological characterization of the marine unicellular cyanobacterium *Synechococcus*. — [In: Platt, T. & Li, W. K.W. (eds.), Photosynthetic Picoplankton.] — Canad. Bull. Fish. Aquat. Sci. **214**: 71-120 — Ottawa.

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