Pseudanabaena sp. – a brown-pigmented cyanophyte (cyanobacterium) with phycobilisomes of uncommon type

Article *in* Algological Studies/Archiv für Hydrobiologie Supplement Volumes · June 1997

DOI: 10.1127/algol_stud/85/1997/1

5 authors, including:

Svetlana Averina
Saint Petersburg State University
28 PUBLICATIONS **189** CITATIONS

SEE PROFILE

Algological Studies **85**	1–11	Stuttgart, Juni 1997

Pseudanabaena sp. – a brown-pigmented cyanophyte (cyanobacterium) with phycobilisomes of uncommon type

By ALEXANDER V. PINEVICH, OLGA V. GAVRILOVA, ANNA A. ZAITSEVA, SVETLANA G. AVERINA, and TATIANA V. USOVA

St. Petersburg University, Institute of Biology, Department of Microbiology, St. Petersburg, Russia

With 4 figures in the text

Abstract: Growth responses, morphology, and phycobiliproteins (PBP) were analyzed in the brown-pigmented, phycoerythrin (PE)-rich cyanophyte (cyanobacterium) *Pseudanabaena* sp. (strain CALU-861) isolated from a soil crust in Central Europe. Its significance issues from the rare occurrence of PE-rich cyanophytes with a terrestrial habitat. The cultures were inhibited by high light intensity. C-PE, which was the major PBP, constituted up to 7% of cell biomass. Purified phycobilisomes (PBS) differed from the usually observed type with respect to the morphology, polypeptide composition, and molecular size of individual polypeptides.

Key words: Cyanophytes (cyanobacteria), *Pseudanabaena*, phycoerythrin, phycobilisome.

Introduction

Chromatic individuality of cyanophytes (cyanobacteria) is integrated from the absorption maxima of (i) green Chl *a*, 440 nm and 680 nm, (ii) orange-yellow carotenoids, 450 nm, (iii) blue phycocyanin (PC), 620 nm, and (iv) red PE, 560 nm (if present), as well as from the relative concentrations of these pigments. In (sub)optimum natural habitats or in cultures, cell masses are coloured (blue-) green, whereas the uncommon, from brown to purple, pigmentation is due to the preponderance of PE. "Red" cyanophytes, primarily the unicellular *Synechococcus* spp. and filamentous *Oscillatoria* spp., are adapted to short-wavelength (near 500 nm) radiation and occupy euphotic niches in both the temperate and tropical oceans, where they are believed to contribute substantially to total primary productivity (WATERBURY et al. 1979). It should be noted that, despite the

DOI:10.1127/algol_stud/85/1997/1

0342-1120/97/0119-001 $ 2.75

interest in PE-rich cyanophytes, their diversity has been only poorly characterized, and data on their biology are limited.

The biogenesis of phycoerythrobilin (PEB)-associated polypeptides, which assemble at the periphery of PBS, is environmentally regulated, and PE accumulation of 20% cell dry weight can be attained (WYMAN et al. 1985). Hence, the study of PE-rich cyanophytes is of dual importance with respect to the physiological ecology and practical application of bilin pigments in these organisms.

Although the general distribution of PE-encoding genes does not match either the morphology-based or molecular sequences-based phylogeny of cyanophytes (APT et al. 1995), the presence of high relative amounts of PE would pinpoint at the peculiarities of PBS organization, including those which associate themselves with the individual stage(s) in evolution of this variant of light-harvesting complex. For example, in *Gloeobacter violaceus* strain PCC 7421 and *Synechococcus* sp. strain PCC 6301, unique architectures of PBS correlate with the affiliation to early branchings of the phylogenetic tree of cyanophytes (GIOVANNONI et al. 1988).

This work centered on the characterization of growth and ultrastructure, as well as on the determination of PE identity and content in the brown-pigmented *Pseudanabaena* sp. strain CALU-861. A separate goal was to characterize the morphology and polypeptide composition of intact PBS, as compared with those in reference strain, *Anabaena* sp. strain ATCC 29413.

Materials and methods

Pseudanabaena sp. strain CALU-861 has been isolated from a soil crust sample collected in Hungary, and kindly supplied by Dr. MIKLÓS SZEKERES (Szeged). *Anabaena* sp. strain ATCC 29413 (CALU-787) was obtained from Dr. PETER WOLK (East Lansing). Axenic cultures were supported on slants of ALLEN's mineral medium solidified with 1% Bacto-Agar (Difco). Test materials were cultivated in sterile air-gassed 50 ml glass fermentors at 20 °C and continuous illumination of 2.5–30 μE photon white light $m^{-2}s^{-1}$. Trichomes from the actively growing (one week-old) cultures were sedimented by centrifugation at 1000× g for 5 min and resuspended in appropriate buffer solutions.

Light microscopy was monitored with a UBI differential-interference (Nomarski) contrast (× 1500). For electron microscopy of cells, pelleted trichomes (resuspended in 5 mM sodium cacodylate buffer, pH 6.8) were (pre)fixed at 0 °C with 1% glutaraldehyde (2 h) and 0.5% osmium tetraoxide (2 h), respectively. After dehydration, the material was embedded in SPURR resin and sectioned with a Reichert ultramicrotome; REINOLDS contrast was universally performed. For electron microscopy of PBS, particles suspended in stabilizing buffer (see below) were absorbed onto carbon films, fixed with 1% glutaraldehyde in 0.75 M potassium phosphate buffer (pH 7.0) for 15 s, rinsed in double distilled water, and

contrasted with 1% uranyl acetate for 15 s. The resulting preparations were observed in a Magiscan at 90 kV.

For pigment analyses, trichomes were lysed by the passage through a French pressure cell (2000 psi). The homogenates were made free of thylakoid membranes with two successive centrifugations at 8000× g for 10 min, followed by Millipore filtration (0.1 μm). To obtain the purified intact PBS, a modified method (GLAZER 1988b) was used: pelleted trichomes were resuspended in 0.75 M potassium phosphate buffer (pH 7.0), 10 mM EDTA, 1 mM 2-mercaptoethanol, 1 mM sodium azide, 0.5 mM 4-(chlormercuri)benzoic acid, 0.25 mM phenylmethanesulfonyl chloride; after a hydraulic treatment, the resulting homogenate was supplemented with 5% (v/v) of Triton X-100, magnetically stirred for 30 min, and centrifugated at 8000× g for 10 min. The resulting lower (hydrous) layer, containing PBS, was removed with a syringe. A crude PBS preparation was purified by centrifugation at 100000× g for 6 h in the step gradient of 0.25 M, 0.5 M, 1 M, and 2 M sucrose in potassium phosphate buffer, at 20 °C. PBS were collected from the zone of 1 M sucrose and used for electron microscopy, or, after the ammonium sulfate precipitation, for SDS-electrophoresis.

PBS polypeptides were separated in 13.5% polyacrylamide gel plates containing 0.1% sodium dodecyl sulfate. The apparent molecular masses were estimated with 10-100 kDa markers (Sigma).

Light absorbance spectra were recorded with a Beckman spectrophotometer, PC concentration was determined using E_{625} (0.1%) = 7.2 L g^{-1} cm^{-1} (RÜDIGER et al. 1980). In the case of PE, E_{560} (0.1%) = 7.0 L g^{-1} cm^{-1} was calculated on the assumption of 47000 M cm^{-1} specific absorbance for polypeptide-bound bilin (MUCKLE & RÜDIGER 1977), and of the trimeric aggregation state for α, β-apoproteins with 2 and 3 attached PEB chromophores, respectively (GLAZER 1988a). PE was purified with ammonium sulfate fractionation, followed by filtration on Sephadex G-100 and ion-exchange chromatography on DEAE-cellulose. Bilin chromophore was analyzed spectrophotometrically after its cleavage with 12 N HCl for 1 h at room temperature.

Results and discussion

The initial indication of a high amount of PE in cells of the cyanophyte (cyanobacterium) strain CALU-861 was unusual colour of slant or liquid cultures. Actually, the optical spectra obtained with unfractionated cell homogenates (Fig. 1a) revealed, beside the sharply defined peaks of Chl *a* (440 nm and 680 nm) and PC (620 nm), intensive absorbance at 565 nm, which was responsible for the reddish-brown pigmentation of dense cell suspensions, and was due to the accumulation of PE.

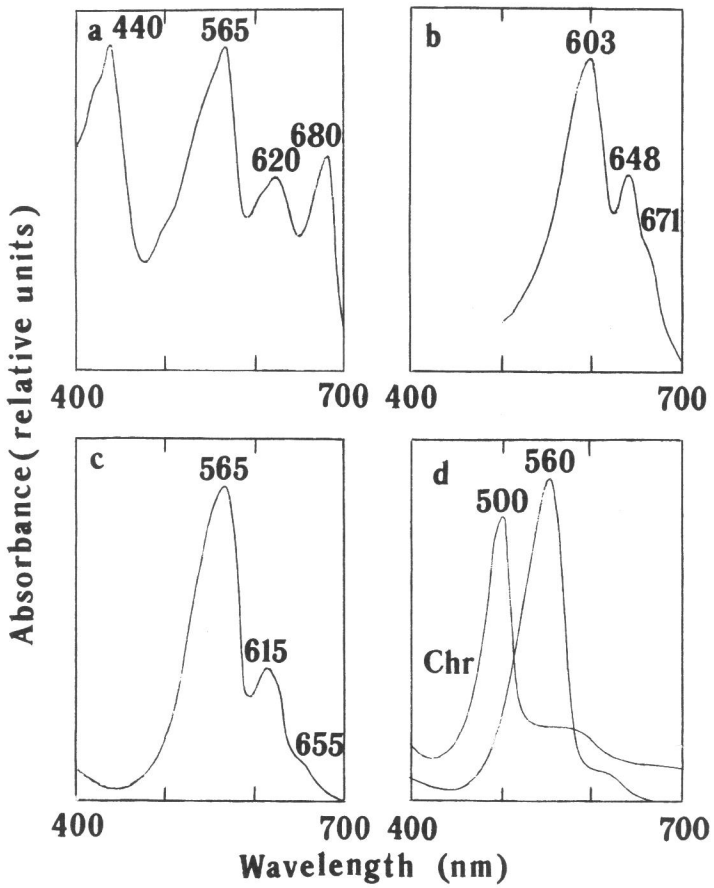

Fig. 1. Light absorption spectra of *Pseudanabaena* sp. strain CALU-861: **a** – Cell homogenate, **b** – Isolated intact PBS, **c** – Cell homogenate free of thylakoid membranes, **d** – Purified PE and its cleaved bilin chromophore (Chr).

When examined light-microscopically (Fig. 2a), the material displays long, flexible, non-spiralized, sheathless trichomes without branching; intercalary cells are uniform, barrel-like in shape, and clearly constricted at the cross walls; terminal cells are isodiametric, with hemispherical free poles. In agreement with a consensus usage of (alternative) botanical and bacteriological approaches to systematics of cyanophytes (BOURRELLY 1970, CASTENHOLZ 1989), this set of markers coincides with diagnosis of the genus *Phormidium* ("LPP-group B", Oscillatoriales). Although the strain CALU-861 has been correspondingly identified as *Phormidium* sp., novel criteria make it necessary to reconsider this taxonomic status. Thus, according to the comprehensive treatment of Oscillatoriales (ANAGNOSTIDIS & KOMÁREK 1988), in all studied strains of *Phormidium*, radially (in cross section) oriented thylakoids occupy whole interior of the cell. In

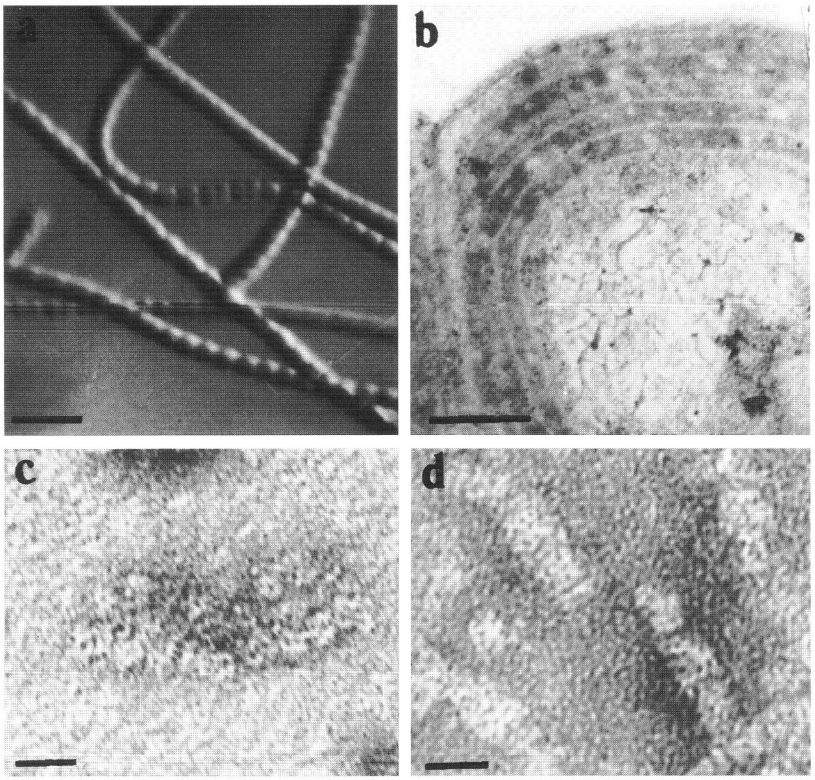

Fig. 2. Morphology of trichomes and isolated PBS: **a** – Light micrograph of *Pseudanabaena* sp. strain CALU-861 trichomes, Nomarski contrast [bar = 5μm], **b** – Transmission electron micrograph of a part of *Pseudanabaena* sp. strain CALU-861 trichome [bar = 0.2 μm], **c** – Electron micrograph of negatively stained PBS in *Anabaena* sp. strain ATCC 29413 [bar = 20 nm], **d** – Electron micrograph of negatively stained PBS in *Pseudanabaena* sp. strain CALU-861 [bar = 20 nm].

contrast, thylakoid pattern demonstrated in the strain CALU-861 is both concentric and peripheral; outermost thylakoids terminate at the cross walls, while the inner ones encircle centroplasm containing DNA fibers. The interthylakoidal space is occupied by electron-dense PBS approximately 50 nm in diameter, with indeterminate morphology (Fig. 2b). The observed arrangement of thylakoids represents a primitive variant of lamellar system and is typical of the unicellular cyanophytes, while in filamentous forms it is restricted to all so far examined strains of *Pseudanabaena* (KOMÁREK & ČÁSLAVSKÁ 1991). Correspondingly, throughout this work, the strain CALU-861 is treated as *Peudanabaena* sp.

The isolation of a new brown-pigmented terrestrial strain of *Pseudanabaena* (see also: RÜDIGER et al. 1980) is intriguing in view of relevant data on the ecological and taxonomical diversity of PE-rich cyanophytes. Noteworthy, the estimated PE contents are usually higher in marine than in fresh water or in soil

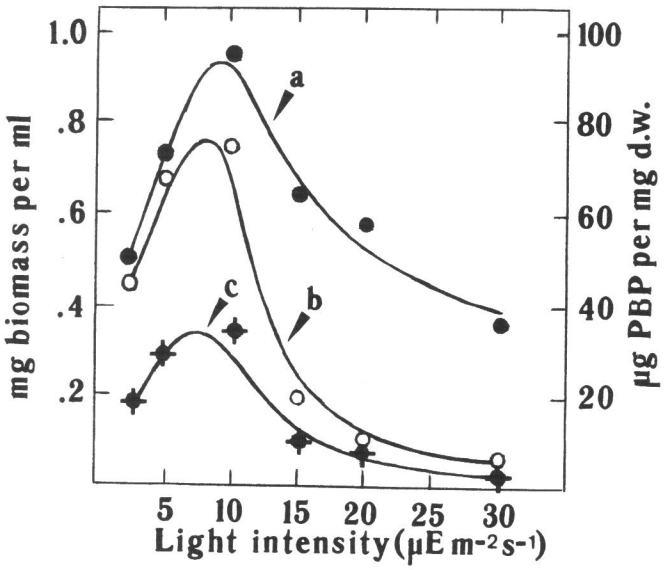

Fig. 3. Growth yield and PBP accumulation in *Pseudanabaena* sp. strain CALU-861 cultivated at different light intensities: **a** – Biomass of the two weeks-old cultures, **b** – PE cellular content, **c** – PC cellular content.

strains; besides, the reports on PE-rich cyanophytes are very unusual for terrestrial ecosystems. Taxonomically, PE-rich strains belong to the unicellular *Synechococcus* (WYMAN et al. 1985, ONG & GLAZER 1991) and *Synechocystis* (PARRY 1984, ONG & GLAZER 1991), as well as to the filamentous *Oscillatoria* (WYMAN et al. 1985, PHILIPS & ZEMAN 1990, CARPENTER et al. 1993), *Pseudanabaena* (RÜDIGER et al. 1980), *Anabaena* (RODRÍGUEZ et al. 1991), and *Nostoc* (RODRÍGUEZ et al. 1991, DE CHAZAL & SMITH 1994, PINEVICH et al. 1994). Of all these cases, only two strains of *Nostoc* sp. (DE CHAZAL & SMITH 1994, PINEVICH et al. 1994) and one strain of *Pseudanabaena* sp. (RÜDIGER et al. 1980) are terrestrial.

Pseudanabaena sp. strain CALU-861 was shown to produce diffuse colonies which gradually dispersed on the agar plates. In liquid cultures, the development of homogeneous suspensions was observed; with more irradiance, the trichomes tended to adhere to the walls of a glass fermentor. Variation of light intensity revealed maximum biomass yield in dim light (10 µE photon m^{-2} s^{-1}), whereas lesser growths were displayed under both low and high illumination (Fig. 3). While the former decline in productivity could be attributed to suboptimum input of energy, the latter one may indicate a marked light-sensitivity typical of many PE-containing cyanophytes (TANDEAU DE MARSAC 1977). Peak amount of PE was associated with the highest biomass yield, and measured ca. 7% by dry weight (Fig. 3). The analogous PE concentrations were previously registered in *Anabaena* sp. and *Pseudanabaena* sp. (RÜDIGER et al. 1980, RODRÍGUEZ et al.

1989), though twice as much PE was reported for the PE-rich strains of *Oscillatoria* sp. (PHLIPS & ZEMAN 1990) and *Nostoc* sp. (PINEVICH et al. 1994). Irrespective of light intensity, the stoichiometry for PE: PC was calculated to be 2–3 : 1 (Fig. 3), which was consistent with the data obtained for other PE-rich filamentous cyanophytes (WYMAN et al. 1985, RODRÍGUEZ et al. 1989, PINEVICH et al. 1994). In contrast, higher PE : PC ratios (10–20 : 1) have been routinely detected in the marine strains of *Synechococcus* sp. (WYMAN et al. 1985).

After the removal of chlorophyll-bearing membrane fragments from the cell homogenate (Fig. 1c), beside the major peak of PE (565 nm) and minor peak of PC (615 nm), a shoulder near 655 nm was observed indicative of the presence of allophycocyanin (APC). The spectrophotometry of purified PE (Fig. 1d) helped to confirm the identity of C-PE, which was based on outline of the spectrum and 560-nm maximum (GLAZER 1988a). Unlike traditional PEB-560 and PEB-590, the acid-cleaved bilin chromophore (Fig. 1d, Chr) had a peak shifted to shorter wavelength (500 nm), suggesting a more extended conjugated double-bond system, in resemblance with that of PEB in B-PE (PINEVICH et al. 1994).

The sample of purified PBS was characterized by absorption maxima at 603 nm and 648 nm, respectively, and by a shoulder at 671 nm (Fig. 1b). Both peaks were unexpectedly shifted to long wavelengths, resembling the PE-less PBS in both the unicellular and filamentous cyanophytes (YAMANAKA & GLAZER 1981, REUTER & NICKEL-REUTER 1993).

The morphology of purified PBS is illustrated by Fig. 2c, d. In *Anabaena* sp. (Fig. 2c), the routine hemidiscoidal PBS are observed, which consist of three coaxial cylinders forming the core, and six radiating rods; in both cases, elementary module is represented by the toroidal trimer of α, β-apoproteins. The cylinders have a diameter of 10 nm, while the rods measure ca. 10×20 nm, which is in agreement with the previously reported data (GLAZER 1988b). At the same time, PBS in *Pseudanabaena* sp. (Fig. 2d) look unusual – instead of hemidiscoids, gigantic 20×60 nm cylinders are present (cf. 50-nm particles in the transmission electron micrograph). A regular striation must be due to the stacked elementary modules (toroidal trimers?). Although it is tempting to consider cylindrical pattern as authentic, the possibility of artifactual disaggregation of a higher-order (hemidiscoidal?) structure should not be completely ignored. However, the PBS isolation protocol used in this work is known to yield intact particles, which was demonstrated by control run with *Anabaena* sp. (Fig. 2c).

Based on morphological data, PBS in cyanophytes can be classified as bundle shaped (in *Gloeobacter violaceus*, see: GUGLIELMI et al. 1981), hemidiscoidal (in most of strains, see: GLAZER 1988b), and hemiellipsoidal. Hemiellipsoids of the same size as hemidiscoidal PBS were found in *Phormidium* sp. C 86; they showed a tight parallel package of ten peripheral rods, whereas the core was of the common tricylindrical type (REUTER & MÜLLER 1993). Interestingly, the fixed, negatively stained PBS in *Anabaena* sp. M3 were found to have a cylindrical

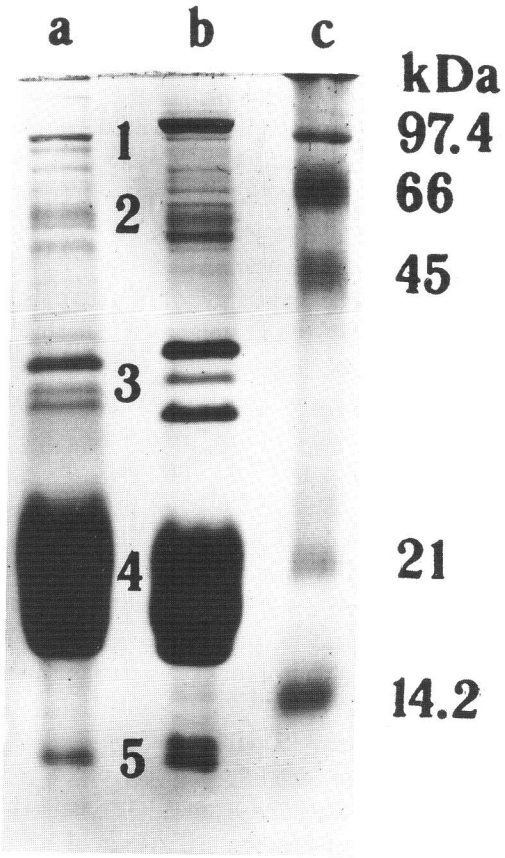

Fig. 4. Separation of polypeptides by SDS-polyacrylamide gel electrophoresis: **a** – PBS of *Pseudanabaena* sp. strain CALU-861, **b** – PBS of *Anabaena* sp. strain ATCC 29413, **c** – Molecular mass standards. For details of polypeptide groups 1–5, see the text.

16×50 nm structure (ISONO & KATOH 1982), which was essentially the same as in Fig. 2d. At the same time, *Synechocystis* sp. BO 8402 was shown to possess the paracrystalline aggregates of PBP arranged in 50×100 nm rods (REUTER et al. 1994), which can further substantiate the authenticity of cylindrical PBS in *Pseudanabaena* sp. strain CALU-861.

A distinction of cylindrical particles from the regularily occurring higher aggregates of PBP is confirmed by the comparison of PBS polypeptides in *Pseudanabaena* sp. and *Anabaena* sp. (the gels were deliberately overloaded, which helped visualize, beside α, β-apoproteins, a complete set of linkers which are known to constitute ca. 15% of PBS mass). A sufficiently high standard of PBS preparations was witnessed by the absence of 15 kDa-bands (contaminating thylakoid membrane polypeptides). In the case of *Pseudanabaena* sp. (Fig. 4, lane a), the heavily stained group-4 polypeptides correspond to apoproteins of PE (21

and 24 kDa), PC (18 kDa), and APC (17 kDa). The estimated M_r for β-subunit of PE is abnormally high (24 kDa) as compared with the reported top value of 22 kDa (REUTER & MÜLLER 1993). In *Anabaena* sp. (Fig. 4, lane b), group-4 is represented by two PC-bands (21 and 18 kDa) and one APC-band (16 kDa). In contrast with PBP apoproteins, linker polypeptides associate themselves with minor bands of group-1 (= core-membrane linkers L_{CM}), group-3 (= rod linkers L_R, and rod-core linkers L_{RC}), and group-5 (= core linkers L_C); group-2 polypeptides are functionally unknown and not localized (REUTER & MÜLLER 1993). In *Pseudanabaena* sp. and *Anabaena* sp., group-1 linkers have similar M_r (78 and 81 kDa). At the same time, group-3 linkers are different: *Pseudanabaena* sp. demonstrates a single strong band (38 kDa) and 34/35 kDa duplex, whereas *Anabaena* sp. shows two intensively stained bands (32 and 40 kDa) together with a faint band of 36 kDa. Another difference is associated with group-5 linkers which are represented by 11 kDa-band in *Pseudanabaena* sp., and 10/12 kDa duplex in *Anabaena* sp.

Despite the apparent symmetry of 20×60 nm cylinders (Fig. 2d), they can be supposed to functionally subdivide into the core and periphery, respectively, which is witnessed by the presence of standard groups of linkers (Fig. 4, lane a), as well as of APC (Fig. 1b, c), which is known to localize at the proximal end of PBS (GLAZER 1988b).

The results of this study contribute to a limited knowledge of PE-rich and, especially, terrestrial PE-rich, cyanophytes. Data on the morphology, light absorption spectrum, and molecular composition indicate an uncommon organization of PBS. However, many aspects remain unknown, including whether a primordial structure, or late evolutionary acquisition, is involved.

Acknowledgement

The authors are indebted to Prof. Dr. BORIS V. GROMOV for his permanent interest in the problem, and valuable suggestions.

References

ANAGNOSTIDIS, K. & KOMÁREK, J. (1988): Modern approaches to the classification system of cyanophytes 3 – Oscillatoriales. – Arch. Hydrobiol./Suppl. 80, Algological Studies **50–53**: 327–472, Stuttgart.

APT, K.; COLLIER, J.L. & GROSSMAN, A.R. (1995): Evolution of the phycobiliproteins. – J. Mol. Biol. **248**: 79–96.

BOURRELLY, P. (1970): Les Algues d'Eau Douce. Tome III: Les Algues Bleues et Rouges. Les Eugléniens, Péridiniens et Cryptomonadines. – 512 pp., Ed. Boubée, Paris.

CARPENTER, E.J.; O'NEIL, J.M.; DAWSON, R., CAPONE, D.G.; SIDDIQUI, P.J.A.; ROENNEBERG, T. & BERGMAN, B. (1993): The tropical diazotrophic phytoplankter *Trichodesmium*: biological characteristics of two common species. – Mar. Ecol. Progr. Ser. **95**: 295–304.

CASTENHOLZ, R.W. (1989): Order Oscillatoriales. - In: STALEY, J.T. et al. (eds.): Bergey's Manual of Systematic Bacteriology, p. 1794–1799. Williams & Wilkins, Baltimore e.a.

CHAZAL, N.M., DE & SMITH, G.D. (1994): Characterization of a brown *Nostoc* species from Jawa that is resistant to high light intensity and UV. - Microbiology **140**: 3183–3189.

GIAVANNONI, S.J.; TURNER, S.; OLSEN, G.; BARNS, S.; LANE, D.J. & PACE, N.R. (1988): Evolutionary relationships among cyanobacteria and green chloroplasts. - J. Bacteriol. **170:** 3584–3592.

GLAZER, A.N. (1988a): Phycobiliproteins. - Meth. Enzymol. **167**: 291–303.

– (1988b): Phycobilisomes. - Meth. Enzymol. **167:** 304–312.

GUGLIELMI, G.; COHEN-BAZIRE, G. & BRYANT, D.A. (1981): The structure of *Gloeobacter violaceus* and its phycobilisomes. - Arch. Microbiol. **129**: 181–189.

ISONO, T. & KATOH, T. (1982): Cylindrical phycobilisomes from a blue-green alga, *Anabaena variabilis*. - Plant & Cell Physiol. **23:** 1347–1355.

KOMÁREK, J. & ČÁSLAVSKÁ, J. (1991): Thylakoid patterns in oscillatorialean cyanophytes. - Algological Studies **64**: 267–270.

MUCKLE, L. & RÜDIGER, W. (1977): Chromophore content of C-phycoerythrin from various cyanobacteria. - Z. Naturforsch. **32c**: 957–960.

ONG, L.J. & GLAZER, A.N. (1991): Phycoerythrins of marine unicellular cyanobacteria. - J. Biol. Chem. **266**: 9515–9527.

PARRY, D.L. (1984): Cyanophytes with R-phycoerythrins in association with seven species of ascidians from the Great Barrier Reef. - Phycologia **23:** 503–505.

PHLIPS, E.J. & ZEMAN, C. (1990): Photosynthesis, growth and nitrogen fixation by epiphytic forms of filamentous cyanobacteria from pelagic *Sargassum*. - Bull. Mar. Sci. **47**: 613–621.

PINEVICH, A.V.; VEPRITSKII, A.A.; GROMOV, B.V.; KRAUTVAL'D, K. & TITOVA, N.N. (1994): Cellular and cultural properties and characterization of the pigment in *Nostoc* sp., a cyanobacterium unusually rich in c-phycoerythrin. - Microbiology [translated from Mikrobiologiya] **63**: 481–485.

REUTER, W. & MÜLLER, C. (1993): Adaptation of the photosynthetic apparatus of cyanobacteria to light and CO_2. - J. Photochem. Photobiol. **21**: 3–27.

REUTER, W. & NICKEL-REUTER, C. (1993): Molecular assembly of the phycobilisomes from the cyanobacterium *Mastigocladus laminosus*. - J. Photochem. Photobiol. **18**: 51–66.

REUTER, W.; WESTERMANN, M.; BRASS, S.; ERNST A.; BÖGER, P. & WEHRMEYER, W. (1994): Structure, composition, and assembly of paracrystalline phycobiliproteins in *Synechocystis* sp. strain BO 8402 and of phycobilisomes in the derivate strain BO 9201. - J. Bacteriol. **176**: 896–904.

RODRÍGUEZ, H.; RIVAS, J.; GUERRERO, M.G. & LOSADA, M. (1989): Nitrogen-fixing cyanobacterium with a high phycoerythrin content. - Appl. Environ. Microbiol. **55**: 758–760.

– – – – (1991): Enhancement of phycobiliprotein production in nitrogen-fixing cyanobacteria. - J. Biotechnol. **20:** 263–270.

RÜDIGER, W.; WAGENMANN, R. & MUCKLE, G. (1980): Investigation of C-phycoerythrin in the cyanobacterium *Pseudanabaena* W 1174. - Arch. Microbiol. **127**: 253–257.

TANDEAU DE MARSAC, N. (1977): Occurrence and nature of chromatic adaptation in cyanobacteria. - J. Bacteriol. **130:** 82–91.

WATERBURY, J.B.; WATSON, S.W.; GUILLARD, R.R.L. & BRAND, L.E. (1979): Widespread occurrence of unicellular, marine planctonic, cyanobacterium. - Nature **277**: 293–294.

WYMAN, M.; GREGORY, R.P.F. & CARR, N.G. (1985): Novel role for phycoerythrin in a marine cyanobacterium, *Synechococcus* strain DC2. - Science **230**: 818–820.

YAMANAKA, G. & GLAZER, A.N. (1981): Dynamic aspects of phycobilisome structure: modulation of phycocyanin content of *Synechococcus* phycobilisomes. - Arch. Microbiol. **130:** 23–30.

Manuscript received July, 30, 1996, accepted October, 10, 1996.

The authors' address:

Prof. Dr. ALEXANDER V. PINEVICH,
Dr. OLGA V. GAVRILOVA,
Dr. ANNA A. ZAITSEVA,
Dr. SVETLANA G. AVERINA,
Dr. TATIANA V. USOVA,
St. Petersburg University,
Institute of Biology,
2 Oranienbaum Chaussee, Old Peterhof,
p/o Box 198904,
St. Petersburg, Russia.
[E-mail: olga@onti.bri.pu.ru]