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Presence of CU-phycoerythrin in the marine benthic blue-green alga *Oscillatoria* cf. *corallinae*

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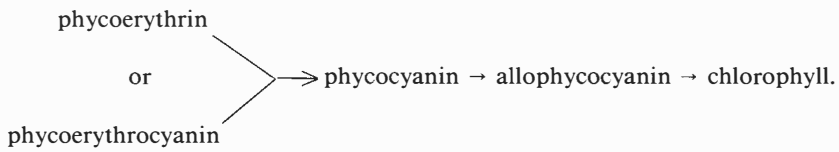
The presence of CU-phycoerythrin, a phycobiliprotein characterized by the presence of phycourobilin chromophores in addition to phycoerythrobilins, and so far found in only eight blue-green algae, is reported for the first time from a marine benthic blue-green alga, *Oscillatoria* cf. *corallinae*.

INTRODUCTION

Phycobiliproteins are the major accessory light-harvesting pigments of blue-green algae and red algae. Their colour is due to the presence of covalently bound open-chain tetrapyrrole prosthetic groups, the phycobilins. Different phycobiliproteins are distinguished in blue-green algae on the basis of their visible absorption spectra (Table 1).

The phycobiliproteins are organized into supramolecular complexes, the phycobilisomes, which are found as regular arrays on the surface of the thylakoid membranes (Gantt 1980, 1981; Glazer 1984). Additional uncoloured polypeptides serve to link biliproteins in the phycobilisomes and to attach them to the thylakoid membranes (Wehrmeyer 1983). Phycobiliproteins constitute an energy-transfer chain through which the incident light energy passes from phycoerythrin or phycoerythrocyanin to chlorophyll *a* (Gray & Gantt 1975; Grabowsky & Gantt 1978; Searle *et al.* 1978; Lundell & Glazer 1981; Pellegrino *et al.* 1981) as shown below:



Phycocyanin and allophycocyanin seem to be universally present in blue-green algae. Allophycocyanin B was identified in many but not all blue-green algae (Glazer & Bryant 1975; Ley *et al.* 1977).

Phycoerythrocyanin, characterized by the presence of the two chromophores phycocyanobilin and phycobiliviolin (Bishop *et al.* 1987), is mainly found in heterocystous blue-green algae. Phycoerythrocyanin and phycoerythrin are mutually exclusive (Bryant 1982).

The phycoerythrins are widely distributed among all the taxonomic groups and form the spectroscopically most variable class of phycobiliproteins. The classical phycoerythrin (CPE) has a single absorption maximum at 560 nm due to the presence of phycoerythrobilin (PEB) as a chromophore. In some blue-green algae, spectral forms with broadened absorption bands and maxima at 550–565 nm, and those possessing two absorption maxima in the 550–570 nm range are found. In many cases, these spectral forms are apparently denatured and dissociated forms of phycoerythrin (MacColl & Guard-Friar 1987), reflecting different types of protein–bilin interaction brought about by variation in pH, concentration of ions and biliproteins in the solution (Glazer 1984). Many, but not all, blue-green algae containing phycoerythrin undergo chromatic adaptation. In fact, three types of response to

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Table 1. Properties of phycobiliproteins present in blue-green algae. Modified from Gantt (1981) and Zilinskas & Greenwald (1986)

Phycobiliprotein	Proteins	Absorption maxima (nm)	Chromophores*	Fluorescence maximum (nm)
APC	Allophycocyanin	650	PCB	660
	Allophycocyanin B	(671 > 618)	PCB	680
	Allophycocyanin I	654	—	680
	Allophycocyanin II	650	PCB	—
	Allophycocyanin III	650	—	—
C-PC	C-Phycocyanin	620	PCB	642
PEC	Phycoerythrocyanin	570 > 595	PCB, PXB	610
C-PE	C-Phycoerythrin	560	PEB	577
	C-Phycoerythrin I	555	PEB	577
	C-Phycoerythrin II	(542 > 565)	PEB	577
CU-PE	CU-Phycoerythrin	540 > 498	PEB, PUB	560–565 573

* PCB: phycocyanobilin; PXB: phycobiliviolin; PEB: phycoerythrobilin; PUB: phycourobilin.

red, green and white light conditions have been observed in blue-green algae (Tandeau de Marsac 1977). Strains designated as type I do not adapt chromatically and the ratio of PE to PC remains constant. Type II strains adapt by modulating PE synthesis alone; its synthesis is promoted in green light and repressed in red light, whereas PC synthesis remains constant. Type III strains are able to alter both PC and PE synthesis. In green light PE synthesis is high and this biliprotein becomes the dominant pigment; in red light PE synthesis is repressed, but the exposure of these strains to red light induces the *de novo* synthesis of a unique PC not present in green-light-grown cells (Bryant 1981; Bryant & Cohen-Bazire 1981).

Another type of phycoerythrin is characterized by the presence of a peak in the 500 nm range, due to the presence of phycourobilin (PUB) chromophore in addition to PEB. This phycoerythrin, called CU-phycoerythrin by MacColl & Guard-Friar (1987), appears to be similar to B- and R-phycoerythrins from red algae in that it contains the same chromophores (PUB, PEB). This pigment class has so far only been demonstrated in eight blue-green algal species belonging to the Chroococcales and the Oscillatoriaceae (Table 2). The pigment was studied in detail for *Synechococcus* sp. DC-2 (Alberte *et al.* 1984; Kursar *et al.* 1981), *Synechococcus* sp. WH 8103 (Ong *et al.* 1984), and *Gloeobacter violaceus* Rippka, Waterbury et Cohen-Bazire (Bryant *et al.* 1981).

The rare occurrence of this pigment in blue-green algae is of interest and adds a marine benthic *Oscillatoria* species to the list.

MATERIALS AND METHODS

Oscillatoria cf. *corallinae* (Kützing) Gomont ex Gomont growing on a calcareous worm tube on the stem of *Posidonia oceanica* Delile was collected by V. Demoulin at a depth of 5 m in July 1984 in the harbour of the oceanographical station STARESO (Calvi, Corsica). The strain CJ1 is maintained in the culture collection of the Department of Botany (University of Liège). The morphological variability of the strain and its growth limits for temperature and irradiance were determined as described by Wilmotte (1988). To determine the growth limits for salinity the strain was grown in MN medium (Rippka *et al.* 1979) with the salinity adjusted to 8, 50, 75, 100, 200, and 500% of seawater at 22°C, and at a continuous illumination of 20 μmol photons m^{-2} s^{-1}. To determine the presence of a chromatic adaptation, cultures were grown for 3 weeks under red and green filters (Lee filters 106 and 124) at 22°C at a continuous illumination of 17 μmol photons m^{-2} s^{-1}. The change of colour was recorded visually.

For pigment analysis, the strain was grown in MN medium in 5 l flasks at 22°C and with a continuous lateral illumination of 30 μmol photons m^{-2} s^{-1} provided by Phytor LF40W cool-white fluorescent tubes. The culture was agitated continuously by magnetic stirring and aerated with 99.5% N_2 and 0.5% CO_2. After 3 weeks, plants were harvested by centrifugation and the pellet was stored at −70°C until use.

Frozen *Oscillatoria* cells were homogenized by a liquid nitrogen-cooled electric grinder. The homogenate was suspended in a 50 mM Na–K

Table 2. Properties of CU-phycoerythrin from blue-green algae

	Habitat	Absorption maxima (nm)	Fluorescence maximum (nm)	Subunits molecular weight (D)	PEB: PUB ratio	Subunit composition*		References
						α	β	
Gloeobacter violaceus Rippka *et al.*	Terrestrial	501, 564	574, 577	α—20 500 β—21 700	6:1			Rippka *et al.* (1974) Bryant *et al.* (1981)
Synechococcus sp. DC-2 (= WH7803)	Marine picoplankton	500, 542	560	α—17000 β—19 500	4:1	2 PEB	2 PEB + 1 PUB	Alberte *et al.* (1984) Kursar *et al.* (1981)
Synechococcus sp. WH8103	Marine picoplankton	492, 543	565	α—19500 β—20 000 γ—29000§	0.6:1		1 PEB + 1 PUB	Ong *et al.* (1984)
Synechocystis cf. *trididemni* Lafargue et Duclaux	Marine symbiont	495, 540 496, 540	 570 569					Parry (1984) Cox *et al.* (1985) Neveux *et al.* (1988)
Oscillatoria irrigua Gomont	Freshwater	495, 565						Hirose *et al.* (1969)
Oscillatoria sp.	Thermal	498, 567		α—18700 β—19 800	5:1	2 PEB	3 PEB + 1 PUB	Stadnichuk *et al.* (1985)
Oscillatoria cf. *corallinae* Gomont	Marine benthic	494, 540	573	α—18 000 β—19 500 γ—29 000	1.76:1			Present study
Oscillatoria spongeliae (Schulze) Hauck	Marine symbiont	498, 542	574	α—18 000 β—20 000				Larkum *et al.* (1987)
Trichodesmium cf. *thiebautii* Gomont	Marine plankton	500, 547, 565 (sh)† 493, 567‡ 495, 550‡ 505, 542, 557 496, 542 495, 547, 565	573					Fujita & Shimura (1974) Shimura & Fujita (1975) Lewis *et al.* (1988) McCarthy & Carpenter (1979) Haxo *et al.* (1987)

* PEB: phycoerythrobilin; PUB: phycourobilin.
† sh: shoulder.
‡ *In vivo* spectrum.
§ Three bands are observed in the 29 kD region.

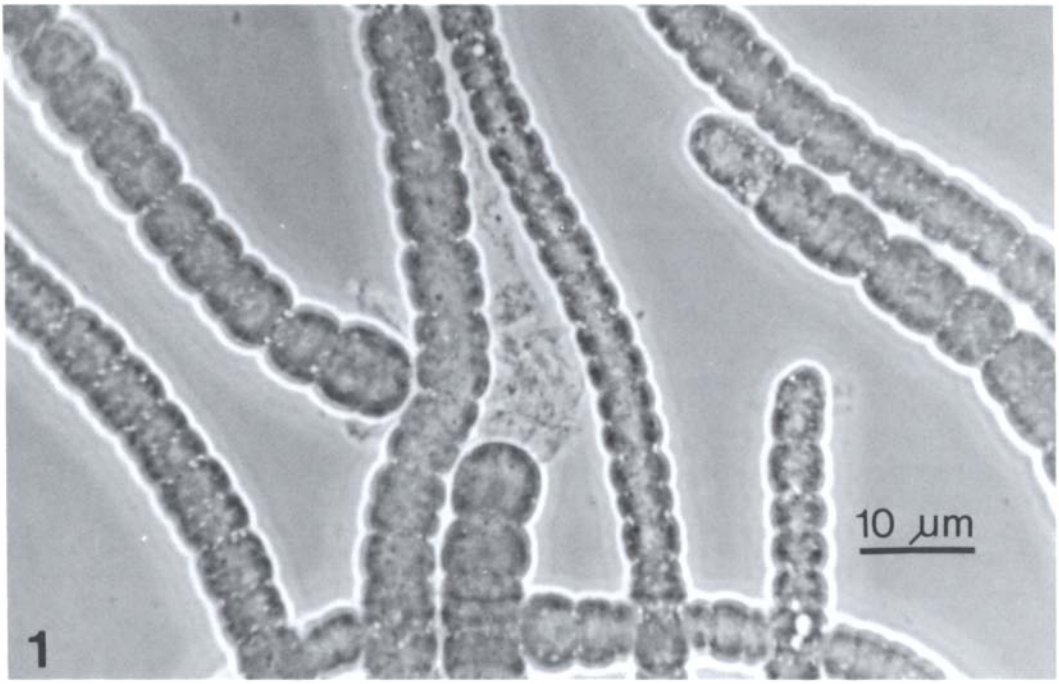

Fig. 1. *Oscillatoria* cf. *corallinae* from culture (phase-contrast microscopy).

phosphate buffer (pH 6.8) in a 1 : 5 (w: v) ratio and kept in the dark at 4°C for 12 h. After centrifugation at 27 000 ***g*** for 20 min at 4°C to remove cellular debris, the aqueous extract was monitored with a Perkin-Elmer 554 spectrophotometer. The extract was then fractionated successively with 30, 40, 50, and 60% ammonium sulphate. At each fractionation step, the extract was left overnight in the dark at 4°C and then centrifuged at 27 000 ***g***; the absorption spectra of the precipitate resuspended in 1 mM phosphate buffer and of the supernatant were taken to check the composition of the fractions. The purest fraction was dialysed against 1 mM phosphate buffer (pH 6.8). Fluorescence emission was monitored with a Perkin-Elmer LS-5 luminescence spectrometer. A pure fraction was denatured with 20% acetic acid. Optical densities at 494 nm (PUB) and 540 nm (PEB) were measured and considered in a linear system of derivation permissible as the absorption spectra of protein bound bilins, when denatured, closely resemble those of free bilins (Glazer *et al.* 1982). The PUB : PEB ratio was calculated with the bilin molar extinction coefficients given by Klotz & Glazer (1985).

SDS–urea gradient gels were used to determine the molecular masses of the subunits. Subunits were prepared by adding 1% dithiothreitol and 0.1% β-mercaptoethanol to the samples and heating them at 100°C for 10 min. Polyacrylamide gel gradients from 10 to 20% in Tris-HCl buffer (pH 8.9) with 4 M urea were used. Lysozyme (14 400 Daltons), soybean trypsin inhibitor (21 500 D), bovine carbonic anhydrase (31 000 D), ovalbumin (45 000 D), bovine serum albumin (66 200 D), and rabbit muscle phosphorylase (97 400 D) were used as markers. Gel slabs were run at 6 mA for 12 h in a Protean II Cell (Bio-Rad) with a circulating water-cooling system. They were stained with Coomassie blue and destained in a mixture of acetic acid (40%) and methanol (10%) in water.

RESULTS

Strain characteristics

The following description is based on a culture grown at 25°C, at a continuous illumination of 7 μmol photons m^{-2} s^{-1}, under which conditions variations in cell length are smallest. Dimensions are expressed as: minimum–maximum (mean) determined from 50 measurements. The trichomes form a red (10D7, Kornerup & Wanscher 1978) cushion-like, loose aggregate in liquid

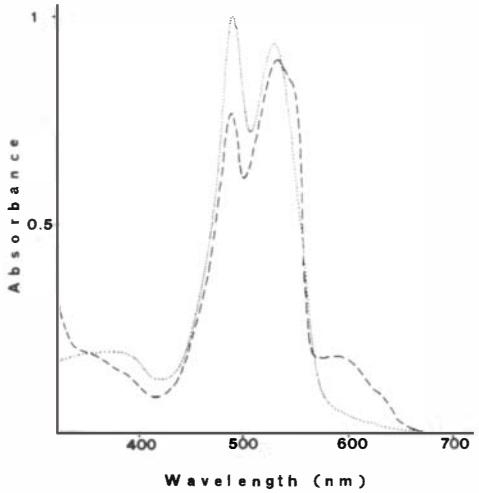

Fig. 2. Absorption spectra of the biliprotein crude extract (– – –) and of the purified CU-phycoerythrin (· · · · ·) from *Oscillatoria* cf. *corallinae*. Note the presence of APC (λ_{max} at 646 nm) and PC (λ_{max} at 608 nm) in the crude extract.

culture. The trichomes are 4.8–6.4 (5.5) μm wide, without any visible sheath, and are flexuous and constricted. The cells are wider than long, 1.9–4.0 (2.8) μm long, with a length: width ratio of 0.3–0.8 (0.5). Newly formed hormogonia are not attenuated at the apex and have rounded apical cells, whereas fully developed trichomes are attenuated towards the apex with a conical, pale apical cell (Fig. 1). The trichomes break by the formation of necridia and move by gliding. In old cultures, dark granules and refringent granules, possibly gas vesicles, are present along the cross-walls.

Culture conditions mainly influence cell width. At 12°C, cell width is narrower (4.1–6.1 μm). At 25°C and at high irradiances (40–74 μmol photons m^{-2} s^{-1}) cell width is slightly larger (5–8 μm). Maximum cell width (10.7 μm) was observed in a 100% salinity medium.

Cell length is less variable and maximum variation is found at 25°C at higher irradiances (1.8–5.8 μm) and at 100% salinity (1.6–5.9 μm).

The strain grows between 7 and 74 μmol photons m^{-2} s^{-1} at 25°C. At 12°C, some filaments survive between 7 and 40 μmol photons m^{-2} s^{-1} and at 35°C complete lysis is observed. Highest yields in MN medium are observed at 25°C and at 17 and 40 μmol photons m^{-2} s^{-1}. At the higher irradiance (74 μmol photons m^{-2} s^{-1}) the colour of the cells turns more orange (8B4, Kornerup & Wanscher 1978). The salinity range tolerated by the alga lies between 50 and 100% of seawater salinity, and best growth is obtained at 100%.

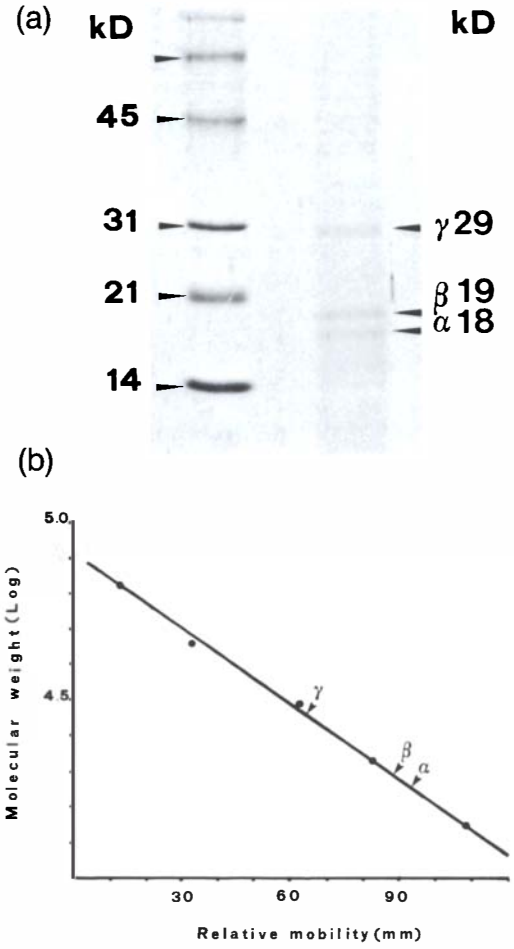

Fig. 3. (a) SDS–urea gradient gel (10–20%) of the purified CU-phycoerythrin after staining with Coomassie blue. Three bands corresponding to the α-, β-, and γ-subunits are visible. (b) Molecular weight determination of the sub-units of CU-phycoerythrin. Estimated values are 18 kD (α), 19 kD (β), and 29 kD (γ).

Pigments

Three different phycobiliproteins have been found in this species of *Oscillatoria* (Fig. 2). The phycocyanins are only present in small amounts under the culture conditions used; the absorption maxima at 608 and 646 nm most probably indicate the presence of C-phycocyanin and allophycocyanin respectively. The absorption spectrum of the isolated phycoerythrin, the major phycobiliprotein of strain CJ1, possesses two maxima at 494 nm and 540 nm. The pigment has a fluorescent emission maximum at 573 nm.

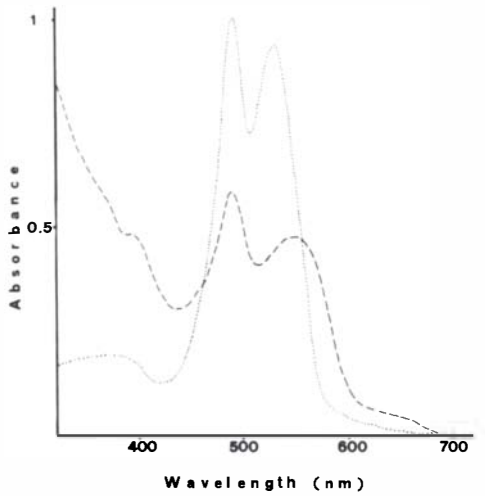

Fig. 4. Absorption spectra of purified (·····) and denatured (– – –) CU-phycoerythrin. PUB : PEB ratio was found to be 0.56.

The alga shows no chromatic adaptation under red light. The molecular weights of the subunits are 18 000 D (α), 19 500 D (β) and 29 000 D (γ) (Fig. 3). After denaturation (Fig. 4) the PEB: PUB ratio was found to be 1.76 : 1, indicating that there are about two phycoerythrobilins for each phycourobilin in the subunits.

DISCUSSION

The marine strain CJ1 most closely resembles descriptions of *Oscillatoria corallinae* and *O. nigroviridis* Thwaites ex Gomont. These two species differ mainly by the presence or absence of granules at the cross-walls, a variable character which depends on the physiological state of the organisms (Anagnostidis & Komárek 1988). Gomont (1890) and Lindstedt (1943) proposed uniting the two species, but Gomont (1893) subsequently treated them as two separate species.

The strain CJ1 differs from these two *Oscillatoria* species by its dimensions, its colour, and the morphology of the apical cell. However, the cell dimensions in the original descriptions of these two species are generally greater than those observed for our strain, but they lie within the possible variation range. Also, the colour of the strain CJ1 is red (even under red light), whereas Gomont (1893) and later authors (e.g. Setchell & Gardner 1919; Lindstedt 1943; Umezaki 1961) mention colours varying from blue-green, olive-green, eruginous to pale brown. According to Anagnostidis & Golubić (1968), *O. corallinae* exhibits chromatic adaptation. No thickening of the cell wall of the apical cell as mentioned by Gomont (1893) is found in strain CJ1. However, Gomont's illustration (1893, pl. 6, fig. 21) shows no such thickening, as has been pointed out by Lindstedt (1943). The conical apical cell of strain CJ1 appears only in fully developed trichomes. Its frequency may thus be variable in the field, depending on the sampling conditions, and it may have been overlooked in the original descriptions.

The morphology of the strain CJ1 is also close to that of *O. boryana* (Bory) Gomont ex Gomont. It differs from this species in having shorter cells and mainly by its habitat, as *O. boryana* is a species found in thermal areas (Geitler 1932). As uncertainties exist about the correct name to apply to this strain, we prefer to refer to it as *Oscillatoria* cf. *corallinae.*

The presence of two peaks at 494 and 540 nm is typical of phycoerythrins carrying phycourobilin and phycoerythrobilin chromophores. This group of pigments, generally simply called phycoerythrin in the literature, was named CU-phycoerythrin (CU-PE) by MacColl & Guard-Friar (1987). The properties of this type of phycoerythrin are still not very well known. It is rather heterogeneous with respect to its spectroscopic and subunit properties. Table 2 summarizes the properties of CU-phycoerythrin. In general, there are two absorbance peaks, one in the 490–505 region and one in the 540–567 region; a supplementary peak or shoulder may be present in *Trichodesmium* sp. (Fujita & Shimura 1974; Haxo *et al.* 1987). Isolation of a phycourobilin-containing phycoerythrin from a species of *Oscillatoria* expands our knowledge about the distribution of similar pigments among blue-green algae. Strain CJ1 is indeed only the ninth entity for which the pigment has been demonstrated. Among the unicellular blue-green algae, CU-phycoerythrin has been identified in four taxa belonging to the genera *Synechococcus* (marine picoplankton), *Synechocystis* (a marine symbiotic species) and *Gloeobacter* (a terrestrial species). For the filamentous blue-green algae, the presence of CU-phycoerythrin has been detected in the genera *Oscillatoria* (symbiont of sponges and ascidians; freshwater and thermal species) and *Trichodesmium* (marine plankton). So far it has not been found in nanocyte- and heterocyst-forming blue-green algae. This is the first report of the presence of CU-phycoerythrin

in a free-living marine *Oscillatoria* species. Owing to the rareness of the pigment among blue-green algae, its presence may be a taxonomic character of some importance.

It is not clear why this pigment replaces phycoerythrin in these blue-green algae, as its presence has been reported from widely different habitats. Wyman *et al.* (1985) suggested that for marine *Synechococcus* species phycoerythrin might function as a nitrogen reserve. CU-phycoerythrin seems especially important for picoplanktonic marine *Synechococcus* species. Alberte *et al.* (1984) showed that when marine *Synechococcus* strains were grown under low irradiances, the phycoerythrin-containing clones showed higher photosynthetic performance than strains lacking phycoerythrin. Furthermore, Glover *et al.* (1986) showed that a *Synechococcus* clone containing the PUB chromophore was able to photosynthesize more efficiently at low fluxes of blue light than a *Synechococcus* clone lacking this chromophore. These results indicate the high photosynthetic efficiency of phycoerythrin-containing organisms in low-light environments common to mid-depth neritic and oceanic habitats. Strain CJ1 was isolated from the infralittoral zone; such environments characteristically have primarily blue and green wavelengths available for photosynthesis because of the preferential absorption of red to yellow wavelengths by the water column. The presence of the phycourobilin chromophore, with an absorbance in the 450–500 nm region, should widen the absorption cross-section in the blue part of the spectrum and would thus be advantageous for organisms inhabiting the infralittoral zone.

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