The spectroscopic properties of two biliproteins, phycocyanin 645 and phycoerythrin 566, have been studied by treating the proteins with two different agents, NaSCN at pH 6.0, or pH 4.0 without NaSCN. For phycoerythrin 566, treatment with NaSCN revealed that the visible CD spectrum of its chromophores was separated into a pair of different spectra, and each of these spectra was observed as a negative and one or more positive bands. For phycocyanin 645, two negative CD bands have been observed previously, together with two or more positive bands, in the dimer \((\alpha_2\beta_2)\) state, and NaSCN treatment caused elimination of one of these negative bands. The dimer was stable at pH 6.0, but at pH 4.0 the spectra of phycocyanin 645 had one less negative band than those at pH 6.0. Chromatography demonstrated that phycocyanin 645 was a monomer \((\alpha\beta)\) at pH 4.0. Monomers of cryptomonad biliproteins have never been observed before. Excitation at 514 nm, in picosecond time-resolved fluorescence studies, produced lifetimes of 11.0 and 45.2 ps for dimers and monomers, respectively. Excitation at 566 nm yielded times of 1.38 and 1.24 ps, for dimers and monomers, respectively. CD in the far UV showed that monomers and dimers had very similar secondary structures. These results have been used to test an hypothesis that proposed two types of exciton splitting among the chromophores of phycocyanin 645, and perhaps phycoerythrin 566 could also have this chromophore organization.

Biliproteins are chromoproteins found in cyanobacteria, red algae, and cryptomonads. In the two former types, biliproteins are organized into phycobilisomes, but phycobilisomes do not occur in the cryptomonads. Light absorbed by biliproteins migrates from the site of absorption to the reaction center of photosystem II through a network of pairwise transfers of energy. These transfers are usually considered to occur via Förster resonance processes (for reviews, see Refs. 1–7).

These investigations are directed at a study of cryptomonad biliproteins by carefully dissociating their dimeric structure. Two directions have been taken: the treatment of phycocyanin 645 and phycoerythrin 566 with NaSCN at pH 6.0 and the effect of pH 4.0 on phycocyanin 645. Very little is known about phycocyanin 566 except that it has the usual cryptomonad dimeric \((\alpha_2\beta_2)\) protein structure and eight chromophores (23–25). These studies will advance insights into the functioning of this protein. For phycocyanin 645, there have been studies on its spectroscopic properties (26–30).

**EXPERIMENTAL PROCEDURES**

Phycocyanin 645 was obtained from the cryptomonad Chroomonas species and phycoerythrin 566 was from Cryptomonas ovata. The proteins were extracted and purified as described previously (30). Cells were grown in the laboratory, harvested, and stored frozen. After addition of pH 6.0, 0.1 ionic strength, sodium phosphate buffer, the frozen cells were thawed, and then the material was refrozen and thawed, which lysed the cells. The crude solution of phycocyanin 645, obtained after pelleting and removing cellular debris, was purified by precipitation with 80% saturated ammonium sulfate and two types of gel-filtration column chromatography (30). Except during chromatography steps, the protein was kept under 80% saturated ammonium sulfate in the cold. A ratio of \(A_{645}/A_{280}\) of 7.4 was considered pure for phycocyanin 645, and a ratio of \(A_{566}/A_{280}\) of 5.4 was the mark for phycoerythrin 566.

The purified proteins were dialyzed into distilled water, lyophilized, and stored in a freezer. As needed, protein was weighed and dissolved into the appropriate solvent. Two buffers were used extensively, pH 6.0, 0.10 ionic strength, sodium phosphate and pH 4.0, 0.10 \(\mu\) sodium acetate. For the pH studies, protein was dissolved into distilled water at a high concentration and then diluted to the proper protein concentration (0.20 \(\mu\)l) with pH 6.0 or pH 4.0 buffers. Measurements were made the same day as the solutions were prepared and were repeated over a 5-h period. A Hanna pH meter was used.

For the NaSCN experiments, a 2.0 M NaSCN solution was prepared in pH 6.0 buffer, and the pH was adjusted back to pH 6.0. A 0.4 \(\mu\) liter protein solution was prepared in pH 6.0 buffer and appropriate solutions were made so that there was a constant protein concentration of 0.10 \(\mu\) liter with varying concentrations of NaSCN. Solutions were stored in a refrigerator, and measurements were made after 1 or 2 days to ensure a completed change in the spectra.

For absorption studies, a Beckman DU 640 spectrophotometer was used. Measurements were made in a 1-cm light path, and the temperature was controlled at 23 °C with a Peltier device. For CD studies, a JASCO J-720 spectropolarimeter was used. The light path for the visible region was 5 or 10 mm, and for the far UV a 0.2- or 0.5-mm light path was used. For visible measurements, the buffers described above were used, and in the far UV the pH 6.0 buffer was the same, but the pH 4.0 buffer was 0.010 \(\mu\) sodium acetate. Temperature was kept at 23 °C with circulating water from a Neslab RTE III refrigerated circulator. A base line was taken with buffer at the same conditions as used for the sample and subtracted from each protein spectrum. Several scans were averaged on each sample to improve the signal-to-noise ratios. Noise was further reduced using a Savitzky-Golay filter. For data in the far UV region, molar units were calculated using a mean residue molecular weight of 105.4.

Fluorescence measurements were carried out using a Perkin-Elmer LS50B luminescence spectrophotometer. The protein concentration was 0.008 \(\mu\) liter for these measurements. Slits were both at 5 nm.
Dynamic light scattering measurements were made using a DP-801 instrument from Protein Solutions. The sample was illuminated at 780 nm using a solid state laser. The protein concentration was 0.40 g/liter. The main purpose of the dynamic light scattering, or quasi-elastic light scattering, was to obtain the diffusion coefficient \( D \) of phycocyanin 645, and then calculate the hydrodynamic radius from the Stokes-Einstein relation and the frictional coefficient \( f \) from \( D = kT f / \eta \). \( D \) was corrected to the value at 20°C and water (Equation 1), where \( T \) was the absolute temperature of the measurement; \( \eta_w \) was the viscosity of water at \( T \); \( \eta_20 \) was the viscosity of water at 20°C; and \( \eta_20 \) was the viscosity of buffer at \( T \).

\[
D_{20,w} = D \left( \frac{293}{T} \right) \left( \frac{\eta_w/\eta_20}{\eta_20/\eta_20} \right) \quad \text{(Eq. 1)}
\]

The DP-801 also allowed a careful scrutiny of the samples in terms of their homogeneity. Solutions of phycocyanin 645 in pH 6.0 buffer were shown to be monodisperse, in terms of size distribution, by this method.

Samples of phycocyanin 645 in pH 6.0 or 4.0 buffer at 0.20 g/liter were analyzed by high performance liquid chromatography using a Waters 625 liquid chromatography system. Samples were injected from an auto sampler (Waters 717 plus) onto a 300 SW Protein Pak column (Waters). The column \((8.0 \times 300 \text{ mm})\) was equilibrated in buffer and run under isocratic conditions. A photodiode array detector (Waters 996) was used to obtain the spectra of the bands. The gel filtration column was calibrated with molecular weight standards of 1,350, 17,000, 44,000, 158,000, and 670,000, which were vitamin B12, myoglobin, ovalbumin, \( \gamma \)-globulin, and thyroglobulin, respectively (Bio-Rad, standards).

The CD and absorption spectra of phycocyanin 645 were deconvoluted using the PeakFit program (Jandel Scientific). Four band types were tried either alone or in couples: Gaussian, Lorentzian, Voight, and Pearson VII. The method used a Levenberg-Marquardt interactive fitting. The spectra were in wave numbers \((\text{cm}^{-1})\) for the fitting.

Time-resolved fluorescence experiments (31–36) with picosecond resolution were performed using the frequency-domain method on an instrument that operated from 4 to 10 GHz. The excitation sources were a mode-locked argon ion laser or a Rhodamine 6G dye laser, which was cavity dumped at 3.81 MHz. The pulse width and wavelength of the argon ion and Rhodamine 6G lasers were 120 ps and 514 nm and 5 ps and 566 nm, respectively, and the number of photons in the pulse was 10^7. The area of the beam was 1 mm^2. The dye laser was pumped with a mode-locked argon ion laser (Coherent, Innova 15). Excitation was observed with a microchannel photomultiplier, and the cross-correlation detection was performed outside the photomultiplier tube. The frequency-domain intensities were fit to:

\[
I(t) = \sum \alpha_i e^{-\lambda_i t} \quad \text{(Eq. 2)}
\]

where \( \alpha_i \) are the pre-exponential factors; \( \lambda_i \), the decay times; \( \Sigma \alpha_i = 1.0 \). The parameters were recovered by a nonlinear least squares protocol. This instrumentation and data analysis have been shown to be useful down to 2 ps from the study of standard methods and materials. Excitation at 566 and 514 nm on samples having absorbances, in a 1-cm light path, between 0.10 and 0.16. A cutoff filter at 640 nm was used for the emission. With these optical conditions, no background signal was observed.

The parameters describing the decay were obtained by minimizing the goodness-of-fit indicator, \( \chi^2 \),

\[
\chi^2 = \frac{1}{v} \sum \frac{\phi_i - \phi_i^c}{\delta \phi_i} + \frac{1}{v} \sum \frac{m_i - m_i^c}{\delta m_i} \quad \text{(Eq. 3)}
\]

where \( \omega \) is the modulation frequency, \( \delta \phi = 0.200 \) and \( \delta m = 0.005 \) were the experimental uncertainties of phase shift \( \phi \) and modulation \( m \); \( v \) is the number of degrees of freedom, and \( c \) indicates a calculated value. The number of components used to fit a particular set of data was determined by trying various numbers and observing \( \chi^2 \) results. The frequency domain instrument was capable of observing a single picosecond with 5% \( \alpha \) contribution.

RESULTS AND DISCUSSION

Treatment with NaSCN—Phycocyanin 566 was treated with varying concentrations, 0–1.0 M, of NaSCN at pH 6.0 and the visible CD (Fig. 1) and absorption (Fig. 2) spectra were obtained. The protein concentration was 0.10 g/liter for all samples, and solutions were measured 1 or 2 days after addition of NaSCN. The absorption spectra in NaSCN (Fig. 2) exhibited a blue shift for the absorption maxima as the thiocyanate concentration was increased. A particularly interesting observation resulted when difference CD spectra were obtained by subtracting the CD in various concentrations of NaSCN from the spectrum in pH 6.0 buffer (Fig. 3). The difference spectra had both a positive and negative band, and the spectra that remained in the various concentrations of NaSCN also had both a positive and a negative band, but the positive bands of the two spectra were at different wavelength maxima (Table I).

These results were intriguing because of a particular feature of CD spectroscopy involving exciton splitting. When two chromophores are sufficiently close together and at a proper orientation, monomer spectra are split into two bands, one higher and one lower in energy. The CD spectrum of such a pair is distinctive, having one positive and one negative band of equal rotational strength, a conservative spectrum (37). In addition, the rotational strength of the bands in the pair should be larger than the bands of the monomers, and the zero crossover of the two bands from the pair should be at the absorption maximum. Results (Figs. 1 and 3; Table I) obtained for phycocyanin 566 suggested that two different pairs of chromophores might be involved in exciton splitting. This observation does not prove that exciton splitting is occurring, but points toward it as a speculative possibility. Another possibility is that the spectrum is a combination of various overlapping individual bands, some positive and some negative.

Experiments with phycocyanin 645 and NaSCN produced similar results to those with phycocyanin 566 (Figs. 4 and 5), but the thiocyanate appeared to have a stronger effect for the phycocyanin. The red-edge negative for phycocyanin 566 persisted even at 1.0 M NaSCN, a condition where very little rotational strength is present at any wavelength. An important difference between the CD spectra of phycocyanin 566 and phycocyanin 645 at pH 6.0 was the appearance of two negative

![CD spectra of phycocyanin 566 in 0–1.0 M NaSCN, pH 6.0. Numbers on curves refer to molarities of NaSCN.](http://www.jbc.org/content/27556/1/55/F1.large.jpg)

![Absorption spectra of phycocyanin 566 in 0–1.0 M NaSCN, pH 6.0. Numbers on curves refer to molarities of NaSCN.](http://www.jbc.org/content/27556/1/55/F2.large.jpg)
bands for the latter and only one for the former. The weak blue-edge negative for phycocyanin 645 is apparently completely removed by concentrations of NaSCN of 0.30 M. The other bands are reduced in intensity under the same conditions. An isosbestic point is observed coincident to the zero crossover point at 626 nm, and there are indications of a second isosbestic points at 550 nm by excluding spectrum of the 1.0 M NaSCN solution of phycocyanin 645 (Fig. 4). The CD spectra of both biliproteins suggested that each has thiocyanate-sensitive and thiocyanate-resistant spectroscopic features, and may further indicate similarities in structure for these proteins. The cyanobacterial biliproteins, C-phycocyanin, allophycocyanin, and phycoerythrocyanin, have been shown to dissociate to monomers in the presence of about 1 M NaSCN (38–40).

Monomers—Phycocyanin 645 is an $\alpha_2\beta_2$ polypeptide dimer at pH 6.0, and there are at least two different $\alpha$ polypeptides (41). The two $\alpha$ polypeptides carry the same tetrapyrrole chromophores (42). The structures of the various chromophores are known (43). The effect of pH was examined at 0.20 g/liter of protein using visible absorption, fluorescence (Fig. 6), and CD spectroscopy (Fig. 7). The results suggested that, at pH 5.0 and 6.0, the dimer is retained, and at pH 2.8 the protein is denatured. At pH 4.0, an intermediate result is observed, and the salient observation is that the negative CD band on the blue-edge of the spectrum is completely eliminated (Fig. 7). The results at pH 4.0 are very suggestive of the effects found by addition of NaSCN above 0.30 M (Figs. 4 and 7).

The pH 4.0 solutions with a 0.20 g/liter protein concentration were analyzed by gel-filtration column chromatography (Fig. 8), as were samples in pH 6.0 (data not shown). The results were analyzed with substances of known molecular weights, and it was determined that the dimer (approximately 50,000 molecular weight) was completely dissociated at pH 4.0 to monomers (approximately 27,000 molecular weight). Chromatography experiments were started as soon as protein was dissolved in buffer. Injections of protein at pH 4.0 on the column continued at 20-min intervals for about three hours. The retention times were essentially identical at all times examined.

Monomers of cryptomonad biliproteins have never been produced before and are of interest because they are the simplest unit of protein structure that possesses single copies of each of the four unique chromophores. Since there are at least two

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**Fig. 3.** CD difference spectrum of phycoerythrin 566. Curves are marked as follows: 0, no NaSCN; 0.4, 0.4 M NaSCN; 0–0.4, difference spectrum of no NaSCN minus 0.4 M NaSCN solution.

**Table I**

The CD maxima for phycoerythrin 566 in NaSCN and the maxima of the difference spectra obtained by subtracting the NaSCN-changed spectra from the spectrum with no NaSCN.

| [NaSCN]  | CD maxima in NaSCN | ΔCD          |
|---------|-------------------|--------------|
|         | [nm]              | [nm]         |
| 0.10    | 574               | 544          |
| 0.30    | 574               | 542          |
| 0.40    | 574               | 542          |
| 0.50    | 574               | 541          |
| 1.00    | 575               | 542          |

**Fig. 4.** CD spectra of phycocyanin 645 in 0–1.0 M NaSCN, pH 6.0. Numbers on curves refer to molarities of NaSCN. One panel (A) shows the whole region, and in B an expanded CD scale of a portion of the spectra is shown.

**Fig. 5.** Absorption spectra of phycocyanin 645 in 0–1.0 M NaSCN, pH 6.0. Numbers on curves refer to molarities of NaSCN.
Biliproteins function by transferring excitation energy from chromophore to chromophore until the energy is passed to the next pigment in the chain. When isolated, the biliproteins instead emit fluorescence from the lowest energy chromophores. Monomers and dimers were excited at 540 nm, and the fluorescence emission spectra obtained (Fig. 6). In both cases, the maxima were at 661.5 nm. This result showed that energy transfer in the monomer still occurs from the high to the low energy chromophores, and the lowest energy chromophore was retained as the principal emitter for the monomer. The monomer emission was hypochromic when compared to the low energy chromophores, and the lowest energy chromophore was retained as the principal emitter for the monomer.

How does monomer formation affect energy migration from the higher to the lowest energy chromophores? This can be considered by using picosecond time-resolved fluorescence methods. Picosecond fluorescence studies have been used previously on phycoerythrin 566 dimers (27, 45–49), but they have never been employed, of course, on monomers and never with dimers at excitation wavelengths in the vicinity of where the blue-edge negative band in dimers, Davydov splitting has previously been estimated at about 91 cm⁻¹ from CD spectra. The estimation of this splitting for the blue-edge negative band is not that reliable because the corresponding positive band is only observed through deconvolution methods.

**FIG. 9.** CD spectra of phycocyanin 645 at pH 6.0 after being pH 4.0 Solutions at pH 4.0 (dashes), original pH 6.0 (dots), pH 6.0 from pH 4.0 (solid line).

**TABLE II**
The deconvolution of the spectra of phycocyanin 645 monomers The presumed Davydov splitting between these bands is, therefore, in the range of 1566 cm⁻¹ (from CD) to 1728 cm⁻¹ (from absorption). For the blue-edge negative band found in dimers, Davydov splitting has previously been estimated at about 91 cm⁻¹ from CD spectra. The estimation of this splitting for the blue-edge negative band is not reliable because the corresponding positive band is only observed through deconvolution methods.

| Wavelength maxima | Types of component | Areas (mded cm⁻¹) |
|-------------------|--------------------|-------------------|
| 561               | Gaussian           | 7,840             |
| 585               | Gaussian           | 20,600            |
| 564               | Gaussian           | 9,204             |
| 613               | Gaussian           | 9,204             |
| 652               | Gaussian           | 341               |
| 630               | Gaussian           | 1,308             |
| 576               | Gaussian           | 989               |
| 554               | Pearson            | 1,328             |
645 (Fig. 11 and Table IV). The fastest times are attributed to energy transfer, and for excitation at 566 nm these times are 1.24 ps (monomer) and 1.38 (dimer), essentially unchanged. When the excitation was at 514 nm, however, the times were quite different, being 45.2 ps (monomer) and 11.0 ps (dimer). The 514-nm excitation will excite chromophores in the region where the blue-edge negative CD band is eliminated by monomer formation (Fig. 7).

CONCLUSIONS

Dynamic light scattering on a 0.4 g/liter solution of phycocyanin 645 at pH 6.0 gave a $D_{20,w}$ of $6.49 \pm 0.10 \times 10^{-7}$ cm$^2$/s with a dynamic radius of 3.3 nm. Using the equation, $f_0 = kT/D$, the frictional coefficient ($f_0$) is calculated to be $6.28 \times 10^{-8}$ g cm$^{-1}$ s$^{-1}$. A frictional coefficient for a spherical molecule, $f_o$, has been calculated, using a molecular weight of 57,000 and a partial specific volume of 0.729, to be $4.80 \times 10^{-8}$ g cm$^{-1}$ s$^{-1}$. The $f/f_o$ was then 1.31. This ratio deviates from that for a perfectly spherical molecule.

Previously, a hypothesis was advanced in which phycocyanin 645 was suggested to have six of its chromophores ordered as two different pairs of chromophores engaged in exciton splitting and two chromophores that are more isolated (29). One of the chromophore pairs produced the red-edge CD negative at 644 nm and the positive band at 585 nm, and there are two such chromophore pairs. The second chromophore pair has the blue-edge negative at about 514 nm, but its corresponding positive component is not discernible in the CD spectrum. This band may be hidden by the stronger neighboring band at 585 nm, and there would be one such chromophore pair in the $\alpha_3\beta_2$ structure. The former of these pairs of chromophores could exist within a monomer, and the latter pair would exist across the monomer-monomer interface. Clearly, if this proposal has any validity when the protein dimer dissociates to monomers, the putative blue-edge exciton splitting would be eliminated and the two bands would be replaced by a single CD band. As noted with pH 4.0 buffer this change occurred (Fig. 7). In the deconvolution of the monomer CD spectrum, a positive band is calculated to be at 561 nm (Table II). This 561-nm band would be the chromophore that would split into higher-and low-energy bands if exciton splitting developed upon dimer formation. The 613-nm CD band is assigned to the chromophores not involved with exciton splitting even when the protein is a dimer.

The second possible case of exciton splitting, found on the red edge of the CD spectra, persisted after monomer formation. The deconvolution of the monomer CD spectrum puts this pair at 644 and 585 nm (Table II). If these bands are produced by a pair of chromophores involved in exciton splitting, then (in addition to one having a positive and a negative CD band) the bands must be equal in rotational strength and must be greater

![Fig. 10. CD spectra in the far UV for phycocyanin 645 at pH 6.0 and 4.0. A 0.2-mm light path was used, and spectra were obtained from 182 to 260 nm. Protein concentration was 0.20 g/liter for these experiments. The pH 4.0 spectrum is dashed and the pH 6.0 is a solid line.](image)

![Fig. 11. Picosecond time-resolved fluorescence results for phycocyanin 645 monomers. Upper panels are for excitation at 514 nm, and lower panels are for 566-nm excitation. The modulation data decline as frequency increases, and the phase angle degrees increase as frequency increases.](image)
in rotational strength than a monomer band. In Table II, both these criteria are observed to be well met. A model based on the monomer data presents a possible chromophore distribution for a dimeric protein (Fig. 12). The model indicates that chromophore dimers may be very important in intraprotein energy migrations. Internal conversion from the high to low energy bands of the chromophore dimers will serve as the main conduits for exciton flow through the molecule. Inspection of the bands of the chromophore dimers will serve as the main conduits for exciton flow through the molecule. Inspection of the bands of the chromophore dimers (Fig. 12). The model indicates that chromophore dimers may be very important in intraprotein energy migration.

The wavelength maxima of the component bands in thiocyanate agree very well with the component bands found for the pH 4.0 monomeric solutions (Table V). The finding that two very different approaches, pH 4.0 and thiocyanate, produced virtually identical spectra suggests that these spectra are not artifacts of a particular method (Tables II and V).

Broadening this discussion, what about the general decline in rotational strength and absorption (Fig. 7) when monomers form? These changes would not occur just because a pair of coupled chromophores became separated, and the hyperchromicity also occurs in spectral regions distal to the changes in the blue edge of the spectrum. When monomers are produced, there is a change in the structural support to each monomer. In the dimer, protein is packed with protein on the monomer-monomer surface, but in the monomer water replaces protein. It can be speculated that the resulting difference in stabilization may produce changes in the tertiary structure of the protein that impacts on the chromophores producing a loss in absorption and rotational strength. For example, a change in the chromophore to a slightly more cyclic conformation could lower its absorption in the region of the first excited state (1), while raising the absorption in the near UV. The CD results in the far UV indicate that the polypeptide portions of the protein retain similar conformations in the dimer and monomer states (Fig. 10). Therefore, the changes in the spectra must stem from changes localized in the vicinity of one or more chromophores. Solvation and conformation changes for the tetrapyrroles are consistent with these experimental results.

Now for phycoerythrin 566, in the comparison of the spectra of this protein in NaSCN with the difference spectra obtained by subtracting the spectra in NaSCN from the spectrum without NaSCN (Fig. 3 and Table I), the possibility of two different sets of chromophores being involved in exciton splitting is brought out. The key is the negative band, if two types of exciton splitting do exist then this negative band must be a composite of two overlapping bands with nearly identical wavelength maxima, but rigorous evidence is lacking on the possibility. Another cryptomonad phycoerythrin, phycoerythrin 545, has been studied spectroscopically and also has CD spectra suggesting the possibility of two different types of exciton splitting (50, 51).

Monomers of phycoerythrin 645 have been produced for the first time for any cryptomonad biliprotein. Monomers lack a small negative CD band found on the blue-edge of the dimer spectrum, and there is a general loss in absorption and rotational strength for all chromophores. Still, the spectra for the chromophores in the monomer of phycoerythrin 645 resemble those of the protein dimer and the secondary structures of their polypeptides are the same; this quaternary form is, therefore, clearly not a denatured state. The maintenance of a very fast energy transfer time upon 566-nm excitation supports the basic integrity of the monomer as a functioning protein.

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