The Crystal Structure of a Novel Unmethylated Form of C-phycocyanin, a Possible Connector Between Cores and Rods in Phycobilisomes

Noam Adir‡ and Natalia Lerner
From the Department of Chemistry and Institute of Catalysis, Science and Technology, Technion, Israel Institute of Technology, Technion City, Haifa 32000, Israel

A novel fraction of c-phycocyanin from the thermophilic cyanobacterium Thermosynechococcus vulcanus, with an absorption maxima blue-shifted to 612 nm (PC_{612}), has been purified from allophycocyanin and crystallized. The crystals belong to the P6_3 space group with cell dimensions of 153 Å × 153 Å × 59 Å with a single (αβ) monomer in the asymmetric unit, resulting in a solvent content of 65%, and diffract to 2.7 Å. The PC_{612} crystal structure has been determined by molecular replacement and refined to a crystallographic R-factor of 20.9% (R_{free} = 27.8%). The crystal packing in this form shows that the PC_{612} form of phycocyanin does not associate into hexamers and that its association with adjacent trimers in the unit cell is very different from that found in a previously determined structure of the normal form of T. vulcanus phycocyanin, which absorbs at 620 nm. Analysis of the PC_{612} structure shows that the α subunits, which typically form the interface between two trimers within a hexamer, have a high degree of flexibility, as indicated by elevated B-factors in portions of helices B, E, and G. Examination of calculated electron density omit maps shows that unlike all other structures of phycobiliproteins determined so far, the Asn^{72} residue is not methylated, explaining the blue-shift in its absorption spectra. On the basis of the results presented here, we suggest that this new form of trimeric phycocyanin may constitute a special minor component of the phycobilisome and may form the contact between the phycocyanin rods and the allophycocyanin core.

Cyanobacteria and red algae efficiently harvest light used for photo-induced electron transfer by a variety of pigment-protein complexes attached to photosynthetic reaction centers. The sizes of such complexes vary between species and growth conditions and can easily reach molecular masses in excess of 2 MDa. The self-association of the protein subunits has been studied and documented for a variety of species and shows different complex forms. All pigment-binding protein species show a canonical first level quaternary structure of the association of two pigment-binding subunits termed α and β into the basic (αβ) monomer. The monomers further assemble into higher organizational levels of (αβ)$_3$ trimers and (αβ)$_6$ hexamers. The trimers (and hexamers) are round disks with dimensions of about 110 × 30 Å (or 60 Å for the hexamers). The hexamer encloses a large internal cavity with triangular shaped openings on both sides. The most prevalent PB forms, found in many cyanobacteria, are made up of a core assembly of three hexamers of allophycocyanin (APC) that are arranged with their ring planes perpendicular to the membrane surface directly above Photosystem II complexes (4). On this core are arranged six rod-like structures, made up of phycocyanin (PC) hexamers. In some species, and under certain environmental conditions, additional phycocerythrin (or other phycobiliprotein variants) hexamers attach at the terminal ends of the PC rods (12). The planes of the rings that make up the hexamers in the rods are perpendicular to both the APC core and to the membrane, so that in essence the APC hexamer disks bind the PC rods by their outer circumference. In addition to the pigment-binding phycobiliproteins, a number of linker proteins have been found associated with PB components (6, 7). It has been suggested that these linker proteins occupy positions running through the internal cavities of the disks and may play roles in complex stabilization, rod-core assembly, and in inducing the directionality of energy transfer toward Photosystem II. Light energy trapped by the most prevalent pigments (phycocerythrobilin, $\lambda_{max} = 560$ nm; phycocyanobilin, $\lambda_{max} = 620$ nm) traverses down through the rods to the APC pigments ($\lambda_{max} = 652$ nm) and from these pigments to the chlorophyll pigments of the reaction center ($\lambda_{max} = 674–680$ nm) (3, 4).

A significant number of PB protein structures have been determined over the past few years (8–25). All of these structures show a very high degree of similarity in the overall structures, the details of the pigment surroundings, the solvent interactions, and the protein residue positions in each structure, and thus have given us an excellent molecular view of the constituents of the PBs. However, a true structural description of how these different components interact is still lacking, due to the fact that the structures of each of the components has been determined separately. Because there appears to be a certain degree of correlation between the formation of hexamers and rods during the crystallization process and the actual
PB rods, it has been suggested that the overall packing of the crystal unit cell can help identify energy transfer pathways between pigments at all levels, including inter-rod energy transfer (9, 20, 21, 24). Biochemical, biophysical, and electron microscopic studies of the PB have been interpreted and promoted a number of models of the entire PB (5, 26–29). These studies were performed on a variety of PB forms, from different species, with different numbers of APC core disks. There are, however, geometric problems with the schematic models of the PB structure. To assemble six PC rods around the three APC disks, interpenetration of the rods must occur, because the circumference if the core is significantly smaller than the sum of the rod diameters. Intercalation of the circumference of one PC hexamer into the molecular circumference of an adjacent hexamer would necessitate the presence of large cavities in the circumference. Analysis of the crystal structures of many PB hexamers has not shown such cavities to exist, indicating that such interpenetration is not possible.

We have recently determined the structure of the PC component of phycobilisomes from the thermophilic cyanobacteria *Thermosynchococcus vulcanus* (*Tv*-PC, formally *Synchococcus vulcanus*) at high resolution (1.6 Å, Protein Data Bank code 1KTP; see Ref. 25). This structure, along with a room-temperature structure at lower resolution (2.5 Å, Protein Data Bank code 1I7Y; see Ref. 23) allowed the detailed analysis of a number of important structural details pertaining to the structure, function, and stability of this protein.

In the present study we have identified and determined the structure of a novel form of *Tv*-PC, which we believe may prove to be a functional and structural link between the rods and cores of the phycobilisomes, helping to avoid the interpenetration problem in PB assembly.

**EXPERIMENTAL PROCEDURES**

**Protein Isolation, Characterization, and Crystallization—Phycocyanin** with an absorption maxima of 612 nm from the thermophilic cyanobacterium *Thermosynchococcus vulcanus* (*PC* 612) was isolated by the following procedure.

Cyanobacterial cells were grown at 55 °C for 3–4 days with 5% CO₂ in air added continuously to the growth medium. Cells were harvested by centrifugation, washed in Buffer A (20 mM Hepes, pH 8.0) and then treated with 1 mg/ml lysozyme (Sigma) at 55 °C for 60 min. The cells were then ruptured using a Yeda Pressure cell using 25 atmospheres of N₂. Broken cell debris was separated from the photosynthetic membranes by centrifugation, and the membranes were then pelleted. The supernatant contained large amounts of PC absorbing at 620 nm (*PC* 620). The membranes were then treated with Buffer A with 2 M KCl, which removed the remaining phycobiliproteins. Following removal of the membranes by centrifugation, the soluble fraction was treated with polyethylene glycol 4000 to precipitate contaminating *PC* 620, and fractions that absorbed at 651 nm (APC) were pooled. The APC-rich fraction was further fractionated by anion-exchange chromatography (DEAE, Toyohashi), using Buffer A as the mobile phase. A salt gradient of 0–300 mM NaCl in Buffer A was used to separate between different protein fractions, with a fraction containing *PC* 612 eluting at 130 mM NaCl and APC eluting at 200 mM NaCl. Protein fractions were analyzed for purity by SDS-PAGE, and the aggregation state was determined by size-exclusion HPLC (PL-GFC 1000 Å, Polymer Laboratories Ltd.).

**Data Collection and Structure Determination—** *PC* 612 crystallized in the P6₃ space group with cell dimensions of a = b = 153 Å = 39 Å and γ = 120° and diffracted maximally to 2.7 Å. A data set was collected using a single crystal on beamline X11 of the EMBL-Hamburg outstation at DESY using an MAR CCD detector (Table I). The data was scaled and merged using the DENZO/SCALEPACK suite (30). The final data was 84.7% complete to 2.7 Å and was used for structure determination by molecular replacement with CNS (31) using the 1.6 Å *Tv*-PC structure (Protein Data Bank code 1KTP; see Ref. 25) as the search model (see “Results” for further details).

**Refinement—** The structure was refined using CNS (31). Following simulated annealing, B-factor refinement, and water molecule addition, the structure was inspected against electron density maps calculated in CNS and examined visually using Quanta (Accelrys). Extensive use of calculated omit maps were used to manually adjust and confirm the positions of all residues and co-factors. The final model had a crystallographic R-factor of 20.9% and a Rfree of 27.8%. The coordinates and structure factors were deposited in the Protein Data Bank under the code 1ON7.

**RESULTS**

**Isolation, Characterization, Crystallization, and Structure Determination**

**PC 612 Isolation and Characterization—** We have previously determined the structure of *Tv*-PC in a rhombohedral crystal space group. Protein for crystallization was isolated in trimeric form from the thylakoid membranes following detergent treatment and anion-exchange chromatography (23). The isolated protein had an absorption maxima at 620 nm, as has been reported previously (4) for PC. This form of *Tv*-PC resulted in two crystal structures, the first from data collected at room temperature (Protein Data Bank code 1I7Y, 2.5 Å resolution; see Ref. 23) and the second from data collected at 100K from frozen crystals (Protein Data Bank code 1KTP, 1.6 Å resolution; see Ref. 25).

Following our successful determination of the *Tv*-PC structure at high resolution, we decided to obtain a more complete picture of this species phycobilisomes by determination of the...
PC$_{612}$ has a single monomer in the asymmetric unit, with two (αβ)$_3$ trimers in the unit cell (Fig. 2). Interestingly, the PC$_{612}$ form of Tc-PC is similar to the first PC structure determined that from *Mastigocladus laminosus* (this structure has not been deposited in the Protein Data Bank; see Ref. 10).

### Refinement

The PC$_{612}$ structure was refined using maximum likelihood simulated annealing (31), followed by multiple rounds of B-factor, coordinate minimization, and manual fitting. The locations of 36 water molecules were identified, and the final refined structure (Table II) had a crystallographic R-factor of 20.9% ($R_{	ext{free}}$ was 27.8%). All geometric constraints were within or better than the mean values as determined by the Protein Data Bank ADIT validation server. Only the highly conserved Thr$^{77}$ residue has non-typical peptide geometry ($\Phi = 76.7^\circ$, $\Psi = 128.3^\circ$), as has been found for this residue in all previously determined PC structures (10, 23).

### Overall Quality of the Structure

The PC$_{612}$ structure shows the typical globin-like fold identified in the past (8). The overall structure is similar to the previously determined high-resolution structure 1KTP with a root mean square deviation coordinate difference of 0.82 and 1.02 Å over all α carbon and all atoms respectively.

However, a number of characteristics make the PC$_{612}$ structure unique. The (αβ)$_3$ monomers are organized into (αβ)$_3$ trimers, which were also the basic unit in solution prior to crystallization. The packing of the unit cell (Fig. 2) shows that the trimers are not associated further into (αβ)$_3$ hexamers, as was previously shown in the 1KTP structure, as well as for many other PC structures (8–9, 11–28). The immediate result of this form of crystal packing is a high solvent content (65%) as opposed to only 42% for the 1KTP structure. One consequence of the high solvent content is the relatively high B-factors, especially those of certain stretches of the α subunit. In crystal structures made up of (αβ)$_3$ hexamers (i.e. 1KTP), the α subunits form most of the trimer-trimer contacts, whereas the β subunits are involved in the formation of both the (αβ) monomer-monomer and in (αβ)$_3$ hexamer-(αβ)$_3$ hexamer interactions. In the PC$_{612}$ structure, the α subunits have few intermolecular contacts (Fig. 3), whereas the β subunits link one another and thus are stabilized (Fig. 3). Each trimer is linked to an adjacent trimer by a very limited contact region formed by residues near the β155 co-factor (Fig. 2). In the 1KTP structure, the mean B-factor is 19.9 Å$^2$ for all protein atoms. In the PC$_{612}$ structure, the overall B-factor is considerably higher, 50.7 Å$^2$. The major source of this higher value is due to residues of the α subunit that has an overall B-factor of 59.8 Å$^2$, whereas the mean value of the β subunit is 38.8 Å$^2$. These values indicate a high degree of disorder in the α subunit, and the calculated electron density is rather weak for side chains of residues located on α-helices B and E (residues Ala$_{50}$–Ala$_{84}$) and helix G (residues 128–140). These residues are intimately involved in the binding of the α84 phycocyanobilin co-factor, and indeed the B-factors of this co-factor are significantly higher (>30 Å$^2$) than those of the other two co-factors.

The trimeric PC$_{612}$ structure has two very different molecular faces (Fig. 3), as opposed to the 1KTP and other hexamer-forming PC types. In the present structure one face is made up of β subunits enclosing a narrow triangular opening (Fig. 3a, blue surface), whereas the opposite face (Fig. 3b, orange surface) is made up of α subunits, which surround a rather large open volume. The β84 co-factors (Fig. 3, red surface) are more accessible from this side than from the β subunit side.

Only 36 solvent molecules could be identified in the PC$_{612}$ structure, as opposed to 377 molecules in the 1KTP structure and 88 in the 1I7Y structure. Although this can certainly be a
result of the lower resolution, we also attribute it to the elevated $B$-factors of the side chains.

Asparagine 72 of the $\beta$ subunit is unmethylated in PC$_{612}$

Another novelty of the PC$_{612}$ structure is found in asparagine 72 of the $\beta$ subunit. This residue has been found to undergo a post-translational modification by methylation of its $\gamma$-nitrogen atom. $\gamma$-N-methylasparagine has been found in many PB-containing species of cyanobacteria and red-algae, both by biochemical and structural analysis (33–35). In the previously determined high resolution Tv-PC structure (25) there was obvious electron density identifying the methyl group as seen in Fig. 4, $a$ and $b$. Similar density could be identified in the lower resolution 1I7Y Tv-PC structure (Ref. 23 and data not shown). When electron density maps surrounding the Asn$_{72}$ residue in the PC$_{612}$ structure were examined, we could not identify any additional density that could be associated with a methyl group. Simulated annealing omit maps (both $2F_o - F_c$ and $F_o - F_c$) were calculated using CNS (31), and although electron density surrounding the residue position itself is very clear, no additional density signifying the presence of the methyl group could be identified (Fig. 4c). The $B$-factors of the Asn$_{72}$ residue and its surroundings are quite low, so it does

| Table II |
| --- |

Refinement statistics

| Resolution range (Å) | 30-2.7 (2.8-2.70) |
| Reflections in work set (test set) | 9088 (1000) |
| $R_{cryst}$, ($\%$) | 20.9 (34.6) |
| $R_{free}$, ($\%$) | 27.8 (32.0) |
| RMS deviations |
| bond length deviation (Å) | 0.0085 |
| angle deviation (degrees) | 1.26 |
| Average $B$-factor ($\AA^2$) | 50.7 |
| $\alpha$ subunit | 59.8 |
| $\beta$ subunit | 38.8 |
| co-factors | 58.5 |
| Final model |
| Total number of atoms | 3035 |
| Protein | 2499 |
| Non-protein atoms | 129 |
| Co-factor | 36 |
| Water | 332 |
| Number of amino acids | 3 |
| Cofactor molecules | 3 |

Statistics for data with $F_o > 1.3\sigma$. Numbers in parenthesis correspond to the highest resolution shell (2.8-2.7Å).

$R_{cryst}$, $R_{free} = \sum |F_o| - |F_c|/\sum |F_o|$ where $R_{cryst}$ and $R_{free}$ are calculated using the working and test reflections, respectively. The test reflections were held aside and not used during the entire refinement process.

Asparagine 72 of the $\beta$ subunit is unmethylated in PC$_{612}$

Another novelty of the PC$_{612}$ structure is found in asparagine 72 of the $\beta$ subunit. This residue has been found to undergo a post-translational modification by methylation of its $\gamma$-nitrogen atom. $\gamma$-N-methylasparagine has been found in many PB-containing species of cyanobacteria and red-algae, both by biochemical and structural analysis (33–35). In the previously determined high resolution Tv-PC structure (25) there was obvious electron density identifying the methyl group as seen in Fig. 4, $a$ and $b$. Similar density could be identified in the lower resolution 1I7Y Tv-PC structure (Ref. 23 and data not shown). When electron density maps surrounding the Asn$_{72}$ residue in the PC$_{612}$ structure were examined, we could not identify any additional density that could be associated with a methyl group. Simulated annealing omit maps (both $2F_o - F_c$ and $F_o - F_c$) were calculated using CNS (31), and although electron density surrounding the residue position itself is very clear, no additional density signifying the presence of the methyl group could be identified (Fig. 4c). The $B$-factors of the Asn$_{72}$ residue and its surroundings are quite low, so it does

FIG. 2. Visualization of the PC$_{612}$ unit cell. $\alpha$ subunits and $\beta$ subunits are in orange and blue, respectively. $\alpha$4, $\beta$84, and $\beta$155 co-factors are in yellow, red, and magenta CPK representation, respectively. The interaction between trimers is limited to a small overlap near the $\beta$155 co-factor. The figure was prepared with InsightII (Accelrys).

FIG. 3. Two views of the molecular surface of the PC$_{612}$ ($\alpha\beta_3$) trimer. The $\alpha$ and $\beta$ subunits are in orange and blue, respectively. The $\beta$84 co-factor is in red (jutting out into the center of the trimer). $a$, the $\beta$ subunit side, showing the small triangular aperture. $b$, the $\alpha$ subunit side, showing the large opening allowing a possible close contact with the $\beta$84 co-factor. The figure was prepared with InsightII (Accelrys).
not appear that the lack of electron density is due to flexibility in the site. We thus propose that the unmethylated PC$_{612}$ is a novel form of Tv-PC. This result concurs with absorption spectra measurements of unmethylated or undermethylated PC species that showed a blue-shift in their absorption spectra (35).

DISCUSSION

The PB is an antenna complex finely tuned to transfer energy to the reaction center of Photosystem II with an efficiency of over 95% (36). It performs this function with a high degree of directionality, even though there are large numbers of similar pigment molecules within each complex (3). A number of possible energy transfer pathways have been described in great detail on the basis of crystal structures and Förster energy transfer theory (10, 12, 20). The initiation point of energy transfer takes into account that each of the different phycobilin pigments has modified absorption/emission properties as a result of the unique chemical background formed by the protein matrix. In PC, the three phycocyanobilin co-factors have slightly different absorption maxima, and in combination with their relative geometric position it has been proposed that the β155 co-factor is a sensitizing type pigment (absorbing to the blue), the β84 co-factor is a fluorescing type pigment (absorbing further to the red), and the α84 co-factor is an intermediate pigment type (4). It has previously been proposed that methylation of Asn$^{β72}$ is required to isolate the β84 co-factor from solvent interactions, thereby altering its absorption and emission properties (34, 35). Indeed, in a cyanobacterial strain deficient in the phycobiliprotein methylation (αβ) monomers had a slightly blue-shifted absorption spectra and showed less PC-APC energy transfer in vivo (35). In studies of a variety of species, different relative amounts of methylated versus unmethylated phycobiliproteins were identified, indicating that at least some fraction of the proteins may be unmethylated (35). One could envision changes in the primary sequence of the
β subunit that could bring about the same result achieved by methylation. Because the machinery required for post-translation methylation is ubiquitous in phycobiliproteins, it would appear that there is an evolutionary advantage to the presence or lack of the methyl group. The state of methylation could represent a site for the fine-tuning of the properties of the β84 co-factor with the existence of non-methylated protein serving a special role.

The PC612 identified in this study was isolated as a fraction of PC that co-purified with the APC core proteins. The co-purification might be an indication of the proximity between the two protein types. If so, what could be the possible role of the PC612 be?

To form a complete PB, a number of architectural problems must be overcome. If the entire PB is made up of disks (hexamers of phycoerythrin, PC, or APC), these disks must fit one onto another in some ordered fashion, as has been seen in electron micrographic studies (4, 5) and at least appears to be simulated in most PB protein crystal structures (20, 21, 24, 25).

Interpretation of these experimental observations suggests that two rods on either side of the APC core lie in a parallel fashion, with a third rod doublet perpendicular to the other rods (3) or at an angle (24). The first problem with this arrangement lies in matching the sizes of the PC rods and APC core (Fig. 5). The first layer is composed of two APC hexamers (Fig. 5, dashed disks), whereas the second layer contains a single APC hexamer, which fits into the “saddle” in the first layer interface. The total height of the core is thus less than twice the diameter of a single disk. If each disk is about 110 Å in diameter, then the total core height (Fig. 5) is only about 190 Å.

When the first layers of rods (Fig. 5, R1, horizontal lines) attach to the core (parallel to the membrane surface) the circumference of the APC disk can attach to the triangular aperture of the terminal PC hexamer and bring the PC β84 co-factors into the direction of the APC β84 co-factors. However, the second layer of PC hexamers (Fig. 5, R2) cannot now fit in a manner similar to that of the first layer because the total height of the two layers is about 220 Å, and the circumference of the top APC hexamer will not be centered in the PC hexamer orifice. Because both R2 rods must contact the single APC hexamer, they are indented in relation to R1 by the radius of the APC disk, which is about 55 Å or less than a complete hexamer (about 60 Å). The last PC rod types (Fig. 5, R3) are layered perpendicular to the R1 and R2 rods (3), and the contact with the top APC hexamer must be different, because both orifices cannot simultaneously meet the disk circumference (if they lie in a parallel fashion). A recent suggestion by Jiang et al. (16) shows the R3 rods as separate, and thus four rods contact a single APC hexamer. However, this would necessitate interpenetration of the rods, because one cannot fit four 110 Å rigid disks around the available circumference of a single APC hexamer (whose total available circumference is less than 350 Å). Examination of the PC hexamer does not show any cavities that might allow the interpenetration of the rods, and thus a different solution is needed. One possibility is that the four rods of type R2 and R3 are positioned further away from the APS core, thus allowing the four rods to be arranged around a single hexamer. This large separation might be performed by as yet unidentified linker proteins (1, 5, 26, 28, 37, 38). This arrangement would, however, separate the terminal PC co-factors from the core co-factors and significantly lower the energy transfer efficiency. Another possibility is that a single, flexible trimer may be situated in between the rods and core. PC612 may serve in this interstitial role (Fig. 5, concave disks). Each P612 trimer has two different faces (unlike PC hexamers in which both outer faces are identical). One face has mostly β subunit residues facing out (Fig. 3a), which could associate with the terminal rod hexamer in a β subunit-β subunit interaction (similar to the interactions used in rod formation). The second face contains mostly α subunit residues, which enclose a larger empty void, with the β84 co-factors pointing out toward the APC core (Fig. 3b). This larger void could accommodate the circumference of APC core hexamers in different orientations. The flexibility of the α subunits may also enable the PC612 to bind the APC core in a tight manner, with a smaller diameter, thus bringing the APC co-factors into close contact with the PC612 β84 co-factors. In addition, the circumference of the trimer has indentations leading to two different diameters, one of which is only 90 Å (Fig. 2). These indentations could serve as the contact points between R1- and R3-type rods, allowing the arrangement of all four rods around a single APC disk.

A question that remains open is the lack of Asnβ72 methyl-
ation in the PC612. Because the absorption spectrum is blue-shifted, it would be less optimal for directed energy transfer from the PC620 to APC (35). However, if the tight binding of the PC612 to the APC brings the APC external α84 co-factors in close contact with the PC612 internal β84 co-factors, solvent could be ejected and the chemical environment of the non-methylated residue may be made hydrophobic, inducing a significant change in absorption further to the red than in PC620. The presence of linker proteins could have an additional modifying effect on absorption and energy transfer from the β84 co-factor to APC. Thus the PC612 may serve as both a structural and functional linker between the PC rods and APC cores. Structural studies on larger complexes containing both APC and PC components are under way to visualize the molecular details of PB assembly.

Acknowledgments—We thank the staff at the EMBL-Hamburg for their help in data collection. We thank Itzhak Ohad for his helpful comments.

REFERENCES
1. Glazer, A. N. (1985) Annu. Rev. Biophys. Biophys. Chem. 14, 47–77
2. Glazer, A. N. (1989) J. Biol. Chem. 264, 1–4
3. Huber, R. (1989) EMBO J. 8, 2125–2147
4. MacColl, R. (1998) J. Struct. Biol. 124, 311–334
5. Anderson, L. K., and Toole, C. M. (1998) Mol. Microbiol. 30, 467–474
6. Tandeau de Marsac, N., and Cohen-Bazire, G. (1977) Proc. Natl. Acad. Sci. U. S. A. 74, 1635–1639
7. Glaser, M., Bryant, D. A., Frank, G., Wehrli, E., Rusconi, S. S., Sidler, W., and Zuber, H. (1992) Eur. J. Biochem. 205, 907–915
8. Schirmer, T., Bode, W., Huber, R., Sidler, W., and Zuber, H. (1985) J. Mol. Biol. 184, 257–277
9. Schirmer, T., Huber, R., Schneider, M., Bode, W., Miller, M., and Hackert, M. L. (1986) J. Mol. Biol. 188, 651–676
10. Schirmer, T., Bode, W., and Huber, R. (1987) J. Mol. Biol. 196, 677–695
11. Duerring, M., Huber, R., Bode, W., Ruembeli, R., and Zuber, H. (1986) J. Mol. Biol. 211, 633–644
12. Duerring, M., Schmidt, G. B., and Huber, R. (1991) J. Mol. Biol. 217, 577–592
13. Finer, R., Lobeck, K., Schmidt, G., and Huber, R. (1992) J. Mol. Biol. 228, 935–950
14. Breje, K., Finer, R., Huber, R., and Steinbacher, S. (1995) J. Mol. Biol. 249, 424–440
15. Chang, W. R., Jiang, T., Wan, Z. L., Zhang, J. P., Yang, Z. X., and Liang, D. C. (1996) J. Mol. Biol. 262, 721–731
16. Jiang, T., Zhang, J., and Liang, D. (1999) Proteins 34, 224–231
17. Liu, J. Y., Jiang, T., Zhang, J. P., and Liang, D. C. (1999) J. Biol. Chem. 274, 16945–16952
18. Rütt, S., Hiller, R. G., Wrench, P. M., Welte, W., and Diederichs, K. (1999) J. Struct. Biol. 126, 86–97
19. Reuter, W., Wiegen, G., Huber, R., and Than, M. E. (1999) Proc. Natl. Acad. Sci. U. S. A. 96, 1363–1368
20. Stee, B., Troxler, R. F., and Teeter, M. M. (1999) Biophys. J. 76, 2912–2921
21. Jiang, T., Zhang, J. P., Chang, W. R., and Liang, D. C. (2001) Biophys. J. 81, 1171–1179
22. Wang, X. Q., Li, L. N., Chang, W. R., Zhang, J. P., Gu, L. L., Guo, B. J., and Liang, D. C. (2001) Acta Crystallogr. D Biol. Crystallogr. 57, 784–792
23. Adir, N., Dobrovetsky, V., and Lerner, N. (2001) J. Mol. Biol. 313, 71–81
24. Padyana, A. K., Bhat, V. B., Madhastha, K. M., Rajashanker, K. R., and Ramakumar, S. (2001) Biophys. J. Biol. Chem. 282, 893–898
25. Adir, N., Vainer, R., and Lerner, N. (2002) Biochim. Biophys. Acta 1556, 168–174
26. Yu, M. H., Glazer, A. N., and Williams, R. C. (1981) J. Biol. Chem. 256, 13130–13136
27. Yamanaka, G., Lundell, D. J., and Glazer, A. N. (1982) J. Biol. Chem. 257, 4077–4086
28. Anderson, L. K., and Eisinger, F. A. (1996) J. Mol. Biol. 191, 441–451
29. Maxson, P., Sauer, K., Zhou, J. H., Bryant, D. A., and Glazer, A. N. (1989) Biochim. Biophys. Acta 977, 40–51
30. Otwinowski, Z. (1993) in Data Collection and Processing (Sawyer, L., Isaacs, L., and Baily, eds) pp. 56–62, SERC Daresbury Laboratory, Daresbury, UK
31. Brunger, A. T., Adams, P. D., Clore, G. M., DeLano, W. L., Gers, P., Grosse-Kunstleve, R. W., Jiang, J. S., Kuszewski, J., Nilges, M., Pannu, N. S., Read, R. J., Rice, L. M., Simonson, T., and Warren, G. L. (1998) Acta Crystallogr. D Biol. Crystallogr. 54, 905–921
32. Matthews, B. W. (1968) J. Mol. Biol. 33, 491–497
33. Klotz, A. V., Leary, J. A., and Glazer, A. N. (1986) J. Biol. Chem. 261, 15891–15894
34. Duerring, M., Huber, R., and Bode, W. (1988) FEBS Lett. 236, 167–170
35. Swanson, R. V., and Glazer, A. N. (1990) J. Mol. Biol. 214, 787–796
36. Sauer, K., and Scheer, H. (1988) Biochim. Biophys. Acta 936, 137–170
37. Bryant, D. A., and Cohen-Bazire, G. (1981) Eur. J. Biochem. 119, 415–424
38. Glazer, A. N., Lundell, D. J., Yamanaka, G., and Williams, R. C. (1985) Ann. Microbiol. (Paris) 134B, 159–189
The Crystal Structure of a Novel Unmethylated Form of C-phycocyanin, a Possible Connector Between Cores and Rods in Phycobilisomes

Noam Adir and Natalia Lerner

*J. Biol. Chem. 2003, 278:25926-25932.*
doi: 10.1074/jbc.M302838200 originally published online April 22, 2003

Access the most updated version of this article at doi: 10.1074/jbc.M302838200

Alerts:
- When this article is cited
- When a correction for this article is posted

Click here to choose from all of JBC’s e-mail alerts

This article cites 37 references, 7 of which can be accessed free at http://www.jbc.org/content/278/28/25926.full.html#ref-list-1