Hoppe-Seyler's Zeitschrift für Physiologische Chemie

Band 360 – 2. Jahreshälfte

Fortgeführt von A. Kossel, F. Knoop und K. Thomas · Herausgegeben von
A. Butenandt, F. Lynen †, G. Weitzel
unter Mitwirkung von K. Bernhard, K. Decker, J. Engel, H. Fritz
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Redaktion A. Dillmann, G. Peters

1979
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Hoppe-Seyler's Zeitschrift für Physiologische Chemie
Begründet 1877 · Fortgeführt von A. Kossel, F. Knoop und K. Thomas

Bd. 360 Juli 1979 Heft 7

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Hoppe-Seyler's Z. Physiol. Chem.
Bd. 360, S. 935–956, Juli 1979

Studies on Plant Bile Pigments, VII*

Preparation and Characterization of Phycobiliproteins with Chromophores Chemically Modified by Reduction

Werner KUFER and Hugo SCHEER

Botanisches Institut der Universität München

(Received 22 December 1978/23 March 1979)

Dedicated to Professor Dr. H. Plieninger on the occasion of his 65th birthday

Summary: The reversible denaturation and reduction with dithionite has been studied for the phycobiliproteins, C-phycocyanin (**1**) and allophycocyanin (**2**) from *Spirulina platensis*, and C-phycoerythrin (**4**) from *Fremyella diplosiphon* (both cyanobacteria).

By treatment with sodium dithionite, the chromophores are selectively reduced at the central (C-10) methine bridge, producing pigments with bilirubinoid (λ_{max} = 418 nm from **1** and **2**), and vinylpyrrolic (λ_{max} = 300 nm from **4**) chromophores. The extent of reduction is dependent on the state of the protein. The chromophores of denatured biliproteins are completely reduced at 0.5mM dithionite. In the native pigments, dithionite concentrations up to 0.5M lead only to partial reduction thus forming products containing both reduced and oxidized chromophores (e.g. "phycocyanorubins" from **1** and **2**). The reduction is non-statistical with respect to the different chromophores present in **1** and **4**, the chromophores absorbing at shorter wavelengths being preferentially reduced.

Renaturation of the proteins containing reduced chromophores is accompanied by their reoxidation. This oxidation is complete in the absence of dithionite or at concentrations up to 0.5mM. At higher dithionite concentrations, the reoxidation is incomplete, and the products are spectroscopically identical to those obtained by reduction of the native pigments at similar concentrations of reductant.

The results are interpreted by a model in which the protein is "transparent" to the reducing agent, dithionite. The difference in the extent of reduction of the native and denatured pigments can only be due to thermodynamic (viz. stability) differences in the susceptibility of the chromophores to reduction.

Specifically, the (extended) chromophore present in the native pigment is much more difficult to reduce than the chromophore (present in a cyclic conformation) in the denatured pigment. The energetics of the process of refolding both the protein and the chromophores are discussed.

Abbreviations:
P_r, P_{fr} = Phytochrome in the red and far-red absorbing forms, respectively;
1 A_{620} unit or 1 A_{563} unit is that amount of substance in 1 *ml* which has an absorbance of 1.00 in a cuvette of path-length = 1 cm at the indicated wavelength.

* The VIth Communication of this series: Krauss, C., Bubenzer, C. & Scheer, H. (1979) Photochem. Photobiol., in press.

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Untersuchungen an pflanzlichen Gallenfarbstoffen, VII: Darstellung und Charakterisierung von Phycobiliproteinen mit chemisch durch Reduktion modifizierten Chromophoren

Zusammenfassung: Die reversible Denaturierung und Dithionit-Reduktion der Phycobiliproteine C-Phycocyanin (**1**) und Allophycocyanin (**2**) aus *Spirulina platensis* und C-Phycoerythrin (**4**) aus *Fremyella diplosiphon* (beides Cyanobakterien) wurde untersucht.

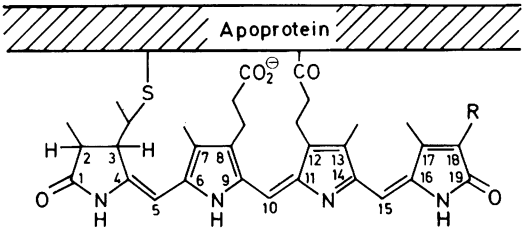
Die Chromophore werden beim Behandeln mit Dithionit selektiv an der zentralen (C-10) Methinbrücke reduziert. Dabei entstehen Pigmente mit Chromophoren vom Typ des Bilirubins (λ_{max} = 418 nm bei **1** und **2**) bzw. des Vinylpyrrols (λ_{max} = 300 nm bei **4**). Das Ausmaß der Reduktion hängt vom Zustand des Proteins ab. In den denaturierten Biliproteinen werden die Chromophore bereits von 0.5mM Dithionit vollständig reduziert. In den nativen Pigmenten werden sie selbst von 0.5M Dithionit nur unvollständig reduziert. Dabei werden Produkte gebildet, welche sowohl oxidierte als auch reduzierte Chromophore enthalten (z.B. „Phycocyanorubin" aus **1** und **2**). Die Reduktion ist nicht statistisch, bei **1** und **4** werden bevorzugt die kürzerwellig absorbierenden Chromophore reduziert.

Die Chromophore der im denaturierten Zustand reduzierten Biliproteine werden beim Renaturieren gleichzeitig wieder oxidiert. In Abwesenheit von Dithionit, oder in Anwesenheit von ≤ 0.5mM Dithonit werden die Chromophore von **1** vollständig oxidiert, bei höheren Konzentrationen ist die Reoxidation unvollständig. Dabei werden nach spektroskopischer Analyse die gleichen Produkte erhalten, wie bei der Reduktion der nativen Biliproteine mit der entsprechenden Konzentration an Dithionit.

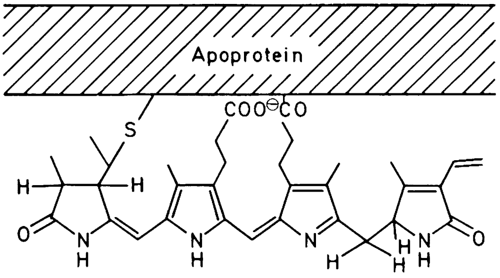
Die Ergebnisse werden durch ein Modell erklärt, bei dem das Protein für das Reduktionsmittel durchlässig ist. Die unterschiedliche Reduzierbarkeit erfordert thermodynamische (d.h. Stabilitäts-) Unterschiede der Chromophore in den nativen bzw. denaturierten Biliproteinen gegenüber Reduktion. Das bedeutet, die (ausgestreckten) Chromophore der nativen Pigmente sind wesentlich schwieriger zu reduzieren als die im denaturierten Zustand vorliegenden (zyklischen) Formen der Chromophore. Die Energetik der Proteinfaltung und -entfaltung und der Konformationsänderungen des Chromophors werden diskutiert.

Key words: Biliproteins, reversible chemical modification, noncovalent protein-chromophore interactions, structure reactivity, conformation-redox potential.

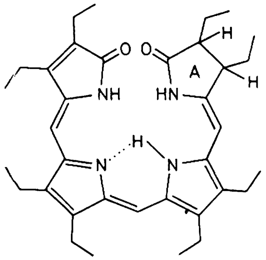
The phycobiliproteins, C-phycocyanin (**1**), allophycocyanin (**2**), and C-phycoerythrin (**4**) are photosynthetic antenna pigments of cyanobacteria, cryptophyceae and red algae[1–7]. Another pigment of this type is phytochrome, the photomorphogenetic reaction center pigment of some algae and higher green plants[1,3,5,8,9]. All of these pigments are chromoproteins with 2,3-di-



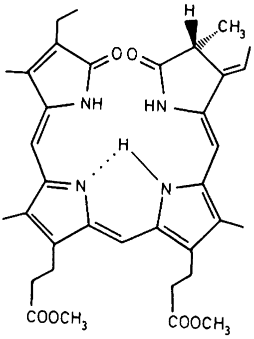
R = C_2H_5: 1 = C-Phycocyanin } 1 and 2 differ
R = C_2H_5: 2 = Allophycocyanin } in the protein
R = C_2H_3: 3 = Phytochrome P_r moiety



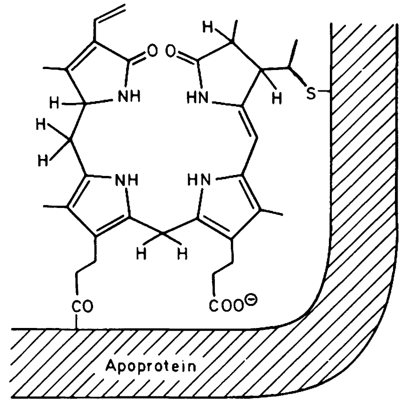
4 = C-Phycoerythrin



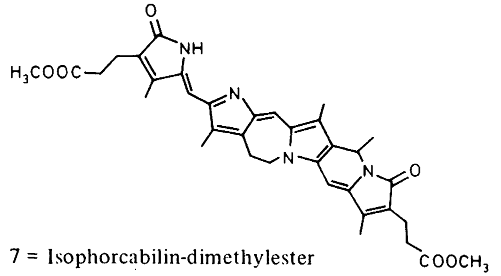
5 = 2,3-Dihydrooctaethyl-1,19(21,24*H*)-bilindione



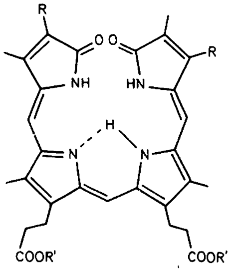
6 = Phycocyanobilin



Formula 9



7 = Isophorcabilin-dimethylester



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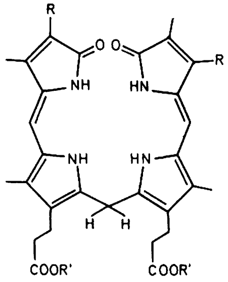
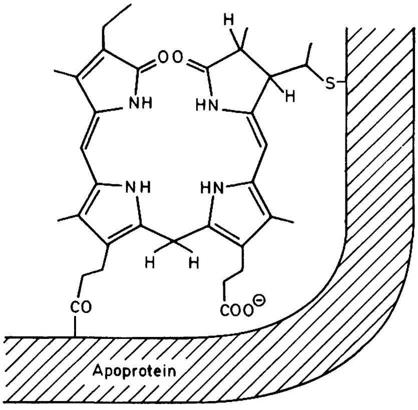


11

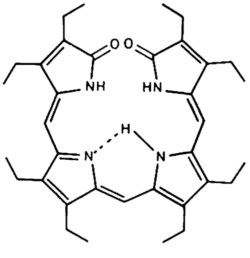
10a = Biliverdin
10b = Mesobiliverdin
10c = Mesobiliverdin dimethyl ester

11a = Bilirubin
11b = Mesobilirubin
11c = Mesobilirubin dimethyl ester

a: $R = C_2H_3, R' = H$
b: $R = C_2H_5, R' = H$
c: $R = C_2H_5, R' = CH_3$



8 = „Phycorubin"



12 = Octaethylbilindione

hydrobilin chromophores *covalently* bound to the protein via a thioether bond (**1**–**4**)[10–17]. In the native phycobiliproteins, the chromophores also interact strongly with the proteins by *non-covalent* interactions. The changes brought about by the latter (Table 1) include pronounced

Table 1. Properties of native biliproteins, as compared to the properties of denatured biliproteins and free bilins. For a recent review of these differences, see Ref.[5].

	Denatured biliproteins and free bilins	Native biliproteins
Absorption spectra	Broad bands, Near UV-band: $\epsilon \approx 4 \times 10^4$ Visible band: $\epsilon \approx 2 \times 10^4$ λ_{max} determined by the chromophore only	Narrow bands, Near UV-band: $\epsilon \approx 2 \times 10^4$ Visible band: $\epsilon \approx 10^5$ λ_{max} influenced by the protein
Photochemistry	Radiationless deactivation predominant, small quantum yield of fluorescence and photochemical reactions	High quantum yield of fluorescence (phycobilins) or photochemical reactions (phytochrome), respectively
Reactions: Complexation	Instantaneous complexation with $Zn^{2\oplus}$ at ambient temperature	Inert with $Zn^{2\oplus}$ at ambient temperature
Reduction	Complete reduction with dithionite ($c \geqslant 0.5$mM)	Partial reduction only with dithionite ($c \geqslant 5$mM)
Oxidation	Oxidative bleaching within days at 4 °C	Stable for months at 4 °C

shifts and intensity variations of the absorption bands, induction of intense fluorescence (in **1**, **2** and **4**) or changes in photochemical properties (in P_r and P_{fr}). At the same time, these interactions render the chromophores inert to externally added chemical reagents[3,5]. The nature of the *non-covalent* interactions is at present only partly understood. From UV-vis spectroscopy, an extended chromophore has been proposed, and from fluorescence and low temperature absorption spectra, a rigid fixation of the chromophore has been inferred[18]. The non-covalent interactions are uncoupled by denaturation of the protein with urea or heat in a stepwise process[18]. In the denatured phycobiliproteins, the chromophore has spectral properties and reacts similarly to free bilins (Tables 1,3). Thus, unfolding with urea or guanidinium chloride has been used to relate the phycobilin chromophores to bile pigments of known structure and to other phycobilins, and to determine the number and kind of chromophores[3,5,12,19–21]. In the denatured state, chemical reactions used for free bilins should also be applicable for selective chemical modifications of the chromophore. Renaturation experiments with phycobilins modified this way are expected to give more specific information on the nature of the *non-covalent* interactions, and on their differences at different chromophore sites. We wish to report the first experiments of this type, in which the chromophore has been modified by chemical reduction.

Materials and Methods

Isolation and purification of biliproteins

1 and **2** were isolated from *Spirulina platensis.* 30 g deep-frozen cells of *Spirulina platensis* were thawed, mixed with glass beads (~ 150 g, 0.17–0.18 mm Ø) and broken in a beaker-type cell mill (Model Vibrogen, Bachofer, Reutlingen) under water cooling for 5 min. The broken cells were suspended in 20 m*l* Tris buffer (10mM Tris, pH 8.0), and centrifuged for 30 min at 7000 × *g*. The pellet was again extracted with 20 m*l* Tris buffer. The crude extract containing biliprotein was freed from chlorophyll by ultracentrifugation (1 h, 78000 × *g*, $A_{620}/A_{280} = 1.4$). Half of this solution was separated on a 2.5 × 18 cm DEAE-cellulose column (DE 52, Whatman, Maidstone, England) equilibrated with Tris buffer (10mM, pH 8.0). The column was developed first with 200 m*l* starting buffer to remove some yellow pigment, then with a linear gradient (0–300mM KCl) of 600 m*l* Tris buffer (10mM, pH 8.0, elution rate 150 m*l*/h). Biliproteins were pooled in 3 fractions according to their spectral properties: 1) **2** I (70 m*l*, $A_{656} = 0.2$); 2) **1** (125 m*l*, $A_{620} = 6.6$, $A_{620}/A_{280} = 3.7$) and 3) **1** and **2** II (220 m*l*, $A_{620} = 1.1$, $A_{620}/A_{280} = 1.6$).

Fraction 1 was further purified on a 1.7 × 15 cm brushite column[22] equilibrated with phosphate buffer (5mM, pH 7.5). A trace contamination of **1** was removed with about 100 m*l* starting buffer; **2** I was then eluted with a linear gradient (5–50mM phosphate) of 200 m*l* phosphate buffer (pH 7.5, elution rate 50 m*l*/h). Fractions with $A_{656}/A_{620} \geqslant 1.6$ were pooled. Yield: 75 m*l* **2** I, $A_{656} = 0.1$, $A_{656}/A_{280} = 3.4$. Fraction 2 was further purified by gel filtration on a 2.5 × 50 cm Biogel P 150 column (Bio-Rad, Richmond, California) equilibrated with Tris buffer (10mM Tris, 100mM KCl, pH 7.5, elution rate 10 m*l*/h). The main fraction of the resulting **1** absorbed with A_{620}/A_{280} = 4.2. Yield: 23 m*l* **1**, A_{620} = 24.

All purification steps were carried out at 4 °C. All buffers contained 1mM NaN_3 and Na_4 EDTA. For storage, biliproteins were dialysed against twice distilled water, lyophilized, and kept at – 20 °C.

4 was obtained from *Fremyella diplosiphon.* Cells were broken with glass beads as described for **1**. The crude extract was purified by gel filtration on Sephadex G-100 and subsequent chromatography on DEAE-cellulose. The procedure is described in detail elsewhere[23].

Modifications of biliproteins

The experiments were carried out at room temperature. Stock solutions for experiments were kept at 0 °C. All solutions were saturated with N_2 before use, unless specified otherwise.

Denaturation: 200 *µl* samples of stock solutions of the biliproteins in phosphate buffer (50mM, pH 7.5) were added to 2.0 m*l* urea buffer (50mM phosphate, 8M urea (p.a., Merck, Darmstadt), pH 7.5). In the case of **2**, 100 *µl* stock solution was added to 1.0 m*l* urea buffer. Denaturation was complete within 10 min.

Chemical modification: Solid sodium dithonite (technical, Merck, Darmstadt) was added to the solution of the *denatured biliprotein* to a final concentration of 5 to 50mM. For lower concentrations of the reductant, portions of a freshly prepared solution of dithionite (50mM) in urea buffer were added instead. Solid sodium sulfite (p.a., Merck, Darmstadt) and 2-mercaptoethanol (p.s., Merck-Schuchard, Hohenbrunn, distilled prior to use) were added to a final concentration of 30mM and 2M, respectively. A change of the colour from blue (**1**, **2**) or red (**4**) to yellow (**1**, **2**) or colourless (**4**) indicated that the reduction had occurred. *Native biliproteins* in phosphate buffer were titrated with a freshly prepared 50mM solution of dithionite in the same buffer. For final concentrations > 5mM, solid sodium dithionite was added.

Renaturation: For removal of urea, 1.0 m*l* of the solution of the denatured biliprotein was passed through a 1.7 x 12 cm Biogel P 2 column (Bio-Rad, Richmond, California) equilibrated with phosphate buffer. Denattured, chemically modified biliproteins were either treated in the same way ("aerobic renaturation"), or the gel filtration was carried out in the presence of the reductant at the appropriate concentration ("anaerobic renaturation").

Reoxidation of the reduced chromophores in the denatured biliproteins: 1.0 m*l* of the solution of the reduced denatured biliproteins was passed through a 1.7 x 12 cm Biogel P 2 column equilibrated with urea buffer (50mM phosphate, 8M urea, pH 7.5).

Preparation and reduction of model bilins

Bilirubin (**11a**) (biochemistry grade, Merck, Darmstadt) was used without further purification. Mesobilirubin (**11b**) was prepared by catalytic hydrogenation of bilirubin[24,25]; its dimethyl ester (**11c**), by reduction of the dimethyl ester (**10c**) with $NaBH_4$[25]. Biliverdin (**10a**) and mesobiliverdin (**10b**) were obtained from the respective rubins by oxidation with 2,3-dichloro-5,6-dicyanobenzoquinone[25], using partition between dichloromethane and water during the work-up procedure. Mesobiliverdin dimethyl ester (**10c**) was prepared from mesobiliverdin by esterification with BF_3/methanol[25]. Octaethyl-1,19 (21,24*H*)-bilindione (**12**) and 2,3-dihydrooctaethyl-1,19 (21,24*H*)-bilindione (**5**) were synthesized from octaethylporphyrin[26,27].

The verdins (≈ 0.5mM) were reduced with sodium dithionite and sodium sulfite (10 mg/2 m*l*) in a mixture of methanol/water = 1 : 1. For workup, the yellow solutions were partitioned between $CHCl_3$ and glycine/HCl buffer, pH = 2.7, in the case of free acids, saturated with $(NH_4)_2SO_4$[28]. The organic phase was dried over NaCl and evaporated to dryness. All reductions including the work-ups were carried out under N_2.

Thin-layer chromatography of the products was carried out on silica HPTLC plates (Merck, Darmstadt) with two published solvent systems[29,30] and with a system consisting of the upper phase of a mixture toluene/acetic acid/water, 5 : 5 : 1. In addition, polyamide 11 F 254 plates (Merck, Darmstadt) were used with the solvent systems of Petryka and Watson[29]. For the reduction experiments with 2-mercaptoethanol (2.5M), methanol was used as a solvent. Work-up by partition between CCl_4 and water resulted in (partial) reoxidation of the yellow pigments to green verdins.

General methods

Gel electrophoresis was performed by the method of Wagenmann[31], in 10-cm diameter 0.6 cm gels, (7.7% polyacrylamide, 2.6% crosslinker) with a Tris gel buffer (pH 8.8) and a Tris/glycine electrode buffer (pH 8.3), for 3 h with 3 mA/gel tube at 4 °C.

UV-vis spectra were determined with a model DMR 22 spectrophotometer (Zeiss, Oberkochen). The extinction coefficient determined by Glazer and Fang[21] for urea-denatured **1** in the cationic form (pH 3.0) was used as a standard for all extinction coefficients of other **1** forms and pigments derived thereof. **2** contains the same chromophore as **1**, so the extinction coefficient for **1** denatured with acidic urea was used for **2** denatured with acidic urea and pigments derived thereof. The extinction coefficient determined by Muckle and Rüdiger[23] for **4** denatured with acidic urea was taken as a standard for the **4** samples.

Redox potentials were determined with a model EA 259 Pt/AgCl electrode (Metrohm, Filderstadt), or by the use of the redox indicator dyes 5-methylphenazinium methylsulfate ($E^{0'}$ = + 8 mV[32], Merck, Darmstadt), indigo bissulfonate ($E^{0'}$ = – 125 mV[32], Riedel de Haen, Seelze), and methylviologen ($E^{0'}$ = – 440 mV[32], Riedel de Haen, Seelze).

Results

Denaturation-renaturation (paths [a] and [b] in reaction scheme, Fig. 1)

Denaturation of the biliproteins is complete at urea concentrations $\geqslant$ 7M. The spectra obtained for all denatured biliproteins were identical, irrespective of the denaturation procedure, e.g. mixing of the native pigment with urea solutions of appropriate concentrations, or addition of solid urea. The products of denaturation by heat[18] or guanidinium chloride[20] have the same UV-vis spectra, while denaturation with sodium dodecylsulfate yields a spectroscopically different product[23,39]. The pigments can be renatured either by dialysis[5,40] against buffer or by gel filtration over a desalting column. Since the chromophores of the denatured pigments are unstable, gel filtration, the more rapid procedure, was used throughout.

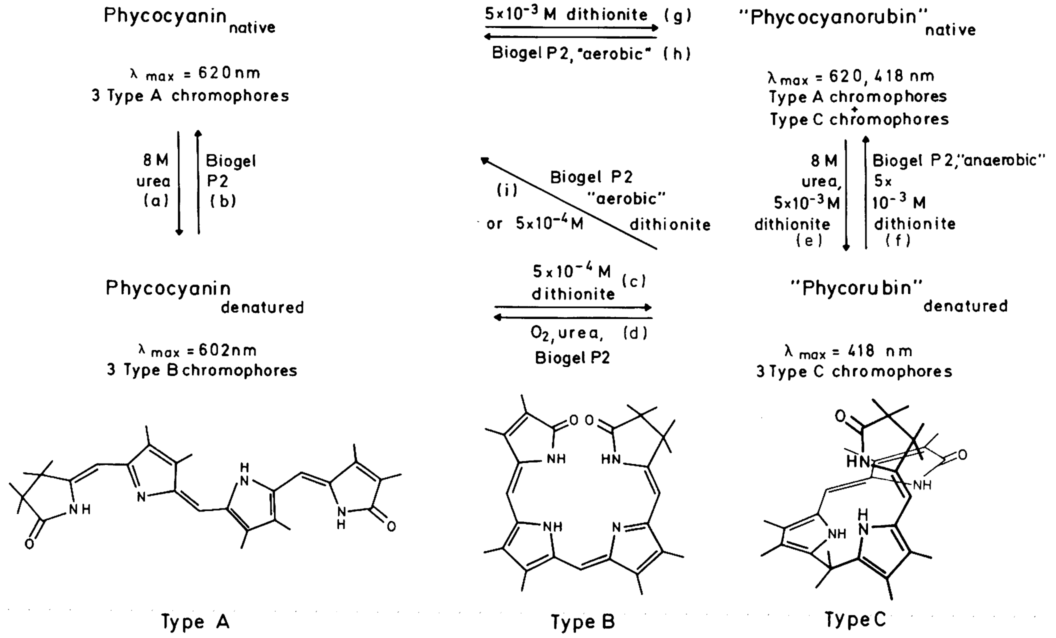


Fig. 1. Reaction scheme of the reversible denaturation-renaturation and reduction-oxidation reactions carried out with 1 from *Spirulina platensis*.

The chromophore structures are schematic representations with the substitutents omitted (see formulas). Structure A is representative of an extended conformation without major steric hindrance of the β-pyrrolic substitutents. Structure B is the porphyrin-type conformation found for biliverdins both in the crystal[33] and in solution[34,35]. Structure C has been drawn with the two dipyrromethene units nearly perpendicular to each other, similar to the X-ray structures found for bilirubins[36,37]. Similar schemes can be drawn for the reactions of 2 and 4, with the following exceptions: a) The renaturation of 2 does not yield native 2 directly, but rather an intermediate (see text).
b) The structure of the reduced chromophore of 4 corresponds to that shown in formula 9. Due to interference of the 300 nm band of this chromophore with the absorption of the dithionite solution, the presence of a pigment with "mixed" chromophores can only be inferred from the decrease in the 560 nm band of native 4 in the presence of dithionite (Fig. 6). c) The conformation of native 4 may be extended, by analogy to that of native 1[3]. The data available by molecular calculations indicate, however, a less pronounced dependence of the oscillator strengths of the conformation[38].

Table 2. Yields of native **1** and **4** after the various treatments shown in Fig. 1.
The % yield was calculated from the volume x absorption of the given solution compared to that of the starting solution (row 1).

Treatment	Compound **1**		Compound **4**	
	A_{620} units[a]	[%]	A_{563} units[b]	[%]
1) Native orginal sample	0.835	100	0.850	100
2) Biogel P2 filtration	0.72	87	0.61	72
3) Denatured, renatured over Biogel P2	0.60	72	0.48	57
4) Denatured, reduced with 0.5mM dithionite, aerobically renatured[c]	0.40	48	0.39	45
5) Denatured, reduced with 0.5mM dithionite, anaerobically renatured[d]	0.41	50	0.20	24
6) Denatured, reduced with 5mM dithionite, aerobically renatured[c]	0.41	49	–	–
7) Denatured, reduced with 5mM dithionite, anaerobically renatured[e]	0.33	39	–	–
8) Native, reduced with 5mM dithionite[f]	0.59	71	0.42	49

[a] 1 A_{620} unit corresponds to 3.4 nmol of native **1**/m*l*, or 3.4μM.
[b] 1 A_{563} unit corresponds to 1.8 nmol of native **4**/m*l*, or 1.8μM.
[c] Renaturation over Biogel P2 in the absence of dithionite.
[d] Renaturation over Biogel P2 in the presence of 0.5mM dithionite.
[e] Renaturation over Biogel P2 in the presence of 5mM dithionite.
[f] See Fig. 3 for the yield with other dithionite concentrations.

At the concentration used throughout this study (3μM), denatured **1** was recovered in 72% yield* by gel filtration. (Table 2). Native **1** gave a recovery of 87% when passed through a desalting column under identical conditions, providing an estimate of losses due to irreversible absorption on the column and losses during the denaturation/renaturation sequence. The corresponding values for **4** (1.5μM) were 57% (denatured/renatured) and 72% (native). Both for **1** and **4**, the renatured pigments were identical to the respective native pigments, if judged from UV-vis spectra. The renaturation product of **2** (starting solutions = 1.5μM) resembled spectroscopically native **1** rather than native **2**, in having an absorption band at 620 nm instead of 656 nm. Subsequent incubation at 35–40 °C led to a progressive rise of a narrow absorption band at 656 nm within 3 h. Even at this stage, however, the value of A_{656}/A_{620} = 1.2 (as compared to 1.8 for native **2**) still indicated only partial renaturation (see discussion). Due to these spectral changes after passage through the gel-filtration column, quantification of the results is less certain than for **1** and **4**.

Reduction of native phycobilins (Path [g] in the reaction scheme)

Titration of native **1** with sodium dithionite led to a gradual decrease in the band at 620 nm, and a simultaneous increase of a band at 418 nm (Fig. 2) with an isosbestic point at 483 nm. Native **1** has an extinction coefficient of 98700 for one chromophore at 620 nm. Assuming a 1 : 1 conversion, an extinction coefficient for the absorption of the reduced chromophores at 418 nm can be calculated from the titration experiment. By using the integrated intensity or the extinction of the 620 nm band as a standard, values of 20500 or 23300, respectively, were obtained. The conversion occured at dithionite concentrations between 0.5 and 5mM. From experiments with indicator dyes, this brackets a range of redox potentials > + 8 mV (5-methylphenazinium methylsulfate) and < – 440 mV (methyl viologen). The spectrum remained essentially unchanged at concentrations up to 50mM.

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* All yields are calculated from the extinction of the visible band at 620 nm for **1** and 563 nm for **4**. For details, see experimental part.

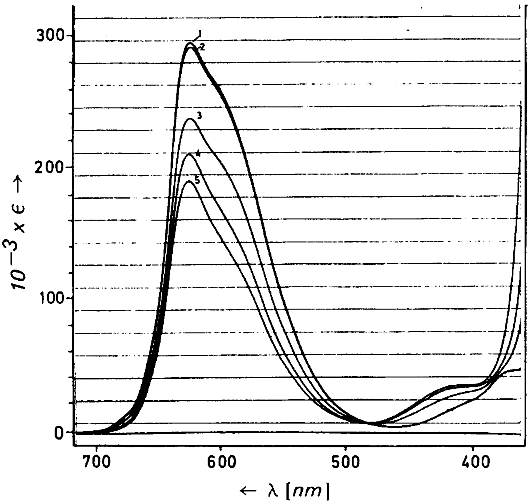

Fig. 2. UV-vis absorption spectra of the titration of 2.2 ml 3μM native 1 in 50mM phosphate buffer, pH 7.5, with 50mM sodium dithionite.

The traces correspond to the following dithionite concentrations (total volume after addition of dithionite in parentheses):
1) 0M, 2) 0.45mM (2.22 ml), 3) 1.3mM (2.26 ml), 4) 2.2mM (2.3 ml), 5) 4.2mM (2.4 ml).
The spectra are not corrected for dilution. The increased absorption at $\lambda \leq 400$ nm is due to the absorption of the dithionite solution.

At higher concentrations, there was even a slight increase of the extinction at 620 nm (Fig. 3), possibly due to a salt effect.* At a dithionite concentration of 5×10^{-2}M, a maximum decrease of the integrated intensity of this band of 45% was observed. The decrease was larger, however, at the short than on the long-wavelength side of the band. This effect is more easily seen in the difference spectrum (Fig. 4), which has a large negative double peak in the red region (λ_{max} = 616, 596 nm) and the corresponding positive peak at 427 nm.

When native 2 was treated with 5mM dithionite, the integrated intensity of the red band decreased by 26%, and a new band appeared as a shoulder at 420 nm, with an isosbestic point at 533 nm (Fig. 5). In this case, the peak shape in the difference spectrum is only slightly different from that of the absorption band of the native pigment.

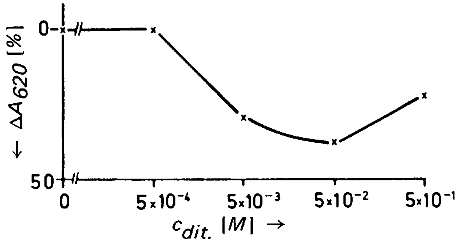

Fig. 3. Decrease in the absorption (ΔA_{620}) of the long wavelength band at 620 nm of native 1 in the presence of increasing concentrations of sodium dithionite ($c_{dit.}$).

During the titration of native 4, the integrated intensity of the 563 nm band decreased by 50% (5mM dithionite), with no corresponding rise in a band in the visible spectral region (Fig. 6). Similar to the findings for 1, the peak in the difference spectrum does not coincide with the absorption maximum of 4, but is blue-shifted to 556 nm (Fig. 7).

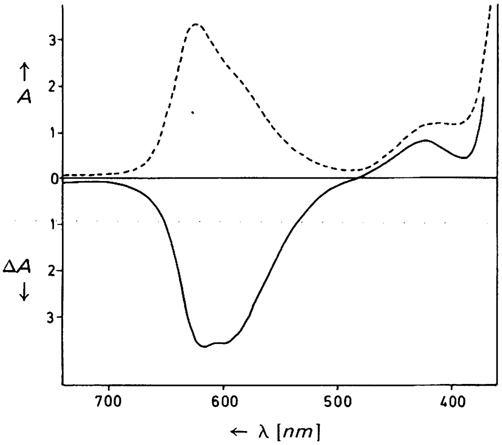

Fig. 4. UV-vis difference spectrum: absorbance of native 1 in the presence of 5mM sodium dithionite, minus the absorbance of native 1 (concentration as in Fig. 1) (——).

For comparison, the spectrum of the reduced pigment is shown in the upper trace (– – –).

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* The extinction coefficient (A_{620}) of 1 was unaltered in 1M NaCl, although a distinct change in the shape of the band indicated a change in the state of the protein, which could alter the stability of the chromophores towards reduction.

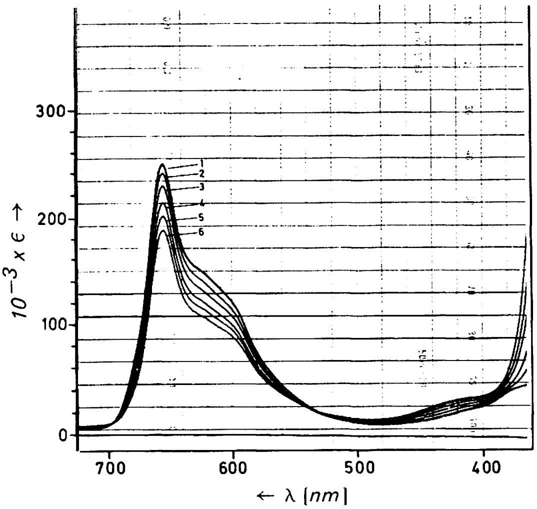

Fig. 5. UV-vis absorption spectra of the titration of 1.2 m*l* 3μM native **2** in 50mM phosphate buffer, pH 7.5, with 50mM sodium dithionite.

The traces correspond to the following dithionite concentrations (total volume after addition of dithionite in parentheses):
1) 0M, 2) 0.82mM (1.22 m*l*), 3) 1.2mM (1.23 m*l*), 4) 2mM (1.25 m*l*), 5) 2.8mM (1.27 m*l*), 6) 3.8mM (1.30 m*l*).

The spectra are not corrected for dilution. The increased absorption at $\lambda \leqslant 400$ nm is due to the absorption of the dithionite solution.

Reduction of denatured phycobilins (path [c] in the reaction scheme)

Addition of dithionite to denatured **1** resulted in a bleaching of the absorption band at 602 nm. A new band appeared instead around 415 nm, and isosbestic points were observed at 446 and 379 nm (Fig. 8). At high concentrations of the reductant, the spectrum of the reduced pigment was red-shifted (dashed line). From the extinction coefficient of denatured **1** (Table 3), the extinction coefficient of the reduced pigment was calculated to be 25 500 at $\lambda_{max} = 418$ nm.

The reaction was complete at dithionite concentrations $\geqslant$ 0.5mM within 20 min at ambient temperature. The spectrum did not change at higher dithionite concentrations, but the reaction was accelerated. At a concentration of 5mM, it

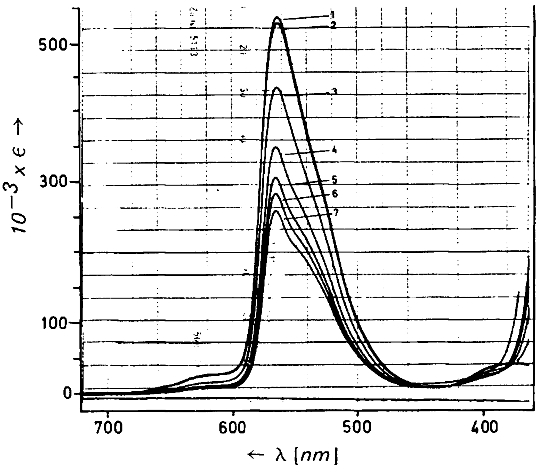

Fig. 6. UV-vis absorption spectra of the titration of 2.2 m*l* 1.5μM native **4** in phosphate buffer (50mM, pH 7.5) with 50mM sodium dithionite.

The traces correspond to the following dithionite concentrations (total volume after addition of dithionite in parentheses): 1) 0M, 2) 0.45mM (2.22 m*l*), 3) 0.89mM (2.24 m*l*), 4) 1.3mM (2.26 m*l*), 5) 1.8mM (2.28 m*l*), 6) 2.2mM (2.30 m*l*), 7) 4.2mM (2.40 m*l*). The spectra are not corrected for dilution. The increased absorption at $\lambda \leqslant 400$ nm is due to the absorption of the dithionite solution.

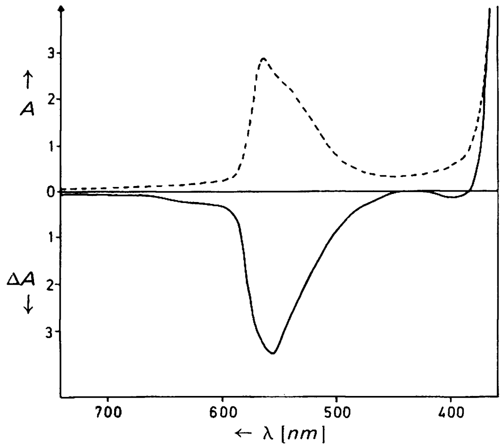

Fig. 7. UV-vis difference spectrum: absorbance of native **4** in the presence of 5mM sodium dithionite, minus the absorbance of native **4** (concentration as in Fig. 6) (——).

For comparison, the spectrum of the reduced pigment is shown in the upper trace (– – –).

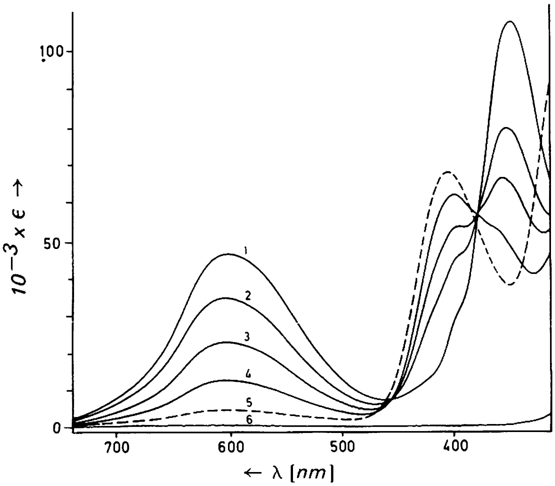

Fig. 8. UV-vis absorption spectra of the titration of 2.5 m*l* 9μM denatured **1** in 50mM, phosphate buffer, pH 7.5, containing 8M urea with 28mM sodium dithionite.

The traces correspond to the following dithionite concentrations (total volume after addition of dithionite in parentheses):
1) 0M, 2) 0.11mM (2.51 m*l*), 3 min after addition, 3) same, 10 min after addition, 4) 0.22mM (2.52 m*l*), 10 min after addition, 5) (– – –). 0.44mM (2.54 m*l*), 10 min after addition, 6) baseline. The traces are not corrected for dilution, the dilution factor for trace 5 is 1.016.

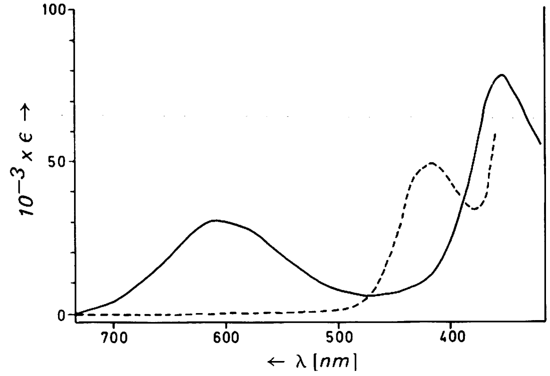

Fig. 9. UV-vis absorption spectra of 1.1 m*l* 1.5μM denatured **2** in 50mM phosphate buffer, pH 7.5, containing 8M urea (—— —) and of the same solution in the presence of 0.5mM sodium dithionite (– – –).

Total volume after addition of dithionite 1.11 m*l*.

was complete within the time required for mixing the solution. The slow reduction with only a small excess of dithionite was paralleled by the titration of mesobiliverdin IXα under anaerobic conditions.* There was no simple stoichiometric relation between the amount of added dithionite and the amount of biliverdin reduced. The reduction was slow in the presence of about equimolar amounts of dithionite, and accelerated with an increasing excess. This effect, which may reflect a kinetic barrier or side reactions of the dithionite [41,42] has precluded the measurement of a redox potential between the verdinoid and rubinoid pigments.

Treatment of denatured **1** with sodium sulfite or 2-mercaptoethanol led to spectroscopically similar products (λ_{max} = 418 nm). At a sodium sulfite concentration of 0.5mM or a 2-mercaptoethanol concentration of 2M, the absorption at 602 nm decreases by 90% within 15 min at ambient temperature, with a simultaneous increase at 418 nm. In spite of their spectral similarities, however, the products are different for the three reducing agents (dithionite, sulfite and 2-mercaptoethanol), as inferred from similar experiments with free bilins (see below).

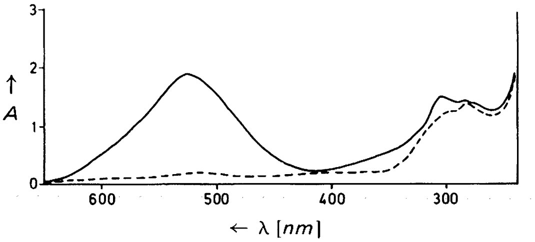

Fig. 10. UV-vis absorption spectra of 1.5μM denatured **4** in 50mM phosphate buffer, pH 7.5, containing 8M urea (——), and of the same solution in the presence of 0.5mM sodium dithionite (– – –).

The dashed trace was obtained by adding a stock solution of **4** to the urea dithionite buffer. It is corrected for dilution and the absorption of dithionite at $\lambda \leqslant 400$ nm.

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* We thank *Dr. L. Fox*, Austin (on leave at the Max-Planck-Institut für Biochemie, Martinsried) for performing this experiment.

Table 3. Extinction coefficients of denatured **1** and **2**, of the model bilin **5**, and of the ethylidenebilin **6**, obtained by cleavage in refluxing methanol and subsequent esterfication.

	Red band λ_{max} ($10^{-3} \times \epsilon$)	Near UV band λ_{max} ($10^{-3} \times \epsilon$)	Q red/UV	Solvent	Ref.
Denatured **1**					
Free base	602 (15.4)	355 (37.0)	0.42	50mM phosphate, 8M urea, pH 7.0	
Cation	661 (35.5)[a]	355 (34.9)	1.02	50mM phosphate, 8M urea, HCl, pH 3.0	
Denatured **2**					
Free base	602 (15.4)[b]	354 (35.4)	0.43	50mM phosphate, 8M urea, pH 7.5	
Cation	661 (30.2)	354 (35.4)	0.85	50mM phosphate, 8M urea, HCl, pH 3.0	
Compound **5**					[19]
Free base	594 (17.6)	347 (39.4)	0.45	Methanol	
Cation	665 (34.0)	351 (36.5)	0.93	Methanol/HCl	
Compound **6**					
Free base	600 (12.3)	362 (41.7)	0.29	Methanol	[45]
Cation	690 (37.9)	374 (47.9)	0.79	Methanol/HCl	[46]

[a] Value for denatured **1** in the cationic form, taken from Ref.[21]. All other extinction coefficients of **1** from *Spirulina platensis* were calculated relative to this standard.
[b] The value was taken identical to that of denatured **1** in the free base form.

The reduction product of denatured **2** was spectroscopically identical to that of denatured **1** (Fig. 9). With **4**, the reduction product had an absorption band around 300 nm (Fig. 10). As dithonite solutions absorb strongly at shorter wavelengths (footnote p. 951), the determination of the extinction coefficient was less accurate in this case, and only arbitrary units are given on the ordinate of Fig. 10.

Reduction of model bilins

Reduction experiments were carried out with biliverdin (**10a**), mesobiliverdin (**10b**) and its dimethyl ester (**10c**), with (**12**) and with (**5**) as a model for the chromophores of **1**, **2** and P_r. Treatment of the verdins with sodium dithionite, sodium sulfite and 2-mercaptoethanol resulted in yellow products spectroscopically similar to the corresponding authentic rubins (**11a**–**11c**) (Table 4). Comparison by thin-layer chromatography in different solvent systems (Table 4) demonstrated the identity of the dithionite reduction products of biliverdin, mesobiliverdin and its dimethyl ester with the authentic rubins. In contrast, the products obtained with sodium sulfite were shown to be different from the rubins by thin-layer chromatography. The products obtained with either dithionite or sulfite remained yellow upon acidification with HCl. If the yellow products obtained after treatment with 2-mercaptoethanol were acidified, the solutions turned green. Their UV-vis spectra became identical to those of the cationic forms of the respective verdins, except for biliverdin, from which a product with the long-wavelength absorption maximum shifted by 21 nm to the blue (as compared to the cation of biliverdin) was obtained (Table 4). Attempts to isolate the products obtained with 2-mercaptoethanol were unsuccessful, because of their instability after removal of the thiol. For this reason, no thin-layer chromatography data are available for these products.

Aerobic renaturation of the reduced phycobilins (path [i] in the reaction scheme)

Chromatography of reduced, denatured **1** on Biogel P2 to remove the urea led to the reappearance of the blue phycocyanin colour after passage of the first quarter of the column. The eluent contained native **1**, as judged from its

Table 4. UV-vis spectra (λ_{max} [nm]) and thin-layer chromatography data ($R_F \times 100$) determined for several 1.19 (21, 24*H*)-bilindiones ("biliverdins") and their reaction products with sodium dithionite, sodium sulfite and 2-mercaptoethanol.

Details will be published elsewhere after completion of this study.

Compound + treatment	λ_{max} [nm]		Chromatography (R_F values × 100) solvent system				
	Free base	After addition of HCl	g	h	i	j	k
Biliverdin (**10a**)	660^{a}; 656^{b}	697^{a}	81	06	00	–	00
Bilirubin (**11a**)	454^{c}; 449/418 (sh)^{d}	458/484^{d,f}	67	00	62^{l}	–	50^{l}
10a, dithionite-treated	418^{b}; 454^{c}; 405/432^{d,f}	402/428^{d,f}	–^{p}	00	62^{l,n}	–	50^{l,n}
10a, sulfite-treated	405^{c}; 403/444^{d,f}	404/431^{d,f}	88	00	00	–	00
10a, 2-mercaptoethanol-treated	436/416 (sh)^{a}	676^{a}	unst.	unst.	unst.	–	unst.
Mesobiliverdin (**10b**)	644^{a}; 657–670^{d}	688^{a}; 690^{d}	80	–	01	03	–
Mesobilirubin (**11b**)	424/398^{d,f}	420^{d}	65	–	66^{m}	69^{m}	–
10b, dithionite-treated	414/398^{d,f}	418/392^{d,f}	65	–	66^{m}	69^{m}	–
10b, sulfite-treated	420/393^{d,f}	420/396^{d,f}	90	–	04^{m,n}	02^{m}	–
10b, 2-mercaptoethanol-treated	422^{a}	688^{a}	unst.	–	unst.	unst.	–
Mesobiliverdin-$(OMe)_2$ (**10c**)			20	–	41	23	–
Mesobilirubin-$(OMe)_2$ (**11c**)			10	–	29	59	–
10c, dithionite-treated			10	–	–	–	–
10c, sulfite-treated			67	–	05^{m}	07^{m}	–
10c, 2-mercaptoethanol-treated			unst.	–	unst.	unst.	–
Dihydrooctaethylbilindione (**5**)	596^{a}	667^{a}					
5, dithionite-treated	398^{d}; 406^{e}	398^{d}					
5, 2-mercaptoethanol-treated	410^{a}	667^{a}					
Octaethylbilindione (**12**)	646^{a}	690^{a}					
12, 2-mercaptoethanol-treated	426^{a}	690^{a}					

[a] in MeOH.
[b] in 50mM phosphate buffer/8M urea, pH 7.5.
[c] in $CHCl_3$.
[d] in $MeOH/H_2O$ 1 : 1 (v/v).
[e] in MeOH/50mM phosphate buffer, pH 7.5, 1 : 1 (v/v).
[f] Two poorly resolved bands were observed with the following absorption ratios: bilirubin in HCl, 1.02; dithonite-treated biliverdin as free base, 1.11, in HCl, 1.11; sulfite-treated biliverdin as free base, 1.40, in HCl, 1.04. Mesobilirubin 1.18; dithonite-treated mesobiliverdin as free base, 0.97, in HCl, 0.84; sulfite-treated mesobiliverdin as free base, 0.83, in HCl, 1.21.
[g] Polyamide, MeOH/10% NH_3/H_2O 9 : 1 : 2 (v/v)[29].
[h] Polyamide, $MeOH/H_2O$ 3 : 1 (v/v)[29].
[i] Silicagel, benzene/abs. ethanol 100 : 8 (v/v)[29].
[j] Silicagel, toluene/acetic acid/water 5 : 5 : 1 upper phase.
[k] Silicagel, chloroform/acetic acid 1% (v/v)[30].
[l] Two further minor spots were detected on the plate: R_F 57, 67^{i}, R_F 41, 60^{k}. From this pattern, they are suggested to correspond to the bilirubin IIIa and XIIIa isomers. They were present only in very small quantities in the commercial bilirubin, but could be well detected in the dithionite reduction product of biliverdin, probably due to "scrambling" conditions[43] during the preparation of the pigment.
[m] Besides the main product, some unidentified minor spots were detected.
[n] Some unidentified material remained at the start.
[p] R_F value undetermined due to extensive tailing.

spectral and electrophoretic properties. The UV-vis spectrum was identical to that of an authentic sample, in particular the asymmetric red band with a peak at 620 nm and a shoulder at shorter wavelengths is restored, and there was no absorption band in the 400–500 nm region (Fig. 11). Likewise, co-electrophoresis with native **1** gave only one single band. The overall yield of the sequence denaturation – reduction – renaturation was 50% (A_{620}). If this "cycled" pigment was again denatured with urea, it gave an absorption band at 602 nm (661 nm after addition of HCl), as did denatured **1**. Renaturation of reduced, denatured **4** was accompanied by a similarily rapid reoxidation to yield native **4** in 45% yield (A_{563}). The renatured pigment was identical to native **4** with respect to UV-vis spectra (Fig. 12), and electrophoretic properties. The denaturation product of the "cycled" **4** was spectroscopically identical to denatured authentic **4**, both in the cationic form (λ_{max} = 559 nm) and as free base (λ_{max} = 525 nm).

Desalting of the reduced, denatured **2** again did not lead to the original pigment, but rather to a product spectroscopically similar to the one obtained after renaturation of **2** (see above).

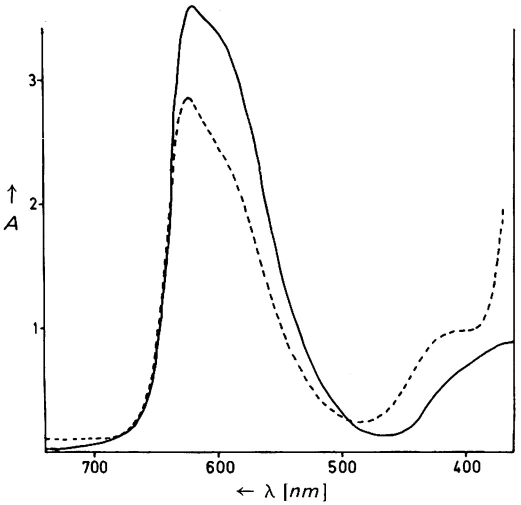

Fig. 11. UV-vis absorption spectra of "cycled" samples of 1.

Reduced, denatured 1 (= denatured phycorubin) was renatured by filtration over Biogel P2 either "aerobically" (——) or "anaerobically" in the presence of 5mM sodium dithionite (– – –).

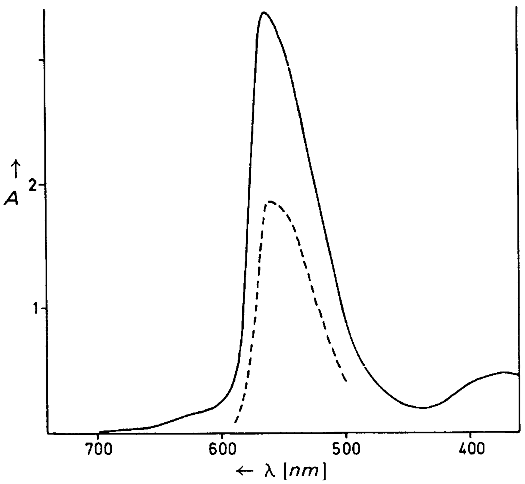

Fig. 12. UV-vis absorption spectra of "cycled" samples of 4.

Reduced, denatured 4 was renatured by filtration over Biogel P2 either "aerobically" (——) or "anaerobically" in the presence of 0.5mM dithionite (– – –).

The spectral changes upon incubation at 35–40 °C gave a similar picture, with a new peak gradually rising at 656 nm and practically no decrease in the 620 nm absorption (Fig. 13). Electrophoretically, the incubation product was identical to native **2**. Thus, in the case of **2**, too, renaturation

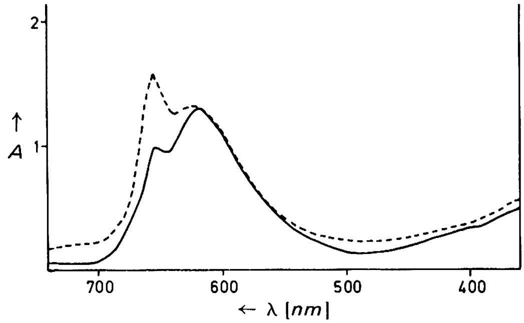

Fig. 13. UV-vis absorption spectra of "cycled" 2.

Reduced, denatured 2 (= denatured allophycorubin): (——), sample renatured "aerobically" by filtration over Biogel P2. (– – –), the same sample after incubation for 3 h at 30 °C.

of the reduced, denatured **2** was accompanied by a rapid reoxidation of the chromophores. The yield of the 620 nm product was comparable in both cases. Denaturation of the "cycled" **2** yielded a pigment spectroscopically identical to denatured **2** in the free base (λ_{max} = 602 nm) and its cationic form (λ_{max} = 662 nm).

Anaerobic renaturation of the reduced phycobilins (path [f] in the reaction scheme)

For renaturation under reducing conditions, reduced **1** was passed over a Biogel P2 column previously equlibrated with dithionite, under conditions maintaining the redox potential < – 440 mV (5mM dithionite) as checked in each case for the eluent at the end of the column with methylviologen. The resulting pigment was not blue but bluish-green, with absorption bands at 620 and 418 nm in the spectrum (Fig. 11)*. The product was stable at the low redox potential over extended times. When stored in air, the redox potential of the solution increased within 12 h due to the oxidation of dithionite. Under these conditions, the band at 418 nm gradually decreased, with a simultaneous increase in the shoulder around 600 nm. If the bluish-green pigment (λ_{max} = 620 and 418 nm) obtained after anaerobic renaturation was again denatured with urea, but without further addition of dithionite, (path [e] in the reaction scheme), the colour turned immediately to yellow. The resulting pigment had a single absorption band at 418 nm identical to that of reduced, denatured **1** (trace 5 in Fig. 8).

The spectrum of the bluish-green product was similar to that obtained after treatment of native **1** with dithionite. The concentrations of dithionite necessary to obtain this species were in the same range, too. Renaturation in the presence of low dithionite concentrations (0.5mM) yielded native **1**, as under aerobic conditions (path [i] in the reaction scheme). Quantitatively, the intensity of the blue band is 39% of that of the native **1** used for the reaction sequence (Table 2). As the control experiment gave a recovery of 49%, the former value corresponds to a corrected recovery of the blue absorption of 79%. The band around 418 nm would then correspond to the remaining 21%.

Renaturation of denatured **2** in the presence of 5mM dithionite led again to partial reoxidation. The resulting pigment still contained chromophores absorbing at 418 nm, and in addition the chromophores of freshly renatured **2** absorbing at 620 nm (see above). The maintenance of the low redox potential during renaturation was ascertained as in the **1** experiment described above. The renaturation of reduced, denatured **4** in the presence of 0.5mM dithionite gave only partial recovery of the absorption at 563 nm (Fig. 12). This demonstrated for **4**, too, a reoxidation of chromophores under reducing conditions. Due to the interference from the dithionite solution at $\lambda < 400$ nm, it could not be established whether the low yield of the 563 nm absorption was due to part of the chromophores being still in the reduced state (λ_{max} = 300 nm), or to irreversible denaturation processes. The low redox potential of the eluent was again ascertained as described above.

Reoxidation of reduced denatured biliproteins (path [d] in the reaction scheme)

Dithionite was removed from a solution of denatured **1** reduced with dithionite (λ_{max} = 418 nm) by gel filtration on a Biogel P2 column equilibrated with 8M urea (or by dialysis against 8M urea). Under these conditions, the pigment is reoxidized to denatured **1** (λ_{max} = 602 nm) in the last quarter of the column (by dialysis for 1 h). Similar results were obtained with **2** and **4**. If these experiments were carried out in the presence of 8M urea/0.5mM dithionite, the pigments remained reduced.

Discussion

Denaturation-renaturation (paths [a] and [b] in the reaction scheme).

The non-covalent interactions between the proteins and the chromophores can be abolished by denaturation of the protein. The spectral properties of **1** from *Spirulina platensis* denatured by heat or by urea are nearly identical[18]. They are similar, too, to that of a model pigment, dihydrooctaethylbilindione (**5**), which contains the same

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* Qualitatively similar results were obtained, if denatured **1** treated with 2-mercaptoethanol or sodium sulfite is renatured in the presence of the respective reagents.

conjugation system as 1[19]. In particular, the position and extinction coefficients of the free base (pH = 7.5) and the cation (pH = 3) are nearly identical to the respective values of the model bilin (Table 3). A residual influence of the protein in the denatured state had been inferred earlier[21] from a comparison with phycocyanobilin 655[44] (= phycobiliverdin[1] = ethylidenebilin 6). The latter has an increased intensity of the near-UV band, but from the data in Table 3 it appears that this difference is due to the additional Δ3,3a double bond present in phycocyanobilin[45–47]. A similar intensity ratio *Q* for denatured 1 and 2 indicates a complete uncoupling for the latter, too. For urea-denatured 4, complete uncoupling had been inferred by Muckle and Rüdiger[23] from proteolysis experiments and comparison with mesobilirhodin.

Spectroscopically different denatured forms of phycobilins have been found after (apparently partial) denaturation with detergents like sodium dodecylsulfate[23,39].

In the case of 1 and 4, removal of the denaturing agent, urea, fully restores the original pigment with respect to the following criteria. Absorption spectroscopy, one of the most sensitive tests for the state of the chromophore and its environment[5], does not show any difference between native and renatured 1. Furthermore, each pigment was denatured again and found spectroscopically identical to the respective denatured phycobilin both at pH 7.5 (free base) and pH 3 (cation).

With 2, the renatured pigment has an absorption maximum at 620 nm, which is close to that of native 1, rather than to that of native 2. This phenomenon was observed first by Erokhina and Krasnovskii[48] and Brown et al.,[49] and has recently been attributed to reaggregation to the trimer of 2[50]. Incubation in phosphate buffer only partly restored the spectrum of native 2, with the shoulder at 610 nm of the long wavelength band remaining too high in intensity. Apparently, reaggregation of the subunits[50] is a much slower process in 2 than in 1 or 4, or the spectroscopic changes due to aggregation are less pronounced in the latter pigments[3,51].

The yields of renatured 1 and 4 are fairly low at the low pigment concentrations used for the spectroscopic studies. The yields are concentration-dependent, however, as the losses are negligible at the much higher concentrations commonly used for desalting in preparative work. As the size of the desalting column is determined by the urea concentration, the low yields obtained with the dilute solutions are probably due to irreversible absorption. This is supported by the blind values obtained after filtration of native phycobilins at the respective concentrations over a desalting column (Table 2). To allow a quantitative comparison (Table 2), all modification and renaturation experiments for a particular pigment have been carried out at the same concentrations.

Reductions

While the chromophores of urea-denatured phycobilins are essentially identical to those of free bilins with the same conjugation system (see above), the properties of the chromophores of native phycobilins are so different (Table 1) that any structural similarity seems unlikely at first sight. The reversible denaturation – renaturation experiments discussed above provide a solid basis, however, for these differences being exclusively due to non-covalent interactions between the protein and the chromophores, as they are completely and reversibly abolished by urea denaturation.

Treatment with a reagent selectively attacking the chromophore is a useful approach to define these interactions more precisely. The reducing agents used in this study are such selective reagents. The only likely point of attack at the protein moiety would be disulfide bonds. These are absent in the phycobiliproteins of known primary structure [16,52]. They also appear to be absent (at least between the two subunits) in other phycobiliproteins, if judged from the identical electrophoretic mobilities in the presence and absence of thiols [22,53,54].

Reduction of denatured pigments and structure of the products (path [c] in the reaction scheme)

Denatured 1 is reduced completely at a dithionite concentration of 0.5mM (Fig. 8). The same reduction product is obtained from 2, as expected, since the two pigments bear chromophores of the same molecular structure. From their absorption at 418 nm and their extinction coefficient and from model studies, the dithionite reduction products of **1** and **2** are proposed to contain bilirubin type chromophores (formula **8**) and have, therefore, been termed "phycorubins".

Bilirubin (**11a**) has been made on a preparative scale from biliverdin (**10a**) by reduction with alkaline dithionite[55]. More recently, the reduction of a biliverdin-iodine complex with sodium dithionite or with sodium borohydride has been reported to yield bilirubin, as identified by UV-vis spectroscopy and thin-layer chromatography [56]. The identity of the dithionite reduction product of biliverdin as bilirubin has been questioned by Foulkes et al.[57], without analytical data*. We have studied the reduction of biliverdin (**10a**), mesobiliverdin (**10b**), its dimethyl ester (**10c**), of **12** and of the A-dihydrobilin (**5**) with three different reductants (Table 4). The verdins yielded the respective rubins only upon reduction with dithionite, as identified by UV-vis spectroscopy, stability under acidic conditions and thin-layer chromatography. By contrast, the reduction products with 2-mercaptoethanol or sodium sulfite had UV-vis spectra similar to those of the authentic rubins, but they differed in their stability under acidic conditions and their behavior in thin-layer chromatography (Table 4). It is concluded that dithonite reduction yields true rubins hydrogenated at C-10 and N-22, whereas the other reagents yield different products, possibly by addition rather than reduction**.

A rubinoid structure **8** for the dithionite-reduced chromophores of **1** is supported by the extinction coefficients of the products. Mesobilirubin contains two dipyrromethene chromophores, but structure **8** has only one identical to the rings C and D of the chromophore of mesobilirubin (**10b**). In $CHCl_3$, the extinction coefficient of the latter pigment (57800 at λ_{max} = 434 nm) is similar to that of bilirubin (**10a**) (58800 at λ_{max} = 453 nm)[64]. The extinction coefficient of bilirubin depends on the solvent[64] and pH[65,66] and is decreased in neutral aqueous solution (46700 at pH = 7.4[67], 46800 at pH = 8.0[55], but 55800 in alkaline solution[65]. The extinction coefficient of 25500 (λ_{max} = 418 nm) determined for the reduction product at pH 7.5 reflects the decrease in the number of chromophores present in structure **8** by 50%.

The reduction of denatured **4** also is complete at 0.5mM dithionite. There are two possible structures for the reduction product of **4**, from attack at either the C-5 or the C-10 methine bridge. No model studies have been done in this case, but the latter product is likely on the basis of the absorption spectrum. Reduction at C-5 would yield a dipyrromethene chromophore of the neotype[68], an example of this class being urobilin with an absorption of the free base around 450 nm[11]. Reduction at C-10 would yield a vinylpyrrole chromophore, for which absorption maxima between 274 and 386 nm[69] (depending on the substituent at the vinyl group) have been reported. Reduction of **4** with dithionite gives a product absorbing at 300 nm (Fig. 10), suggesting a reduction at the C-10 methine bridge (formula **9**).

Reduction of the native pigments

By contrast to denatured **1**, the reduction of the native pigments is incomplete, and requires much higher concentrations of reductant. Assuming the same oscillator strengths for the three chromophores present in the α, β-monomer of **1**, the integrated intensity change of the red band of 40% indicates the reduction of approximately one out of three chromophores. The question then arises whether this reduction is statistical or selective for one of the three chromophores. The decreased shoulder of the red absorption band of partially reduced native **1** and the correspondingly blue-shifted difference spectrum against native **1** (Fig. 4) support a non-statistical reduction. Distinctly different absorption spectra for the three chromophores had been inferred earlier from fluorescence[70,71], fluorescence polarization[72] and low temperature absorption spectra [18,73], and from partial denaturation studies[18]. Different primary structures at the chromophore sites provide a common basis for the spectral dif-

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* Biliverdin is susceptible to attack at its vinyl group(s) [58,59], and we have observed unidentified products of this spectral type after 2-mercaptoethanol reduction/acid reoxidation of biliverdin, if judged from the blue-shifted absorption spectrum. For the lack of experimental data, it is difficult to judge whether the different results cited[57] are due to side reactions of this type. The chromophores of 1 and 2 are devoid of vinyl groups.

** Rubinoid pigments are accessible from verdinoid pigments not only by reduction, but also by nucleophilic addition, as suggested recently[60,61], and by C-protonation[62,63]. See also note added in proof, p. 954.

ferences[14–17,52]. The double maximum in the difference spectrum (Fig. 4) is, however, indicative that the reduction is not an all-or-nothing process for any of the three chromophores, but that there is only a preference for the short wavelength forms. The reduction of native **1**, has been studied at concentrations of dithionite up to 0.5M. At concentrations less than 0.5mM it is negligible, although this amount of reductant is already almost an order of magnitude in excess of the chromophores present. An increase to 5mM dithionite is necessary to reach a saturating, but still incomplete reduction. At higher concentrations, there is no significant further reduction. By contrast, the extinction of the oxidized form at 620 nm even increases again at a dithionite concentration of 0.5M, but this may be an artefact due to the high salt concentrations and has not been analysed further.

The absorption maximum at 418 nm suggests that some of the chromophores are reduced at the C-10 methine bridge. Thus, the point of attack is the same as in the denatured pigments, but the reduction is more difficult. The state of the reduced chromophores is less certain to assess. The same extinction coefficient has been found within the limits of error for the 418 nm band of the reduced chromophores both in the denatured and the native pigments. While this indicates a *similar* conformation in both cases, it appears from the work of Blauer and Wagnière[74] that the spectrum of bilirubin is not as strongly dependent on its conformation as is that of biliverdin[75,76]. CD experiments are in progress to further clarify this point.

The results obtained with **4** are similar and can be rationalized in the same way. **4** from *Fremyella diplosiphon* contains six chromophores[23]. As in other C-phycoerythrins, they are more difficult to separate spectroscopically[3] than in **1**. Different environments for each chromophore present have been established for two phycoerythrins [14]. Again assuming equal oscillator strengths for the chromophores, the decrease in the integrated intensity of the 560 nm band corresponds to the reaction of 50% of the chromophores. The difference spectrum (Fig. 7) again supports a non-statistical reduction of the chromophores, with the ones absorbing at shorter wavelengths being preferentially reduced. In the formalistic description derived from fluorescence polarization data[70], these would again correspond to the sensitizing chromophores. Due to the lack of absorption of the reduction product (**9**) of **4** in the visible spectral range, no positive band is seen in the difference spectrum (Fig. 7). Measurements below 400 nm are obscured by the high absorption of the dithionite solution*.

In **2**, the decrease in the integrated intensity of the absorption band at 656 nm corresponds to the reduction of 26% of the two chromophores present. The simultaneous rise of an absorption band around 418 nm again supports the reduction to a product hydrogenated at the C-10 methine bridge, as in **1**. As discussed above, the absorption spectrum of **2** is more sensitive to the state of the protein than those of **1** and **4**. It is, therefore, surprising that the difference spectrum upon reduction indicates a more random reduction than for **1** and **4**. This indicates that the chromophores present in native **2** are in similar environments, at least with respect to reduction. This similarity is supported by recent fluorescence polarization data[72] and the sequence determination[52] of an allophycocyanin.

Reoxidation and renaturation of the reduced pigments (paths [d], [f] and [i] in the reaction scheme)

The reactions of native and denatured phycobilins, e.g. with reductants, may be explained by two mechanisms: a kinetic mechanism in which the protein increases the activation energy or acts as a shield separating the interior from the aqueous environment, and a thermodynamic mechanism in which the chromophore-protein interactions (conformation, H-bonds and others) change the stabilities of the chromophores in such a way that they no longer react as free bilins. A distinction between the two mechanisms should be possible by treating the native biliprotein with the chromophore-selective reagent, and comparing it to the denatured pigment treated with the reagent and subsequently renatured in the presence of the same reagent at the same concentration. If the protein acts as a shield, the two procedures should yield different products. In this case, the modi-

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* A 5mM solution has the following absorbances: $A_{400} = 0, A_{380} = 0.03, A_{360} = 0.55$.

fied chromophore would have to be accomodated by the protein. If the protein interactions do not prevent the approach of the reagent, but rather change the stability of the chromophore, one would expect identical products from the two treatments.

If the criterion of renaturation is applied to the dithionite reduction studied here (see the reaction scheme for a survey) the results obtained are strong arguments in favor of the thermodynamic mechanism, in which the protein is transparent to the reductant*, but the chromophore stabilized towards reduction. Renaturation of reduced, denatured **1** (= "phycorubin") is always accompanied by reoxidation of the type C to the type A chromophores. The oxidation is complete if the renaturation is carried out in the absence of dithionite, or at a concentration of dithionite $\leqslant 0.5$mM (path [i] and Fig. 11). Renaturation of the protein in the presence of 5mM dithionite still leads to partial reoxidation. In the product, about 79% of the chromophores are oxidized, and 21% stay reduced (Table 2). The onset of the partial reduction of native **1** (path [g]) is bracketed by the same two concentrations, and a similar ratio between oxidized and reduced chromophores is obtained after reducing native **1** at a dithionite concentration of 5mM. If judged from the spectroscopic similarity, the same state is reached, independently of the way it is reached (paths [a, c, i] or [a, c, f] as compared to native **1** treated with the appropriate dithionite concentration).

As dithionite solutions can be unstable in open systems like the column chromatography used [41,42], the actual concentration of dithionite may be lower at the end of the column than originally adjusted. While the final concentration has not been determined quantitatively, the redox potential of the eluent has been checked routinely with redox indicators.

In the experiments with 5mM dithionite (original) leading to the partially oxidized "phycocyanorubins", the redox potential of the eluent was in each case < -440 mV, the standard potential of methylviologen. Thus, the chromophores are obviously reoxidized during the renaturation process at a redox potential sufficiently negative to reduce all chromophores of denatured **1**. This is illustrated best by a subsequent denaturation of the samples, which produced, without further addition of dithionite, fully reduced, denatured **1** ("phycorubin", path [e] in the reaction scheme), thus excluding any artefacts due to the possible destruction of dithionite.

Free bilirubins are autooxidizable to biliverdins

The slow oxidation of bilirubin in $CHCl_3$ was an early indication[78] of the intramolecular H-bonds present[36]. The dimethyl esters[78], non-IXα isomers[36] and octamethylbilirubin[79] incapable of forming such bonds are oxidized more rapidly, and oxidation is promoted especially by $Zn^{2\oplus}$[65] and other metals preferring square-planar ligands, probably due to a template effect of the metal[80]. The reoxidation of "phycorubin" under denaturing conditions to denatured **1** (path [d] in the reaction scheme) has been studied by removal of the dithionite either by dialysis against buffer containing 8M urea, or by filtration over a desalting column in the presence of urea. In both cases, the chromophores are reoxidized to form denatured phycocyanin. This process is slow, however, if compared to the rapid oxidation if both urea and dithonite are removed simultaneously. The latter transformation is already visible at the first quarter of the column, if judged from the colour change and the reappearance of the red fluorescence. While these processes may be under kinetic control, the (partial) reoxidation which occurs in the presence of dithionite cannot be explained by a kinetic control mechanism. Under these conditions, free biliverdins and denatured phycobiliproteins become completely reduced, and bilirubins or denatured phycorubins remain so, e.g. the reduced form is thermodynamically stable. If the chromophores are nonetheless oxidized during renaturation, this implies that the redox potential of the chromophores* becomes more negative during this process.

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* Frackowiak and Skowron[77] have recently observed the electrooxidation of phycobiliproteins. The electron transfer from the chromophores in the native pigments also indicates the transparency of the proteins towards redox reagents.

* We have been unable so far to define conditions under which bilirubin and biliverdin are in rapid thermodynamic equilibrium to permit the measurement of redox poten-

It has been suggested recently that a major change in the chromophores during renaturation is a conformational one. Based on spectroscopic arguments a rigid, extended conformation has been proposed for the chromophores of native **1** and other biliproteins, vs. a cyclic structure in free bilins and denatured biliproteins[18]. This proposal has gained strong support recently from spectral studies[83,84] of isophorcabilin (7) and sarpedobilins. These pigments are derivatives of biliverdin IX γ which are held in an extended conformation by additional bridges between the pyrrolic rings[85]. Spectroscopically, they are very similar to *native* **1**. In particular, the high intensity of the band around 600 nm and the low intensity of the near UV band is similar in both pigments, and they show a high fluorescence[84] as compared to biliverdins[60,84]. If such a conformational change is indeed the major difference between native and denatured biliproteins, the results suggest a pronounced conformational dependence of the stability of bilins to redox reagents. Specifically, the extended conformation present in native phycobiliproteins would have a redox potential similar to or below that of the dithionite solution (e.g. < -440 mV), because the chromophores are not reduced with a large excess of the reductant present, and if previously reduced, become even oxidized.

A mechanism to explain this change in the redox potential could be the change of the ridge-tile conformation typical for bilirubins[36,37] (C in Fig. 1) into a coplanar, extended conformation[18] (like A) during the refolding of the protein. While in the former, the two π-systems are efficiently uncoupled, the interactions between the two coplanar halves in the latter conformation would facilitate its oxidation. A similar template effect has been invoked to account for the decreased oxidation potential of bilirubin complexes with metals preferring a square-planar configuration[80].

Assuming such a conformational change between a noncoplanar ridge-tile structure (C in the reaction scheme) and a coplanar extended structure (like A in the reaction scheme) as the crucial step during renaturation, it is possible to estimate the upper limits for the energetics of this process.

The known activation energies for geometric changes of bile pigments are $\Delta G^* = 74.8$ kJ/mol for the inversion of a derivative of bilirubin[86], $\Delta G^* = 42$ kJ/mol for the inversion of a biliverdin[87] and $\Delta G^* = 105$ kJ/mol for the Z, E isomerization of a biliverdin[88]. For the latter process, a free energy difference of $\Delta G^0 = 20$ kJ/mol has been determined[88] which probably reflects mainly the increased steric hindrance in the E-isomer. Studies with space-filling models for the stepwise unfolding of the bilin chromophore (Fig. 14) indicate that the first step always increases the steric hindrance and decreases the possibility of forming H-bonds, but that these factors balance for each subsequent step, as long as the strongly hindered E, *anti*-conformations are avoided.

Under these assumptions, the energetics of, for example, the cited Z, E-isomerisation[88] as the first step give a first order estimate for the entire unfolding process in the range $\Delta G^* \leqslant 100$ kJ/mol and $\Delta G^0 \leqslant 20$ kJ/mol.*

The free activation enthalpy is in a range thermally accessible at room temperature, and there are, besides the cited quantitatively studied processes, a variety of isomerizations of bile pigments known to occur at room temperature. These include (probably Z, E) isomerizations of bilirubins[90], conformational changes of bilirubin and biliverdin bound to serum albumin[74,75], induction of optical activity in chiral solutions[34], and the like.

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tials (see above). The observation of irreversible steps in the electrochemical oxidation of bilirubin to biliverdin [80,81] and vice versa point to the same difficulty. Thus the ΔG^0 of the reaction between dithionite and biliverdin is not yet accessible *experimentally* from a redox titration, but the above results demonstrate that a reduction – reoxidation equilibrium must exist, and that it is different for the native and the denatured pigments. The molecular orbital calculations of Pullman[82] indicate a high electron affinity of biliverdin in an unspecified conformation. To our knowledge, a conformation dependence of the redox properties has not yet been investigated.

* This reasoning has ignored any possible stabilizing interactions between the bilin chromophore and the protein. It is interesting in this respect, that nicotinamide dinucleotides bind in a maximally extended conformation to flexible protein regions in certain reductases[89].

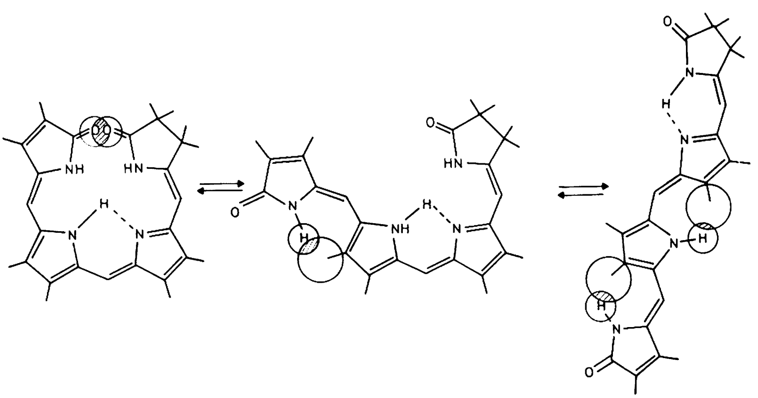

Fig. 14. The interconversion of cyclic and extended conformations of bile pigments by rotation around the 14,15-single and Δ10,11-double bond.

Steric hindrance and H-bonding between adjacent groups are indicated. The cyclic structure is predominant in solution [33–35]. In this conformation, the steric hindrance is relieved only by small deformations of the methine bridges from planarity, thus forming a helix.

The required free energy would have to be provided by the protein. The free stabilization energy of macromolecules, e.g. the free energy differences $\Delta G^0_{H_2O}$ of native vs. forms denatured by urea or quanidinium chloride, at or near neutral pH, and at ambient temperature, have been determined carefully for several substances: ribonuclease (40.5[91] and 54.3 kJ/mol[92]), lysozyme (59.3 kJ/mol[93], α-chrymotrypsin (51.4 kJ/mol[94]), several cytochromes *c* (53.1–64.4 kJ/mol[94]) and myoglobins (49.3–59.8 kJ/mol[92]).

Although the values vary considerably, depending on the corrections used (see Lapanje[95] and Pace[96] for a discussion), these values would suffice to unfold at least two to three chromophores, if the proteins of **1**, **2** and **4** had similar stabilization energies. The molecular weights of the enzymes cited are similar to or less than that of one subunit of a biliprotein bearing one to a maximum of four chromophores[1,2,4,7]. Recently, $\Delta G^0_{H_2O}$ has been determined for phycocyanins from a variety of cyanobacteria of different biotopes[97]. With the exception of a **1** from a halophilic cyanobacterium, values between 10.0 and 22.2 kJ/mol at pH = 6.0 have been found, using corrections similar to those used in the enzyme studies cited above. The highest value for the **1** from a mesophilic organism is as low as 17.6 kJ/mol. One might speculate that the pronounced decrease in $\Delta G^0_{H_2O}$ from the enzymes cited above to **1** is due to the free energy required to bring the chromophores from the cyclic into an extended conformation.

Conclusions

One of the remarkable aspects of proteins is their ability profoundly to alter the properties of small molecules bound to them. In the case of biliproteins, these alterations are entirely due to non-covalent interactions between the linear tetrapyrrolic chromophores, and the proteins, even though they are covalently linked. There are two principal control mechanisms of the protein, a *kinetic* and a *thermodynamic* one. The results of denaturation – renaturation and reduction – oxidation experiments summarized in the reaction scheme can only be explained by a *thermodynamic* control mechanism. While the results do not allow any conclusions about an additional kinetic control, a purely kinetic effect cannot explain the cyclic scheme leading to the same pigments irrespective of the reaction pathway.

On a molecular level, the factors responsible for the increased stability towards reduction are still open to speculation. One such speculation, derived from the known conformational change of the flexible tetrapyrrole chromophore induced by the protein, implies different chemical stabilities for different conformations of the chromophores. This working hypothesis, which has obvious implications for chromoproteins with similarly flexible chromophores (e.g. carotenoproteins, rhodopsins), has to be tested by other modification procedures and studies with suitable model compounds.

Note added in proof (18 Mai 1979): We are aware of the work of G. Blankenhorn and E.G. Moore[98] on the stepwise reduction of $NAD^{\oplus}$ analogs with sodium dithionite via a reversibly formed sulfinate addition product, which is stable only at high pH (> 8.5). All experiments with biliproteins in the preceding study have been performed at pH 7.5, and the model reactions with free bile pigments included acidification to pH 2.7 during workup. The latter gave no indications of intermediates, but studies at higher pH and with other reductants shall clarify if sulfinate adducts are accessible, too, from bilindiones and in case establish their properties.

This work was supported by a grant of the *Deutsche Forschungsgemeinschaft*. We thank *Prof. W. Rüdiger* for continuing support and helpful discussions. A generous gift of frozen cells of *Spirulina platensis* from *Prof. C. Soeder*, Gesellschaft für Strahlenforschung, Dortmund, is acknowledged. We thank Ms. *B. Zickendraht-Wendelstadt* for a gift of 4 from *Fremyella diplosiphon* and Ms. *C. Bubenzer* for valuable technical assistance.

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Gesamtregister 1979

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Hinsichtlich der *Nomenklatur* richte man sich nach der IUPAC-Nomenklatur sowie nach den Empfehlungen der "IUPAC-IUB Commission on Biochemical Nomenclature": Kohlenhydrate, *Eur. J. Biochem.* **21**, 455–477 (1971); **25**, 4 (1972); α-Aminosäuren, *Eur. J. Biochem.* **53**, 1–14 (1975);

Tab. 1. Symbole für Größen und ihre Einheiten

Größe		Einheit[a]
l	Länge	m, mm, µm, nm, etc.
V	Volumen	m^3, l (dm^3), ml, etc.
λ	Wellenlänge	nm (nicht mµ oder Å)
t	Zeit	h, min, s, ms, µs, etc.
ν	Frequenz	Hz
m	Masse	kg, g, mg, µg, etc.
ρ	Dichte	g/cm^3
s	Sedimentationskoeffizient	$S = 10^{-13}s$
n	Substanzmenge	mol, mmol, etc.
M	molare Masse (m/n)	g/mol
–	Masse eines Moleküls	Dalton[b]
M_r	Molekulargewicht	(dimensionslos)
c_B, [B]	molare Konzentration einer Substanz B	M, mM, µM, etc. (besser als 10^{-3}M, etc.)
T	Temperatur (absolut)	K (nicht °K)
t, θ	Temperatur	°C
q, Q	Wärmemenge	J (besser als cal)[c]
I	Ionenstärke	M (mol/l), mM, etc.
K	Gleichgewichtskonstante	
K_m	Michaeliskonstante	
K_i	Inhibitorkonstante	
k	Geschwindigkeitskonstante	
v	Reaktionsgeschwindigkeit	mol/s (oder mmol, µmol oder nmol/s, etc.), besser als µmol/min
V (nicht V_{max})	Geschwindigkeit der enzymkatalysierten Reaktion bei unendlich großer Substratkonzentration	
I	Lichtintensität	cd
T	Durchlässigkeit (I/I_0)	(dimensionslos)
A	Absorption[d] (– lg T)	(dimensionslos)
ϵ	molarer Extinktionskoeffizient	$M^{-1} \times cm^{-1}$

[a] Präfixe für Einheiten: T, Tera (10^{12}); G, Giga (10^9); M, Mega (10^6), k, Kilo (10^3); m, Milli (10^{-3}); µ, Mikro (10^{-6}); n, Nano (10^{-9}); p, Piko (10^{-12}); f, Femto (10^{-15}); a, Atto (10^{-18}).

[b] Das Dalton ist 1/12 der Masse eines Atoms des Nuklids ^{12}C.

[c] Das Joule ist die SI-Einheit der Energie. Die Kalorie (1 cal = 4.184 J; 1 J = 0.239 cal) ist für eine Übergangszeit noch zugelassen; in jedem Fall sollten aber die Angaben auch in Joule ausgedrückt werden.

[d] Die Ausdrücke optische Dichte, Extinktion oder Absorbancy sollen nicht mehr verwendet werden.

Cyclite, *diese Z.* **350**, 523–535 (1969), *Eur. J. Biochem.* **57**, 1–7 (1975); Lipide, *diese Z.* **358**, 617–631 (1977); Phosphorhaltige Verbindungen, *diese Z.* **358**, 599–616 (1977); Steroide, *diese Z.* **351**, 663–689 (1970); Chinone mit isoprenoiden Seitenketten, *Eur. J. Biochem.* **53**, 15–18 (1975); Folsäure u. verschiedene andere Verbindungen, *diese Z.* **348**, 266–276 (1967); Corrinoide, *Eur. J. Biochem.* **45**, 7–12 (1974); Vitamine B_6, *Eur. J. Biochem.* **40**, 325–327 (1973); Carotinoide, *Eur. J. Biochem.* **25**, 397–408 (1972), **57**, 317–318 (1975); synthetische Analoga natürlicher Peptide, *diese Z.* **348**, 262–265 (1967); Enzyme Nomenclature, Recommendations (1972), Elsevier Publ. Comp., Amsterdam; multiple Enzymformen, *diese Z.* **353**, 852–854 (1972); Eisen-Schwefel-Proteine, *Eur. J. Biochem.* **35**, 1–2 (1973); Human-Immunglobuline, *Eur. J. Biochem.* **45**, 5–6 (1974); Peptidhormone, *Eur. J. Biochem.* **55**, 485–486 (1975). Für die Rechtschreibung ist „Jansen/Mackensen, Rechtschreibung der technischen und chemischen Fremdwörter" maßgebend.

Tab. 2 Empfohlene Abkürzungen.

Atome, isotope = z.B. [16-^{14}C]Östron
Atome, numeriert = z.B. C-5
Curie = Ci
Impulse pro Minute = Ipm (engl. cpm)
Prozent der Theorie = % d. Th.
prozentig = proz. (nicht %-ig)
Relative Wanderungsgeschwindigkeit = R_F
Schmelzpunkt = Schmp. (engl. m.p.)
Siedepunkt = Sdp. (engl. b.p.)
Umdrehungen pro Minute = U./min (engl. rpm)
Zerfälle pro Minute = Zpm (engl. dpm)
Zersetzung = Zers. (engl. decomp.)

Bezüglich der *Abkürzungen und Symbole für chemische Namen*, die in der biologischen Chemie von besonderem Interesse sind, wird auf die Empfehlungen der „IUPAC-IUB Commission on Biochemical Nomenclature" verwiesen (siehe z.B.: Allgemeines, Aminosäuren, Zucker, Phosphate, Coenzyme, *diese Z.* **348**, 245–265 (1967); Aminosäurederivate und Peptide, *Eur. J. Biochem.* **27**, 201–207 (1972); synthet. Polypeptide, *diese Z.* **349**, 1013–1016 (1968); Nucleinsäuren, Polynucleotide und deren Bestandteile, *diese Z.* **351**, 1055–1063 (1970). Andere als die dort empfohlenen Abkürzungen werden nur in seltenen Ausnahmefällen zugelassen. Sie müssen am Beginn jeder Arbeit in einer Fußnote erklärt werden.

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Die folgenden Damen und Herren haben in diesem Jahr als Gutachter mitgewirkt. Herausgeber, Schriftleitung und Verlag danken ihnen für ihre freundliche Unterstützung.

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