Review Letter

LIGHT-HARVESTING PIGMENT–PROTEIN COMPLEXES OF PURPLE PHOTOSYNTHETIC BACTERIA

R. J. COGDELL and J. P. THORNBER+

Department of Botany, University of Glasgow, Glasgow G12 8QQ, Scotland and +*Department of Biology and Molecular Biology Institute, University of California, Los Angeles, CA 90024, USA*

Received 10 October 1980

1. Introduction

The light-absorbing pigments (bacteriochlorophyll and carotenoid) in the purple photosynthetic bacteria exist in vivo as well-defined pigment–protein complexes [1,2]. In general the polypeptides associated with the pigments are low molecular weight (or M_r), hydrophobic, intrinsic membrane proteins. There is a division of labour among the pigment molecules in the photosynthetic process: The majority serve as a light-harvesting antenna and funnel absorbed incident radiation to a few specialised sites (the photochemical reaction centres) where the light energy is trapped and converted into chemical potential energy. The combination of reaction centres with their associated antenna forms the so-called photosynthetic unit.

The structure and function of the reaction centre is now quite well understood [3–6], mainly because of the availability of isolated, highly purified reaction centres [3,6,7]. In contrast, the light-harvesting pigment–proteins have been rather neglected. However, now that biochemists have learned how to isolate and purify the antenna complexes, the structure of this interesting class of proteins is receiving more attention. It is our purpose here to summarise the recent advances in the area.

2. Nomenclature

Purple photosynthetic bacteria exhibit intense, reasonably well-separated absorption bands in the near infrared (NIR) between 800 and 900 nm due to bacteriochlorophyll (Bchl) *a* contained in the light-harvesting complexes. It is most practical and informative to name the fractionated complex(es) after their NIR absorbance maxima. For example, *Rhodopseudomonas (Rps.) sphaeroides* contains two antenna complexes, one absorbing maximally at 870 nm, termed B870–protein, and the other at 800 and 850 nm, termed B800-850–protein; each of these spectral forms of Bchl can be observed to occur in the intact bacterium (cf. fig.1). We shall use this nomenclature for Bchl *a*-containing complexes of purple bacteria in this article. It has been proposed from fractionation [1,2,8], developmental [8,9], and genetic [10] studies that all purple bacteria contain either a B870–protein type or both types of antenna complex; however, the exact NIR maximum(a) in either type may differ slightly between different species of bacteria or between different strains of a bacterium [1]. On this basis two classes of purple bacteria have been recognised:

(i) One (typified by *Rhodospirillum (Rsp.) rubrum*) has an antenna composed only of the B870–protein;

(ii) The other (e.g., *Rps. sphaeroides, Rps. capsulata,* and *Chromatium* spp.) contains both types (fig.1).

There are, of course, a few exceptions to this rule-of-thumb (e.g., *Chr. acabenum* [11]).

3. Isolation and purification of light-harvesting pigment–protein complexes

In comparison with water-soluble proteins, purification of antenna pigment–proteins is not so easily achieved. A brief discussion of purification procedures will pinpoint the difficulties.

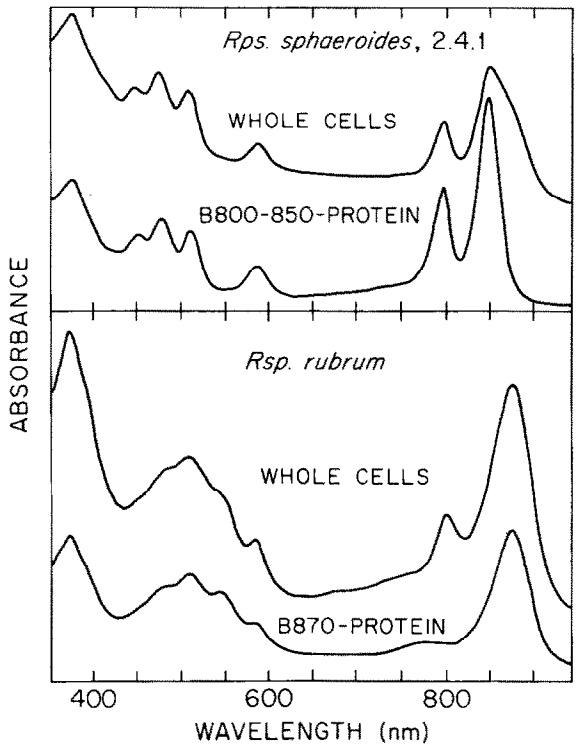

Fig.1. Room temperature absorption spectra of two purple bacteria and antenna caroteno–Bchl–proteins prepared isolated from them. *Rps. sphaeroides* contains two antenna complexes: the B800-850–protein shown here and a B870–protein (not shown); the presence of the latter complex in the whole cell spectrum can be deduced from the ~870 nm shoulder. *Rsp. rubrum* contains a single antenna complex, the B870–protein shown in the lower portion of the figure. The 800 nm absorption peak in the whole cell spectrum is due to the absorbance of reaction centre chromophores (cf. [47]).

The antenna complexes are membrane-bound and not extracted therefrom by aqueous salt solutions. Their isolation requires disruption of the membrane structure and the concomitant liberation of the complexes as soluble entities. This has generally been achieved by the use of detergents. Thereafter the object is to obtain the smallest possible, homogeneous, pigmented entity which is still representative of its in situ state. This is done empirically and the objective can be hard to achieve when a protein denaturant (i.e., a detergent) has to be used to disrupt the membrane.

The four most widely used detergents are sodium and lithium dodecylsulfate, lauryl dimethylamine-oxide and Triton X-100 [1–3,12–15]. The selection of the detergent to be used is, at present, empirical and a compromise (see philosophy in [2]): It must be harsh enough to give a reasonable degree of membrane disruption in the organism under study, and yet not be so harsh that it causes significant denaturation of the required complex. Once the membrane has been disrupted, the antenna complexes are purified by various fractionation procedures, most of which are carried out in the presence of detergent. The applicable fractionation procedures are DEAE-cellulose and hydroxylapatite chromatography, ammonium sulphate precipitation, sucrose gradient centrifugation, and polyacrylamide gel electrophoresis [2,12–15]. Usually purification involves a combination of procedures (e.g. [2,14]).

It is worth emphasising that preparation of a complex demands a flexible approach. Unlike the case for water-soluble proteins, the exact details of the preparative method can be expected (cf. [2]) to vary slightly from time to time. Since it is difficult always to obtain membranes from a photosynthetic bacterium with the same protein:lipid:pigment ratios, the quantity of detergent required for the same degree of membrane disruption may alter for each batch of the bacterium (cf. [2]); the amount of detergent added is usually estimated from the easily measured pigment content of the membranes. This variation largely explains why published purification procedures may not always prove to be exactly repeatable from one laboratory to another. We stress the philosophy presented in [2] for investigators who attempt to repeat a published method. This in essence said:

> Start with a large batch of cells so that one can vary the detergent: Bchl ratio on aliquots of cells until a procedure that works is obtained, then it can be repeated exactly several times before a new batch of cells must be used and the procedure modified slightly.

Secondly, we advised that one can waste much time pursuing an attempt at a preparation long after it has become obvious that it is not going to work; one should not hesitate to abandon a preparation that is obviously not going correctly and make a fresh start.

The first test applied to an isolated complex to see whether purification has caused significant alterations to its native structure is to record its NIR absorption spectrum and compare it with that of the intact membrane. The NIR wavelength maximum(a) is a sensitive indicator of the delicate Bchl–protein interaction [1,2] and thus if purification has altered the interaction (i.e., denatured the complex), then the

spectral forms will be shifted from their wavelength maximum(a) in situ. It is worth mentioning here that this test cannot be applied to some preparative procedures which treat the photosynthetic membrane with organic solvents to obtain the apo-protein of the antenna complex [16,17]. This procedure solubilises some polypeptides, including perhaps the desired one(s), but also strips the pigment from the complex and thereby presents a serious problem. Without the 'marker' pigment it is obviously very difficult to be absolutely certain that the polypeptide(s) ultimately purified is(are) indeed associated with the light-harvesting pigments in vivo.

Other useful tests are fluorescence excitation spectra and Bchl:carotenoid ratios. The pigment ratio in the isolated complexes may be compared with those of the intact membranes of mutant strains which contain only that type of antenna complex under study. For example, analysis of *Rps. capsulata* Y5 enables one to determine the ratio and spectrum which should be obtained in the purified B800-850 complex since this mutant lacks the reaction centre and the B870 complex [20].

Circular dichroism (CD) spectra offer another useful indicator of the integrity of the purified complexes; the carotenoid–protein interaction in a complex is particularly sensitive to denaturation [18]. For example, in the B800-850 complex from *Rps. sphaeroides* the carotenoids show a large, induced CD spectrum; carotenoids dissolved in petroleum ether show no CD spectrum [19]. This induced CD arises from the specific binding of the carotenoid to the protein, and if the protein is denatured or digested by proteolysis this CD spectrum collapses ([18], G. D. Webster and R. J. C., in preparation).

4. Spectral and biochemical characterisation of the antenna complexes

Rather than provide a complete catalogue of all the different antenna complexes described so far, we have selected one or two representatives of the two types, and will discuss recent studies on them in some detail. The reader is referred to [1] for a 1976 perspective of all isolated complexes.

4.2. *The B800-850 light-harvesting pigment–protein complexes of* Rps. sphaeroides *and* Rps. capsulata

The B800-850–protein antenna complex isolated from *Rps. sphaeroides* (fig.1) contains Bchl *a* and carotenoid in a ratio of 3:1 (mol/mol) [2,18,21]. There does not seem to be any specificity as to which carotenoid type is present; rather it is just the same as that of the strain from which it was prepared (cf. fig.1). Resonance-Raman studies indicate that the carotenoid is most probably in all-*trans* configuration (Lutz and R. J. C., unpublished). The B800-850 complex shows strong CD bands in the NIR Bchl *a* absorptions [15]. These have been interpreted to show that the 850 nm band represents a pair of excitonically coupled Bchls, whereas the 800 nm band is monomeric. Similar conclusions were reached by fourth derivative analysis of the NIR absorption bands [2,18].

The polypeptide subunit composition of this complex was first analysed by electrophoresis on 10% polyacrylamide gels [14]. Pure preparations gave a single broad band with app. M_r 9000. However, using both polyacrylamide gradient gels and isoelectric focusing gels, this apparently single protein band has been resolved into two ([22], L. Cohen and S. Kaplan, unpublished). The pigments of the B800-850 complex could therefore be bound to both polypeptides. The minimal M_r values of these polypeptides, calculated [22] from their amino acid analyses are 5800 and 6400 and they are present in the intact complex in a ratio of 1:1 [22]. L. Cohen and S. Kaplan (unpublished) find both polypeptides to have very similar amino acid compositions and minimum $M_r \sim 9000$. Using a Lowry protein assay and assuming M_r 9000 for the light-harvesting polypeptides, the measured pigment to protein ratio suggests that 3 Bchl molecules/pair of 9000 M_r polypeptides are present [14,15]. However, until unequivocal M_r values for the polypeptides are available, this ratio is still open to question. Also it is not certain that a Lowry assay, using the water-soluble protein bovine serum albumin as the standard, is really quantitatively applicable to hydrophobic proteins. But notwithstanding this, the most likely model for the 'minimal unit' of the B800-850 complex is the simplest: 3 Bchls and 1 carotenoid/pair of polypeptides. In vivo the complex is undoubtedly an aggregated form of this 'minimal unit', and indeed electrophoresis of the undenatured pigment–protein gives a zone of >100 000 M_r [14].

A limited amount of structural work has been undertaken on this B800-850 complex. Bolt and Sauer [23] incorporated the complex into polyvinyl

alcohol films and induced orientation by stretching the film. From the linear dichroism spectra they were able to deduce some of the angles between the optical transition moments of the pigment molecules and the particle axis (q.v. [23]).

Similar conclusions have been reached regarding the structure of the B800-850 complex obtained from *Rps. capsulata* [20,24–26]. The isolated complex has a Bchl:carotenoid ratio of 3:1 [2,26]; no carbohydrate is seemingly present in the isolated material [26]. In contrast to the *Rps. sphaeroides* complex, the *Rps. capsulata* component contains three polypeptides with app. M_r 14 000, 10 000 and 8000 as judged by SDS–polyacrylamide gel electrophoresis of the denatured complex [24,26]. Amino acid analysis studies [26] have given minimum M_r for the three of 11 900, 9200 and 5100. The specific Bchl content is 100 μg/mg protein, but as yet the stoichiometry of the three polypeptides is not known.

The size of the isolated complex has been estimated by gel filtration to be 170 000 M_r, while on electrophoresis under non-denaturing conditions a colored B800-850–protein zone of 118 000 app. M_r was obtained; this zone contained only the two smaller polypeptides [26]. A chance occurrence in the way in which this complex is inserted into the chromatophore membrane has allowed a further insight into its structure [20,25]. If chromatophores from *Rps. capsulata* are treated with a low concentration of pronase, initially only the 14 000 M_r polypeptide is digested. This has no apparent effect upon the absorption spectrum of the complex, confirming the observations [24,26] that this polypeptide is not involved in binding pigment. Then over a time the 8000 M_r polypeptide is cleaved. The 10 000 M_r polypeptide is only digested after the 8000 M_r polypeptide has been attacked. When the 8000 M_r polypeptide is digested the 800 nm absorption band shifts and the carotenoid is dissociated from the complex. The 850 nm absorption band is removed in concert with cleavage of the 10 000 M_r polypeptide. These results locate the carotenoid and 1 Bchl molecule (the 800 nm absorber) with the 8000 M_r polypeptide, and the other 2 Bchl (the 850 nm absorbers) with the 10 000 M_r polypeptide (fig.2). Interestingly, when the carotenoid is removed from the B800-850 complex in the membrane, the light-induced electrochromic carotenoid bandshift is lost, even though the chromatophores remain ion-tight and retain their primary photochemistry [27]. This result, together

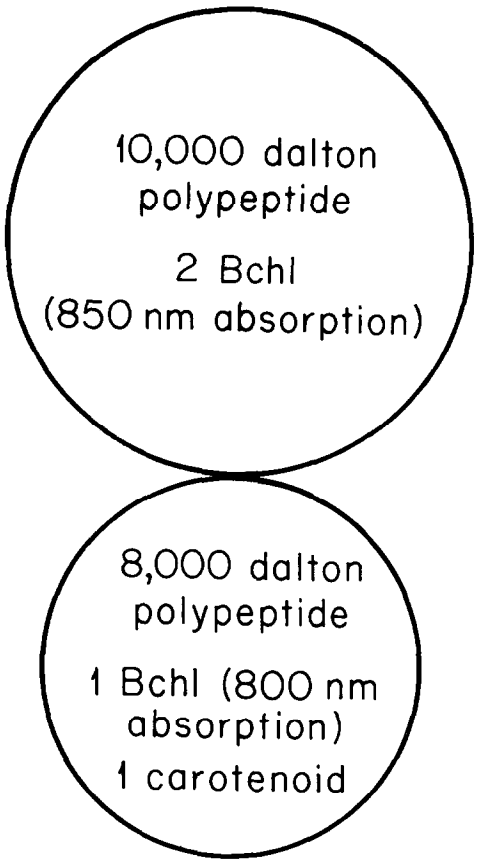

Fig.2. Current model of the arrangement of pigments and polypeptides in the minimal unit of the B800-850–protein of *Rps. capsulata*.

with similar evidence from genetic [28] and developmental studies ([29,30], R. K. Clayton, personal communication) have shown that it is only the carotenoid in the B800-850 complex which is responsible for the membrane-potential-linked carotenoid bandshift. The N-terminal amino acid sequence up to residue 24 for each of the two smaller polypeptides has been obtained [26]. No homology between the two is observed.

When the B800-850 complex isolated from *Rps. sphaeroides* (fig.1) is illuminated, it shows a single strong fluorescence emission band centered at 872 nm [13]. This presumably comes from the 850 nm chromophores. There is also a small emission from the 800 nm absorption band which confirms earlier studies [31] that energy transfer from the 800 nm Bchl to the 850 nm Bchl is not 100% efficient [32]. The fluorescence yield of the isolated complex has been found to be rather variable

(~5–30%) [15,33]. The variation seems to depend on the amount of detergent in which the complex is dissolved; higher detergent:protein ratios give higher fluorescence yields.

Light absorbed by the carotenoid as well as the Bchl sensitises Bchl fluorescence [28,32,34]. The efficiency of this energy transfer is high (85–100%) and relatively independent of the carotenoid type present. When light is absorbed by the B800-850 complex, triplet states are generated [32] which have been detected optically and by ESR. The car^T is formed by a triplet–triplet exchange reaction with $Bchl^T$, and it is thought that this reaction is the major mechanism whereby the carotenoid protects the complex from the 'photodynamic reaction' [32,35].

4.2. *The B870 antenna pigment–protein complex*

Compared to the other antenna type this complex has received less attention. It has been most studied in *Rsp. rubrum*, in which it accounts for all the antenna Bchl [1]. The B870–protein (fig.1) has been obtained by detergent treatment [2,15] and a pigment-free protein, presumably its apo-protein, by organic solvent extraction of chromatophores [17,36,37]. The pigmented complex has a Bchl *a*: carotenoid ratio of 2:1; the carotenoid is almost entirely spirilloxanthin [2]. Investigations of the apoprotein preparations have shown that the complex is probably composed of a single polypeptide having, on SDS–polyacrylamide gel electrophoresis, app. M_r 12 000 [17] or 14 000 [37]. Amino acid analysis indicates minimum M_r 19 000 [17]. Amino acid sequence determination has been started by two groups [36,37]. The N-terminal sequence and C-terminal residue has been reported [37] as:

N-formyl-Met–Trp–Arg–(Ile–Trp–Gln–Leu–
Phe–Asp–Pro–Arg–Gln–Ala–Leu–Val–
Gly–Leu–Ala–Thr–Phe–Leu–Phe–Val–
Leu–Ala . . . Ser-COOH.

Tonn et al. [17] determined that 3–7 Bchl and 1–2 carotenoid molecules were associated with one 19 000 M_r polypeptide. Little biophysical characterisation of the complex has been reported. CD spectra of the 890 nm peak show exciton coupling [15], suggesting that the band represents the absorption of dimeric Bchl; these researchers also reported a fluorescence yield of ~6% for the complex in Triton X-100. Cogdell and Thornber [2] also showed that the 890 nm peak is composed of 2 spectral forms of Bchl by fourth derivative analysis. A seemingly homologous complex has been obtained from *Chr. vinosum* [2]. In light of all the data it seems reasonable to suppose that the 'minimal unit' of this complex, at least in *Rsp. rubrum* and *Chr. vinosum*, is one of ~20 000 M_r of protein together with 2 Bchl and 1 carotenoid (mainly spirilloxanthin) molecules.

Very recently a B870–protein complex has been fractionated from *Rps. sphaeroides* by polyacrylamide gel electrophoresis at 4°C in the presence of lithium dodecylsulfate [13]. This component has a Bchl:carotenoid ratio of 1:1, and has its pigments bound to two different, low M_r polypeptides [13,21]. Since these characteristics differ from those of the purportedly homologous *Rsp. rubrum* and *Chr. vinosum* complexes, it will be interesting to await further characterisation of this antenna type to see whether all of the single-peaked, longest wavelength antenna Bchl–proteins should really be grouped together in one class.

5. The origin of the large spectral shift of bacteriochlorophyll in the antenna complexes

Before the role of the protein in binding chlorophyll was appreciated, a problem existed of how to account for the 30–120 nm shift to longer wavelengths which occurred in the NIR absorption maximum of Bchl *a* when it was bound to the membrane from that (~770 nm) of monomeric Bchl *a* in organic solvents. It was discovered that if Bchl *a* (or indeed Chl *a*) was aggregated in the form of Bchl *a*–H_2O–Bchl *a* adducts, the absorption spectrum was shifted to longer wavelengths. It was therefore suggested that a good model for the antenna Bchl would be such an extended aggregate structure (cf. [38]).

However, some recent experiments have shown this idea is incorrect in one case, and have emphasised the role of the pigment–protein interaction in this shift [39]: Chromatophores from the carotenoidless mutant of *Rps. sphaeroides* (R26) were subjected to strong illumination in the presence of oxygen. In this mutant under these conditions the antenna Bchl, a single peak at 860 nm, is irreversibly photodestroyed. At various times during the progress of the photodestruction the absorption and CD spectra were recorded. Initially the NIR absorption maximum was at 860.2 nm, but during the photodestruction it diminished in intensity and shifted to 851.9 nm. The

CD spectrum showed initially the presence of Bchl dimers, then as the absorption peak shifted and decreased, the dimer spectrum was replaced by a CD spectrum of monomeric Bchl *a*. When the absorption spectrum had a maximum of 851.9 nm, the CD spectrum was totally that of monomeric Bchl. The occurrence of an absorption maximum at 852 nm for monomeric Bchl *a* in a protein complex demonstrates that the majority of the spectral shift in vivo reflects a pigment–protein interaction rather than pigment–pigment aggregation. Whether pigment–protein interactions account for the major portion of the shift of other antenna forms to longer wavelengths requires further studies. However the current view that very few Bchl molecules occur in the basic building blocks of the antenna complexes favours the shifts being due mainly to pigment–protein interactions rather than to pigment–pigment interactions.

6. The organisation of the antenna complexes in the membrane

There is no definitive biochemical evidence as yet about how the antenna complexes are organised into photosynthetic units. However from biophysical studies on the antenna system in intact chromatophores, Monger and Parson [40] showed that the model depicted in fig.3 gave the best fit to their data; they were studying the interaction of excited states as they migrated around the photosynthetic unit. The model shows how the B870–protein complexes are arranged nearest to the reaction centres with the B800-850 antenna complexes peripheral. Note also how several reaction centres plus B870–protein molecules interact, i.e., a reaction centre–B870–protein complex is not separated from all others by the B800-850 complex (see discussion added to [2]). This model has the advantage of downhill energy gradient such that absorbed energy can proceed from B800-850 Bchl to the reaction centre via the B870 Bchl, and permits excitation energy in the B870 complex to visit more than one reaction centre until it is quenched. The model receives circumstantial support from studies on how the photosynthetic membranes develop: When *Rps. sphaeroides* or *Rps. capsulata* are grown aerobically in the dark their membranes are non-pigmented and almost completely lack any invaginations. If they are transferred to the light and the oxygen tension is lowered they begin to synthesise the components required for photosynthesis. The membranes invaginate and become highly pigmented [41]. Initially the reaction centres and B870 complexes are synthesized in concert. Only later do they extend their antenna system with the addition of B800-850 complexes [41]. Indeed if they are grown at sufficiently high light intensities the formation of B800-850 is largely suppressed and the photosynthetic units consist only of B870 and the reaction centre complexes. It is clear from these studies that there is much more intimate relationship of the reaction centre with B870 than with the B800-850 pigments.

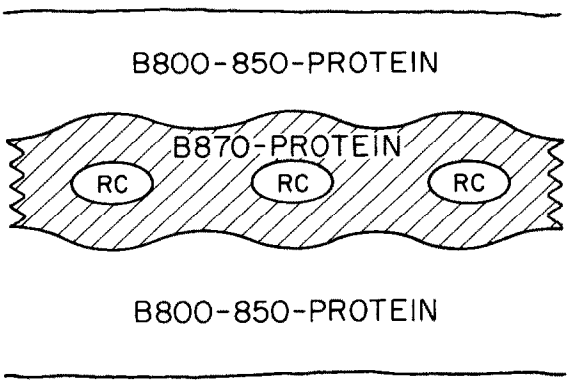

Fig.3. Model depicting the organisation of the reaction centre and the two antenna complexes in the chromatophore membrane of a purple bacterium such as *Rps. sphaeroides* (cf. [2,40]).

7. Concluding remarks

Our knowledge of the organisation of antenna Bchl in purple bacteria is growing rapidly but still has some way to go before it is equivalent in depth to our understanding of the reaction centre complex. The B800-850 component is better described biochemically than the B870 complex; this probably reflects the relative difficulty in isolating the two types in a pigmented form. Perhaps the most needed characteristics which remain to be determined precisely are the pigment:protein ratio of the complexes and the molecular weight of the isolated, pigmented complexes. Surprisingly we are apparently going to know their amino acid sequences before we know their specific Bchl content! Also, few analyses have been made of the presence of constituents other than Bchl,

carotenoid and protein in the complexes. The first indications are appearing that the notion may not be correct that only two classes of antenna complex exist in Bchl *a*-containing purple bacteria. Further studies on the recently isolated B870-protein of *Rps. sphaeroides* and new studies on complexes of other bacteria should show whether the original idea [1] was too simple.

The ultimate aim of research in this area is to understand fully the structure, function and biosynthesis of the energy-transducing system. To deduce the structure requires the availability for X-ray or electron microscopic analysis of some ordered array (hopefully crystals) of each component; alternatively a plethora of biochemical and biophysical data must be obtained on each complex. Obviously the former route is quicker and less equivocal but, at present, not attained for any detergent-soluble complex. The macromolecular structure of the membrane is being studied both directly, by examining the location and size of the components in the intact membrane [42–45], and indirectly by reassembling antenna complexes with reaction centre components [33,46]. The mechanism of energy migration to the reaction centre and its conversion into chemical energy should be fully understood once the three-dimensional structure of the complexes and the intact membrane is obtained. The current availability of isolated reaction centres and antenna complexes that have been described biochemically enables the biosynthesis of the photosynthetic unit, in particular the control of its biosynthesis, to be investigated by molecular biologists. We anticipate that there will be soon further, very intense activity in what is sure to be a very interesting molecular biology problem.

Acknowledgements

The writing of this review and the research of the two authors on purple bacterial antenna complexes was supported by NSF grant 78-15835 to J. P. T. and a SRC grant to R. J. C. We would like to thank Sam Kaplan and Larry Cohen for showing us their unpublished data.

References

[1] Thornber, J. P., Trosper, T. L. and Strouse, C. E. (1978) in: The Photosynthetic Bacteria (Clayton, R. K. and Sistrom, W. R. eds) pp. 113–160, Plenum Press, New York.
[2] Cogdell, R. J. and Thornber, J. P. (1979) in: Ciba Found. Symp. 61 (new ser.) (Wolstenholme, G. and Fitzsimons, D. W. eds) pp. 61–79, Elsevier/Excerpta Medica, Amsterdam, New York.
[3] Feher, G. and Okamura, M. Y. (1978) in: The Photosynthetic Bacteria (Clayton, R. K. and Sistrom, W. R. eds) pp. 349–386, Plenum Press, New York.
[4] Blankenship, R. E. and Parson, W. W. (1978) Annu. Rev. Biochem. 47, 635–653.
[5] Dutton, P. L. and Prince, R. C. (1978) in: The Bacteria (Ornston, L. N. and Sokatch, J. R. eds) vol. 6, pp. 523–584, Academic Press, New York.
[6] Gingras, G. (1978) in: The Photosynthetic Bacteria (Clayton, R. K. and Sistrom, W. R. eds) pp. 119–132, Plenum, New York.
[7] Clayton, R. K. (1963) in: Bacterial Photosynthesis (Gest, H. et al. eds) pp. 495–500, Antioch Press, Yellow Springs OH.
[8] Lien, S., Gest, H. and San Pietro, A. (1973) J. Bioenerget. 4, 423–434.
[9] Aagard, J. and Sistrom, W. R. (1972) Photochem. Photobiol. 15, 209–225.
[10] Drews, G., Dierstein, R. and Schumacher, A. (1976) FEBS Lett. 68, 132–136.
[11] Haswha, F. (1979) III Int. Cong. Photosynthetic Prokaryotes, Oxford, England, abst.
[12] Thornber, J. P. (1970) Biochemistry 9, 2688–2698.
[13] Broglie, R. M., Hunter, C. N., Delepelaire, P., Niederman, R. A., Chua, N.-H. and Clayton, R. K. (1979) Proc. Nat. Acad. Sci. USA 77, 87–91.
[14] Clayton, R. K. and Clayton, B. J. (1972) Biochim. Biophys. Acta 283, 492–504.
[15] Sauer, K. and Austin, L. A. (1978) Biochemistry 17, 2011–2019.
[16] Fraker, P. and Kaplan, S. (1972) J. Biol. Chem. 247, 2732–2737.
[17] Tonn, S. J., Gogel, G. E. and Loach, P. A. (1977) Biochemistry 16, 877–885.
[18] Cogdell, R. J. and Crofts, A. R. (1978) Biochim. Biophys. Acta 502, 409–416.
[19] Cogdell, R. J., Parson, W. W. and Kerr, M. A. (1976) Biochim. Biophys. Acta 430, 89–93.
[20] Feick, R. and Drews, G. (1979) Z. Naturforsch. 340, 196–199.
[21] Clayton, R. K., Clayton, B. J., Conway, K. C., Cooke, M. T. and Williams, D. M. (1980) Fed. Proc. FASEB 39, 1801.
[22] Cogdell, R. J., Lindsay, J. G., Reid, G. P. and Webster, G. D. (1980) Biochim. Biophys. Acta 591, 312–320.
[23] Bolt, J. and Sauer, K. (1979) Biochim. Biophys. Acta 346, 54–63.
[24] Feick, R. and Drews, G. (1978) Biochim. Biophys. Acta 501, 499–513.
[25] Webster, G. D., Cogdell, R. J. and Lindsay, J. G. (1980) FEBS Lett. 111, 391–394.
[26] Shiozawa, J. A., Cuendet, P., Zuber, H. and Drews, G. (1980) Proc. V Int. Congr. Photosynthesis, Greece, in press.
[27] Webster, G. D., Cogdell, R. J. and Lindsay, J. G. (1980) Biochim. Biophys. Acta 591, 321–330.

[28] Scolnik, P. A., Zannoni, D. and Marrs, B. L. (1980) Biochim. Biophys. Acta 593, 230–240.
[29] Matsuura K., Ishikawa, T. and Nishimura, M. (1980) Biochim. Biophys. Acta 590, 339–344.
[30] Holmes, N. G., Hunter, C. N., Niederman, R. A. and Crofts, A. R. (1980) FEBS Lett, 115, 43–48.
[31] Zankel, K. L. and Clayton, R. K. (1969) Photochem. Photobiol. 9, 7–15.
[32] Cogdell, R. J., Hipkins, M. F., MacDonald, W. and Truscott, T. G. (1980) Biochim. Biophys. Acta in press.
[33] Heathcote, P. and Clayton, R. K. (1977) Biochim. Biophys. Acta 549, 506–515.
[34] Hunter, C. N. and Holmes, N. G. (1980) Fed. Proc. FASEB 39, 1801.
[35] Monger, T. G., Cogdell, R. J. and Parson, W. W. (1976) Biochim. Biophys. Acta 449, 136–153.
[36] Gogel, G. E., Bering, C. L. and Loach, P. A. (1980) Fed. Proc. FASEB 39, 1801.
[37] Cuendet, P. A. and Zuber, H. (1980) Proc. V Int. Cong. Photosynthesis, Greece, in press.
[38] Katz, J. J., Norris, J. R. and Shipman, L. L. (1977) Brookhaven Symp. Biol. 28, 16–55.
[39] Rafferty, C. N., Bolt, J. R., Sauer, K. and Clayton, R. K. (1979) Proc. Natl. Acad. Sci. USA 76, 4429–4432.
[40] Monger, T. G. and Parson, W. W. (1977) Biochim. Biophys. Acta 460, 393–407.
[41] Niederman, R. A. and Gibson, K. D. (1978) in: The Photosynthetic Bacteria (Clayton, R. K. and Sistrom, W. R. eds) pp. 78–118, Plenum Press, New York.
[42] Zurrer, H., Snozzi, M., Hanselma, K. and Bachofen, R. (1977) Biochim. Biophys. Acta 460, 273–279.
[43] Cuendet, P. A., Zurrer, H., Snozzi, M. and Zuber, H. (1978) FEBS Lett. 88, 309–312.
[44] Oelze, J. (1978) Biochim. Biophys. Acta 509, 450–461.
[45] Golecki, J., Drews, G. and Buehler, R. (1979) Cytobiologie 18, 381–389.
[46] Hunter, C. N., Van Grondelle, R., Holmes, N. G. and Jones, O. T. G. (1979) Biochim. Biophys. Acta 548, 458–470.
[47] Prince, R. C. and Thornber, J. P. (1977) FEBS Lett. 81, 233–237.