Towards an understanding of the structural mechanism of state transitions in photosynthesis

Professor John F Allen
2008/09 Rudi Lemberg Travelling Fellow
Professor of Biochemistry
Queen Mary, University of London

12.05 pm, Friday 27 February 2009

Robertson Seminar Room

The Research School of Biological Sciences

The Australian National University

The Australian National University
The Research School of Biological Sciences
27 February 2009

Towards a structural description of the mechanism of state transitions

John F. Allen
Australian Academy of Science Rudi Lemberg Travelling Fellow

School of Biological and Chemical Sciences, Queen Mary, University of London

Queen Mary
University of London

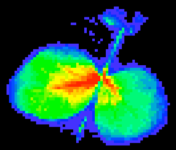
http://jfallen.org

Max Rudolph Lemberg

1896-1975

Acknowledgements

Lund University, Department of Plant Cell Biology



Anders Nilsson

Dalibor Stys

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Queen Mary, University of London, School of Biological and Chemical Sciences

Sujith Puthiyaveetil

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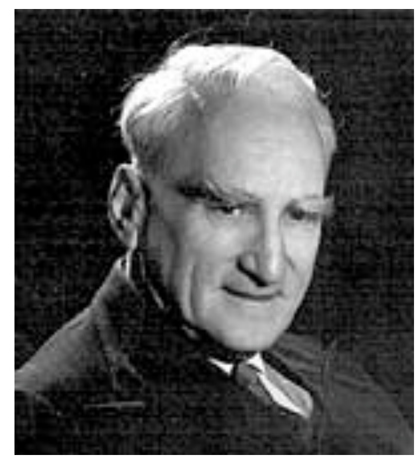

Rudi Lemberg
1896-1975

Jack Myers

Photosynthesis Research **73:** 21–28, 2002.

Personal perspective

In one era and out the other

Jack Myers
Section of Integrative Biology, University of Texas, Austin, TX 78712, USA
(e-mail: txjack10@aol.com)

Received 4 July 2001; accepted in revised form 24 October 2001

Key words: William Arnold, Chlorella, cyanobacteria, Emerson enhancement effect, Robert Emerson, C. Stacy French, Bessel Kok

Abstract

A guided tour through much of photosynthesis research as I saw it, 1936–2001, is presented here. For earlier perspectives, see Myers 1974 (Plant Physiol 54: 420–426) and 1996 (Photosynth Res 50: 195–208).

Figure 1. Stacy French.

Figure 2. William Arnold.

Figure 3. Bessel Kok.


June 9, 06
Advances in Photosynthesis and Respiration
Discoveries in Photosynthesis
Govindjee,
J.T. Beatty, H. Gest and J.F. Allen (Eds.)
Springer
Prof.Jack Myers
Photo by Govindjee

On December 7, 2004, Jack Myers wrote:

Gov: I have no muse that easily turns on. The following is the best thoughts I have:

"The book encompasses a tumultous period of photosynthetic research. For those who lived through the period it will be a reminder of old arguments now moot. For those who find this part of history newly displayed it will reveal the raggedness of science in the changing of paradigms."

www.statetransitions.org.uk Photosynthesis Research 2009...?

Chlamydomonas – conditions for states 1 and 2

Chlamydomonas – conditions for states 1 and 2

Chlamydomonas – conditions for states 1 and 2

Action spectrum and Emerson Enhancement

Chlamydomonas – conditions for states 1 and 2

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Advice to young scientists - move out of your comfort zone

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State 1 or state 2 in the dark?

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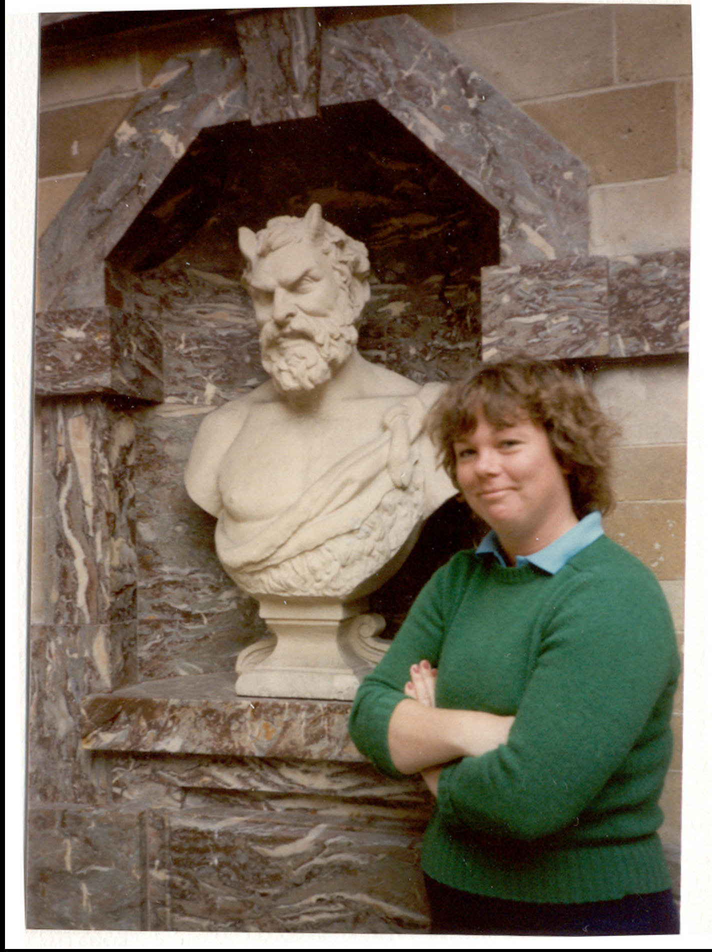
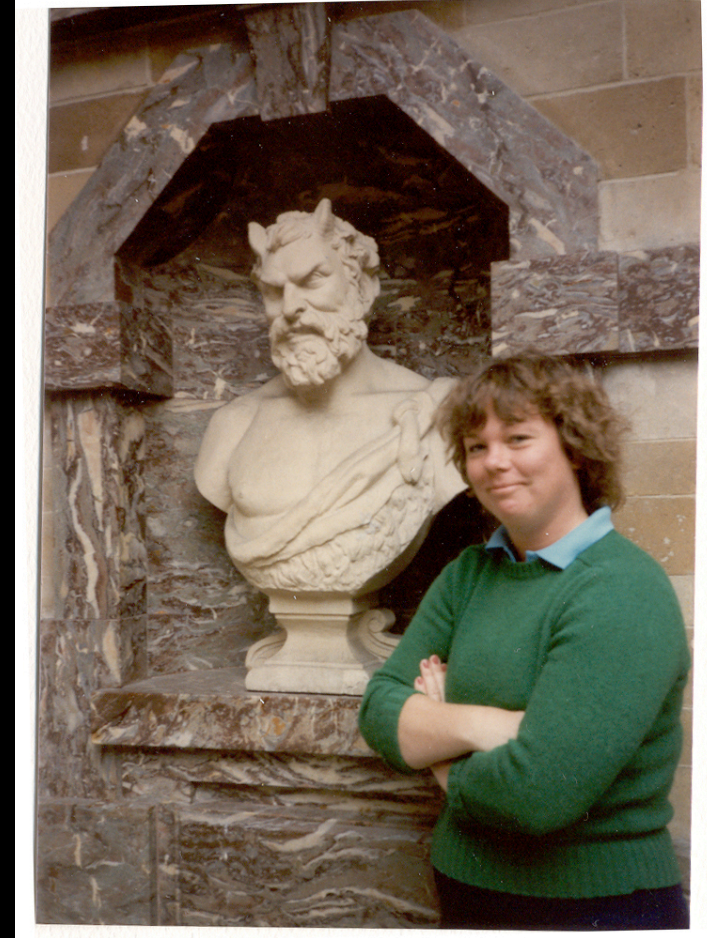
Alpha-changes

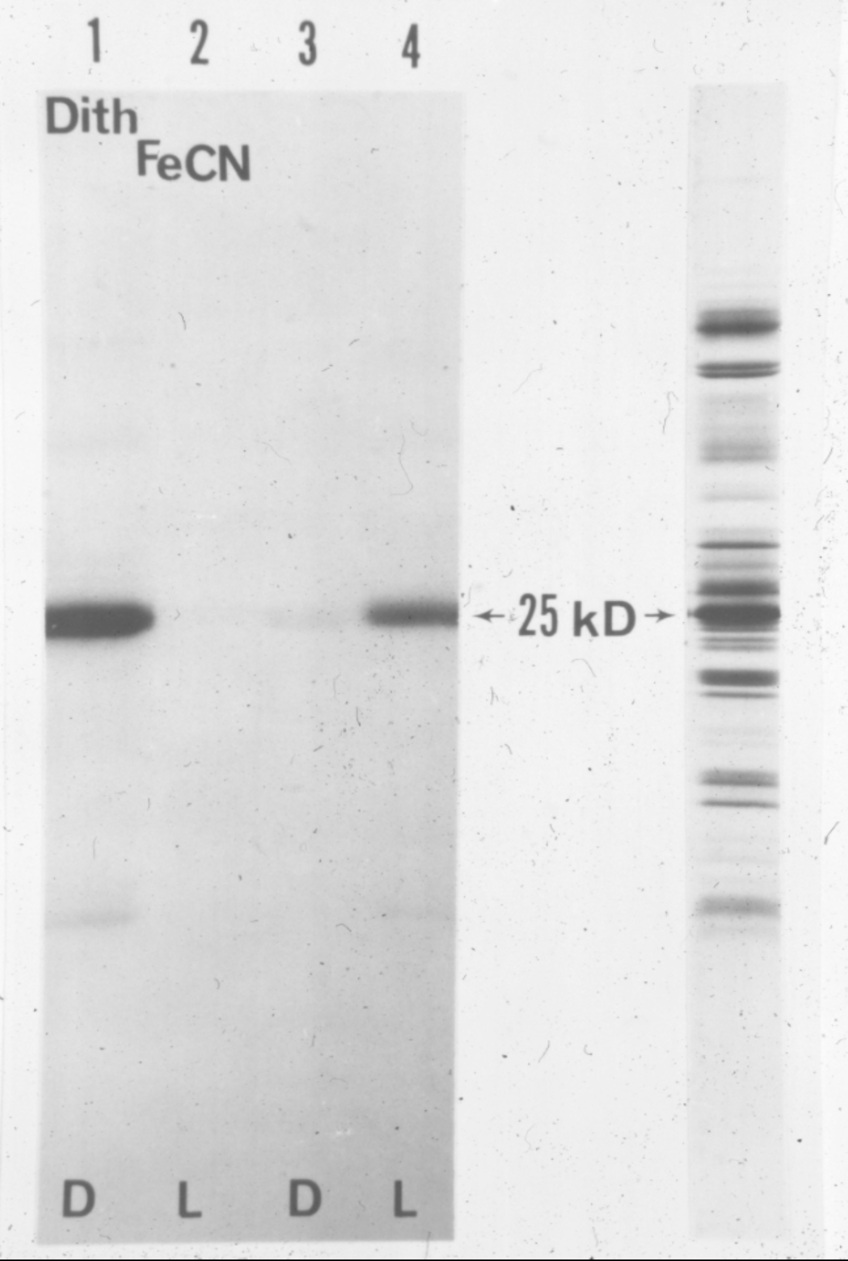
State 1 or state 2 in the dark?

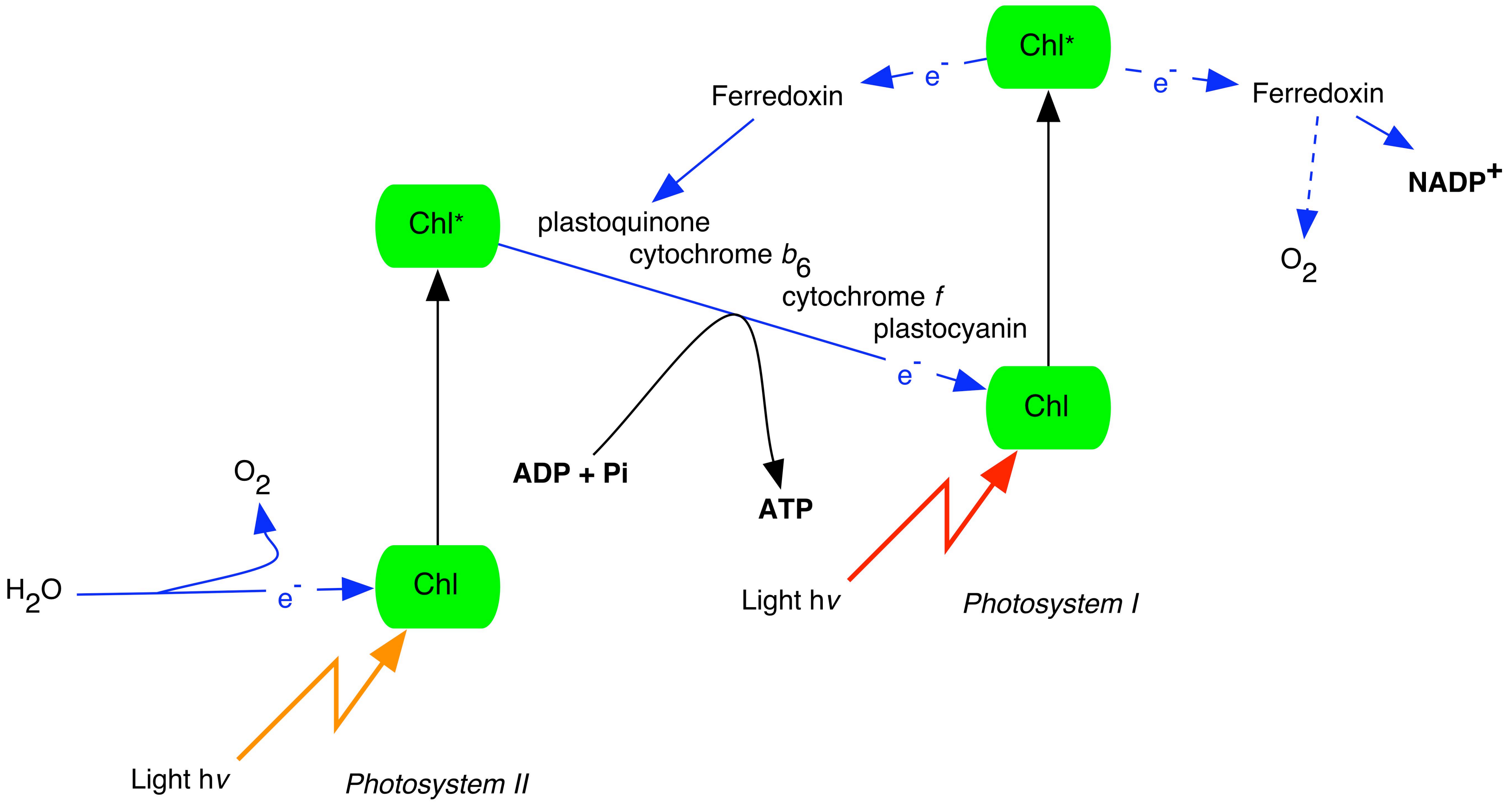
Why state transitions? What do they do in the real world?



Autoradiograph of pea chloroplast phosphoproteins separated by SDS-PAGE.





Photosynthetic phosphorylation 1960

Photosynthesis Research **73:** 21–28, 2002.

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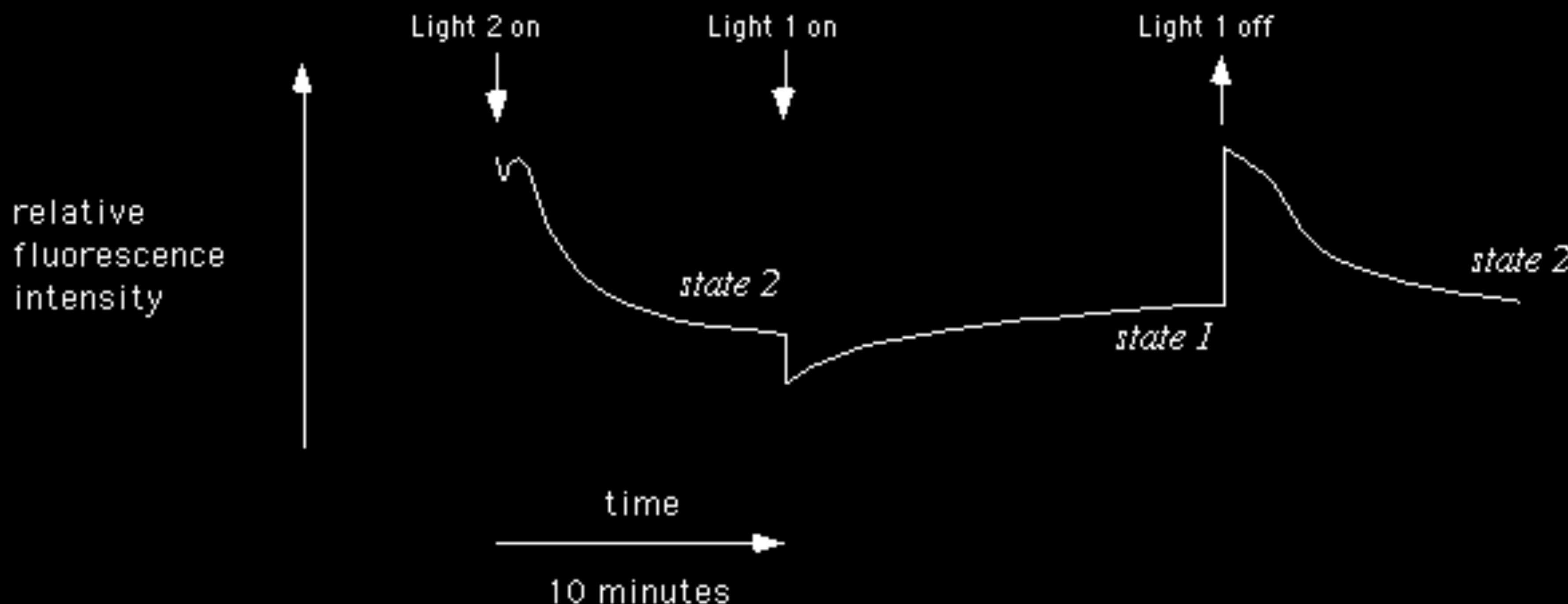
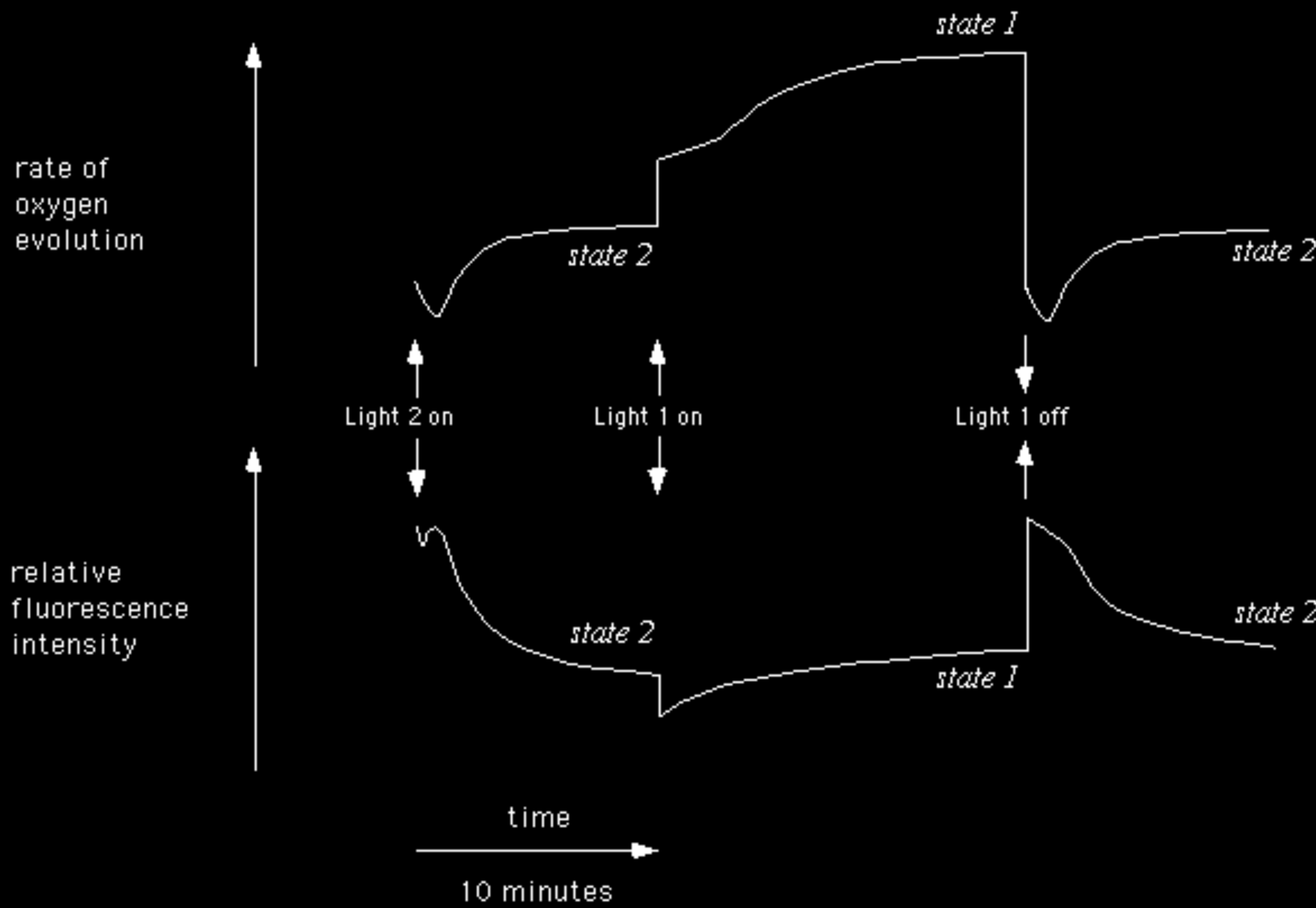
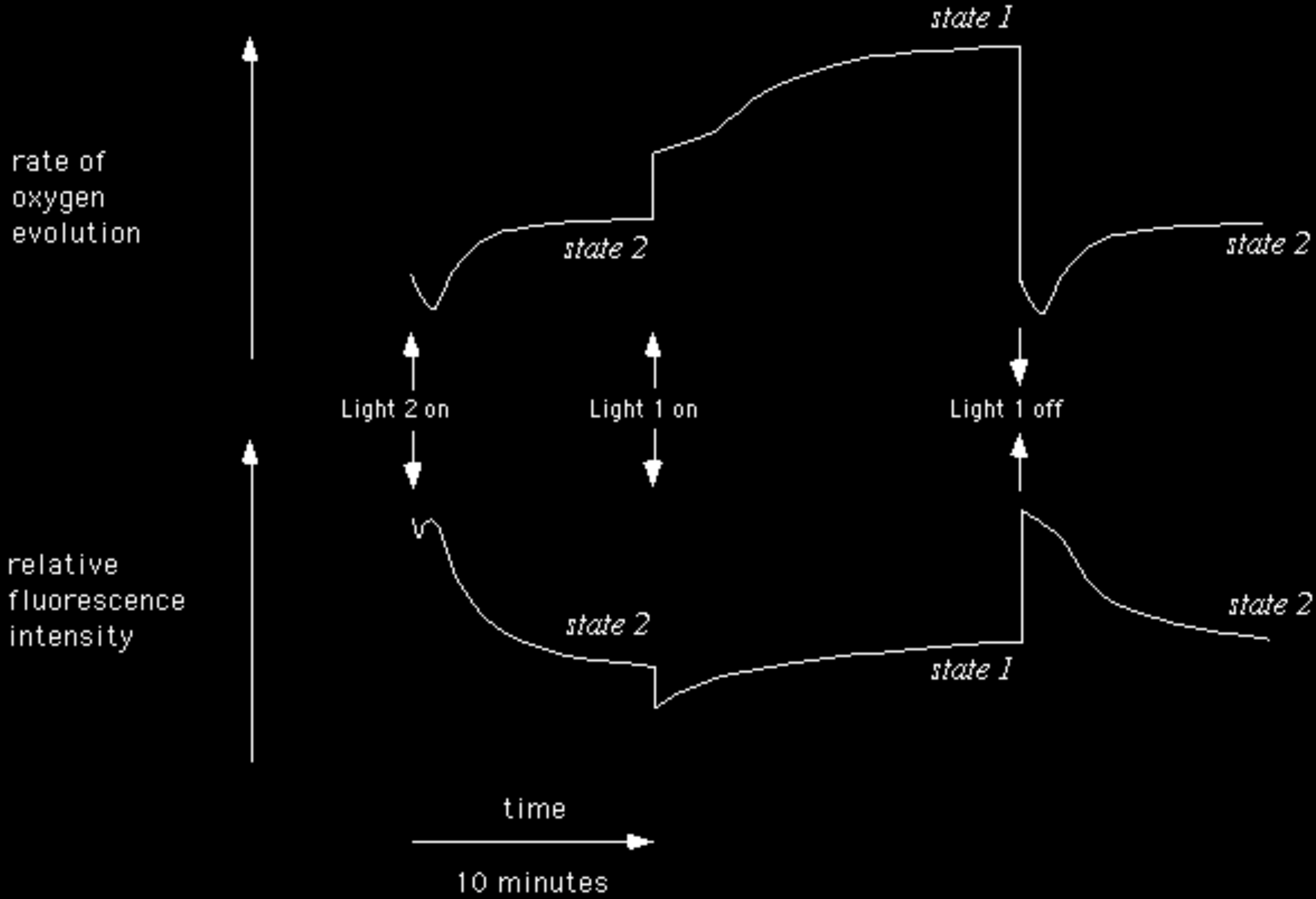

Light 2 on
Light 1 on
Light 1 off
relative fluorescence intensity
state 2
state 1
state 2
time
10 minutes



rate of
oxygen
evolution
relative
fluorescence
intensity
state 1
state 2
state 2
Light 2 on
Light 1 on
Light 1 off
state 2
state 2
state 1
time
10 minutes



Allen, J. F. (1992) BBA 1098, 275-225. Redrawn from Bonaventura, C. and Myers, J. (1969) 189, 366-383

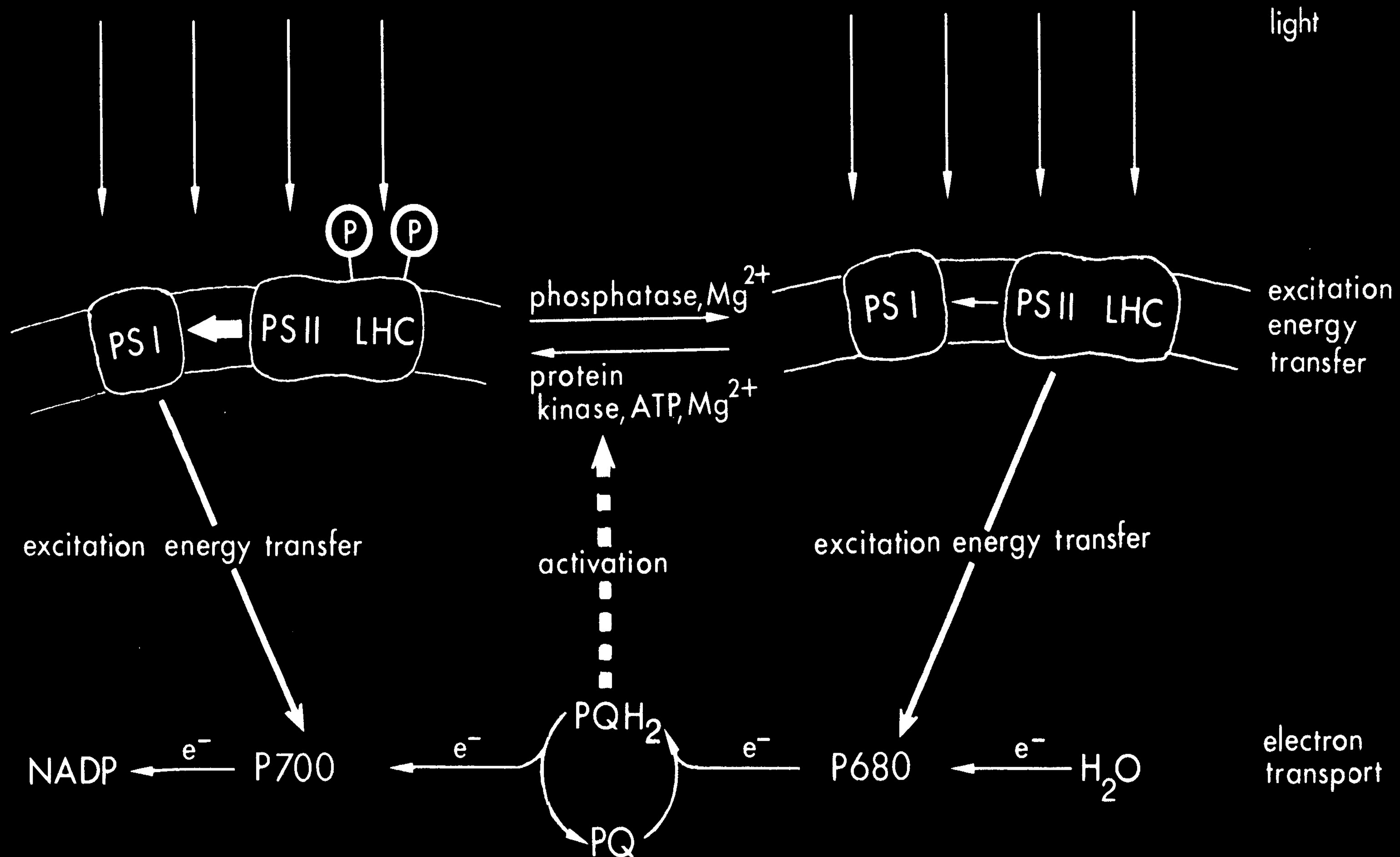
Reprinted from Nature, Vol. 291, No. 5810, pp. 21-25, May 7 1981

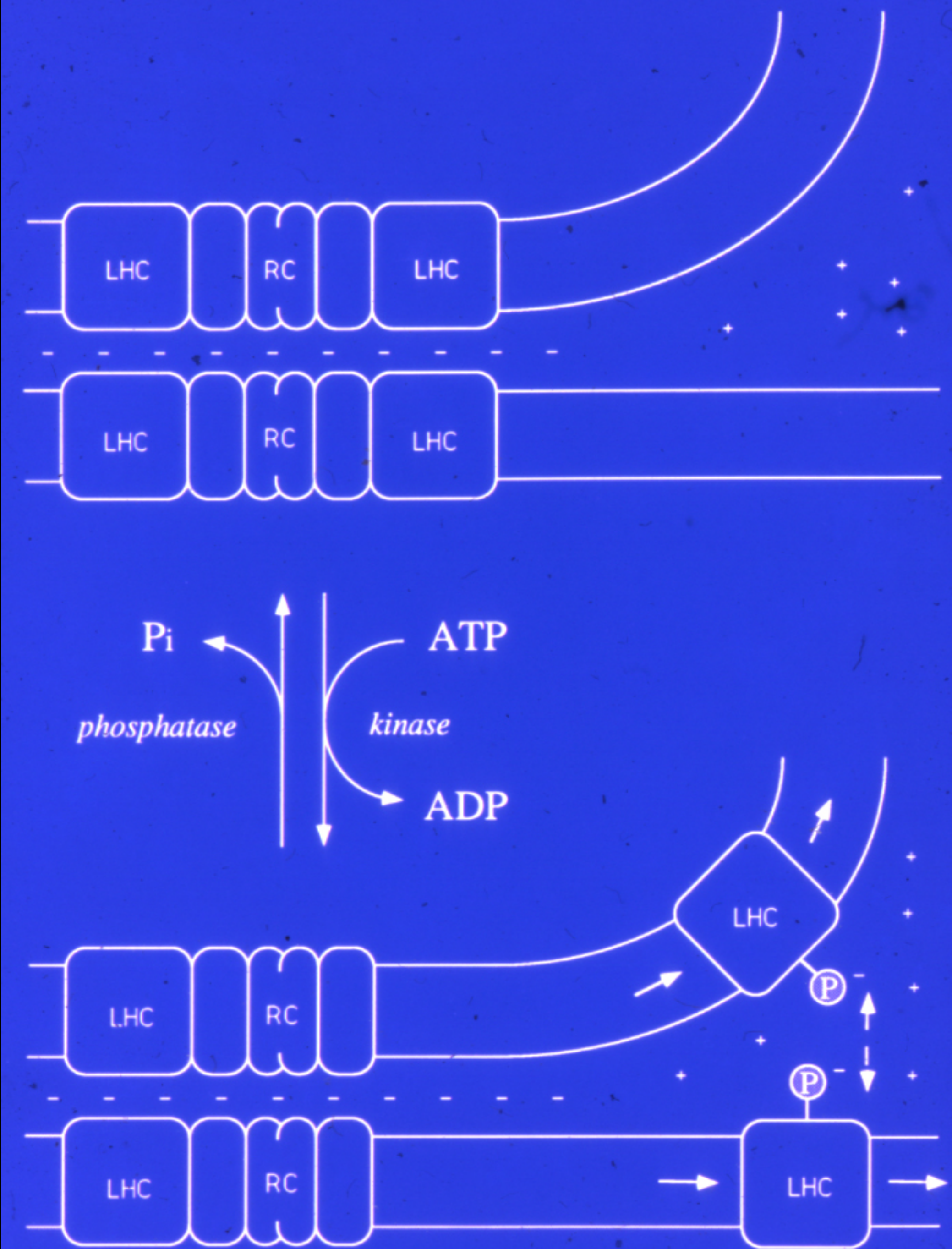
Chloroplast protein phosphorylation couples plastoquinone redox state to distribution of excitation energy between photosystems

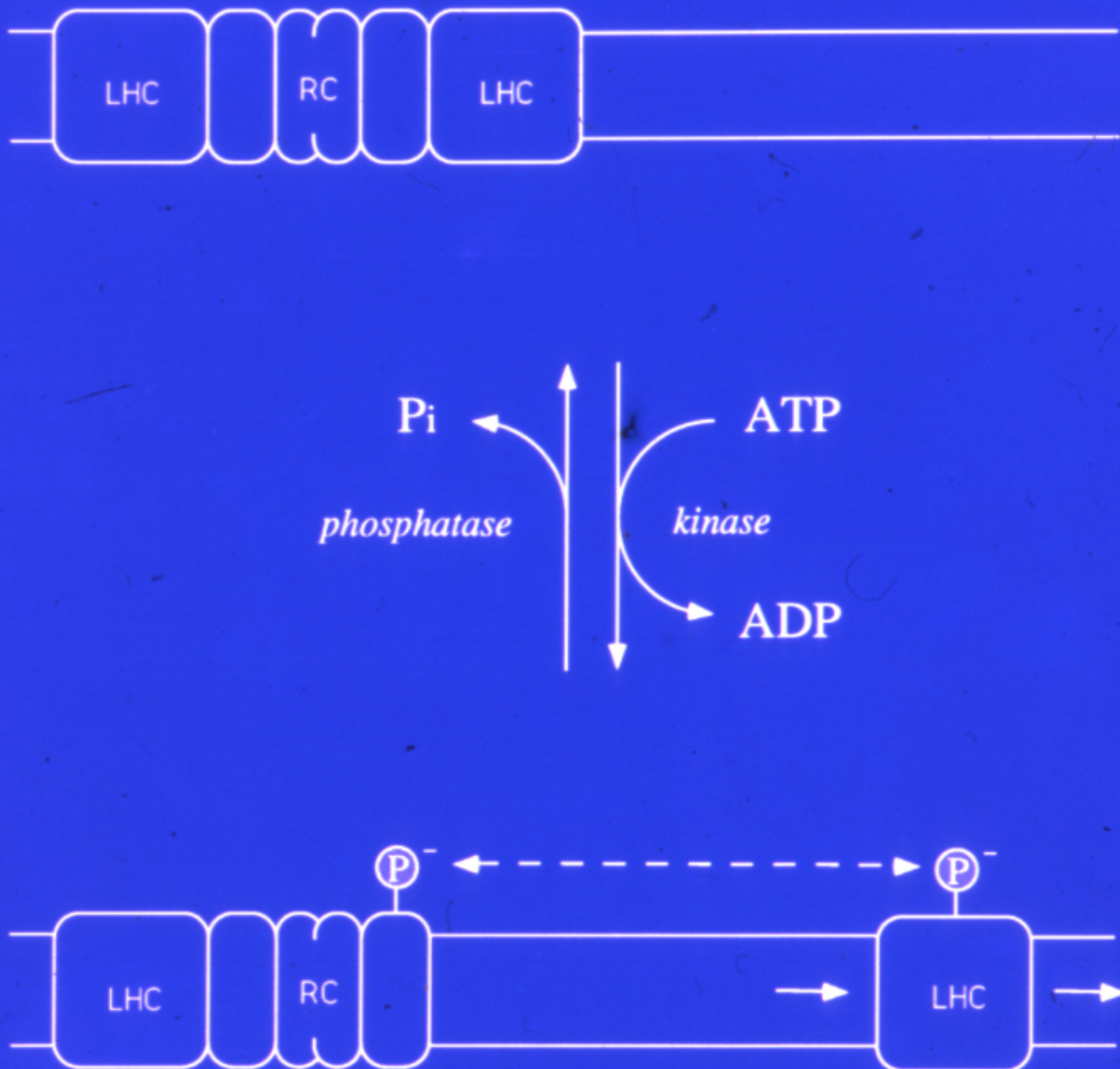
John F. Allen[*,†], John Bennett[†], Katherine E. Steinback[*,‡] & Charles J. Arntzen[*,‡]

[*] USDA-SEA-AR, Department of Botany, University of Illinois, Urbana, Illinois 61801, USA
[†] Department of Biological Sciences, University of Warwick, Coventry CV4 7AL, UK
[‡] MSU/DOE Plant Research Laboratory, Michigan State University, East Lansing, Michigan 48824, USA

In photosynthetic membranes isolated from pea leaves, the redox state of the plastoquinone pool controls both the level of phosphorylation of the chloroplast light-harvesting pigment–protein complex (LHC) and distribution of absorbed excitation energy between the two photosystems. Phosphorylation of LHC polypeptides is proposed as the regulatory mechanism by which photosynthetic systems adapt to changing wavelengths of light.


light
P
P
PS I
PS II LHC
phosphatase, Mg2+
protein kinase, ATP, Mg2+
PS I
PS II LHC
excitation energy transfer
excitation energy transfer
activation
excitation energy transfer
NADP
e⁻
P700
e⁻
PQH2
PQ
e⁻
P680
e⁻
H2O
electron transport


LHC
RC
LHC
LHC
RC
LHC
Pi
ATP
phosphatase
kinase
ADP
LHC
P
LHC
RC
P
LHC
RC
LHC



LHC
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LHC
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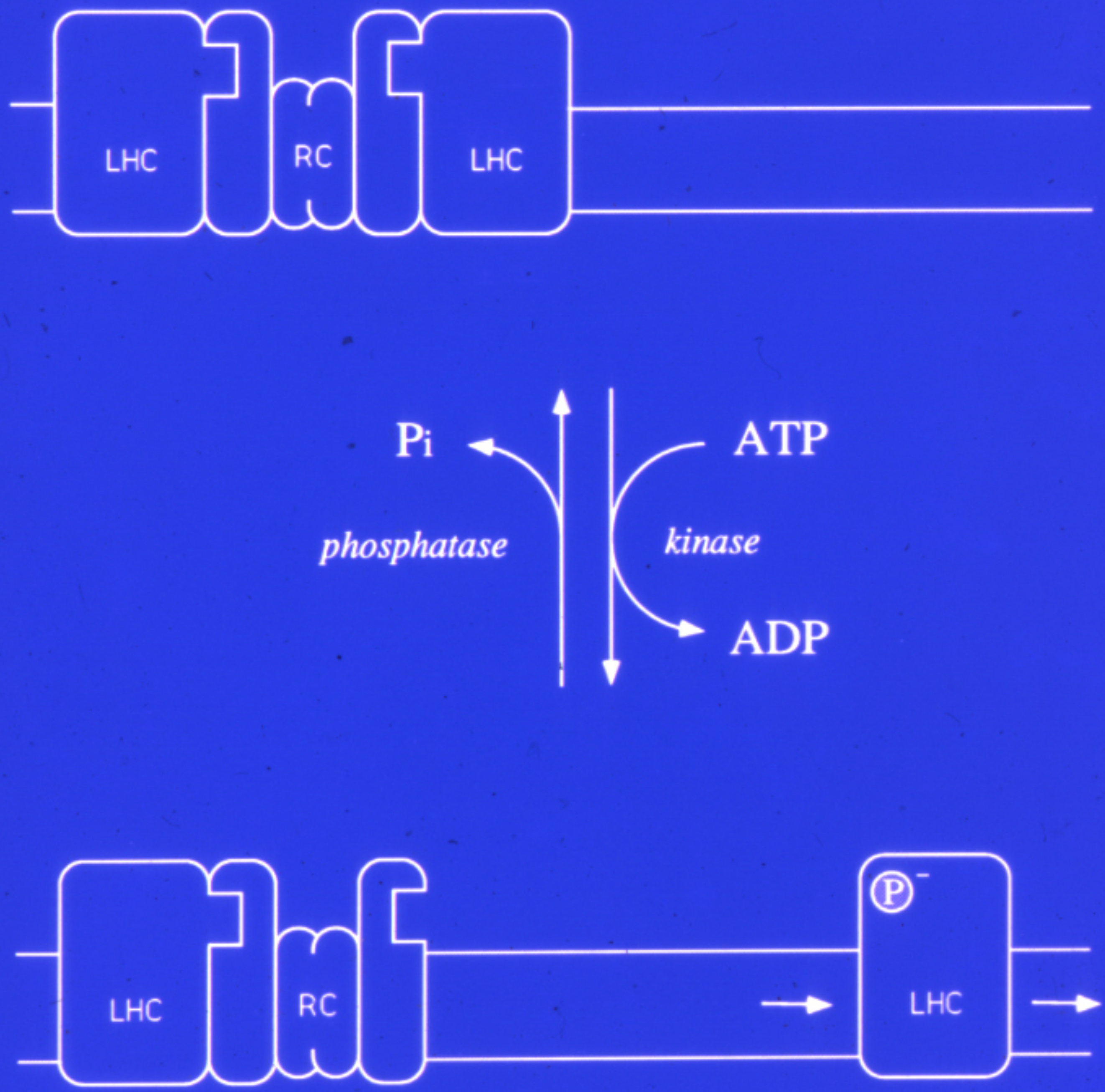
ATP
phosphatase
kinase
ADP
P
P
LHC
RC
LHC


LHC
RC
LHC
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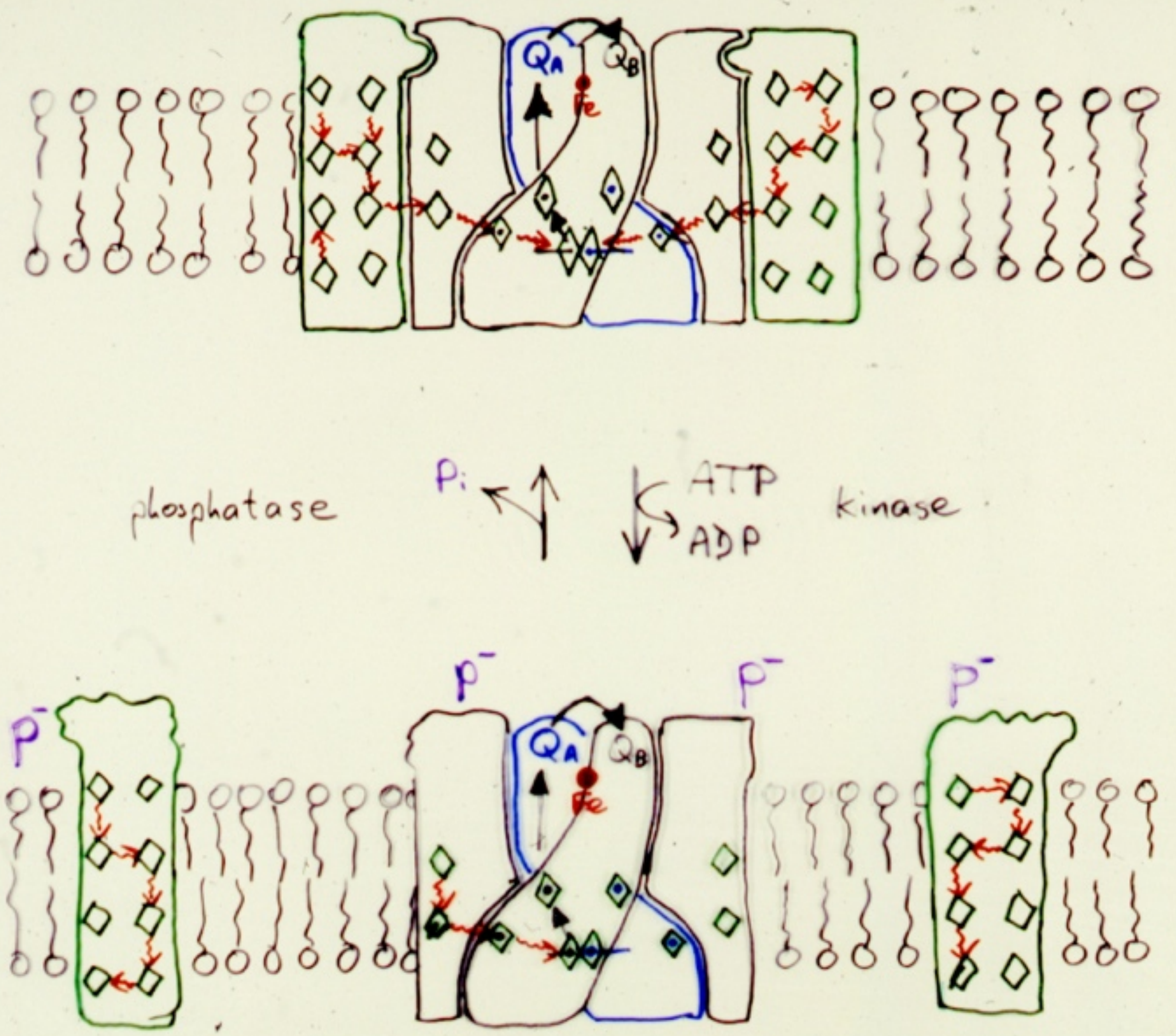
ATP
phosphatase
kinase
ADP
P
LHC
RC
LHC



Q_A
Q_B
Fe
phosphatase
P_i
ATP
ADP
kinase
P^-
P^-
P^-
P^-
Q_A
Q_B
Fe

nature

INTERNATIONAL WEEKLY JOURNAL OF SCIENCE

Volume 336 No.6196 17 November 1988 £1.95

CONFORMATIONAL EFFECTS OF PROTEIN PHOSPHORYLATION

AUTUMN BOOKS

including

John Cairns and William Cooper
(on Francis Crick and Lord Zuckerman)

John Tyler Bonner
(Edelman's embryology)

Roy Porter
(vampires)

John Yudkin
(palaeodiets)

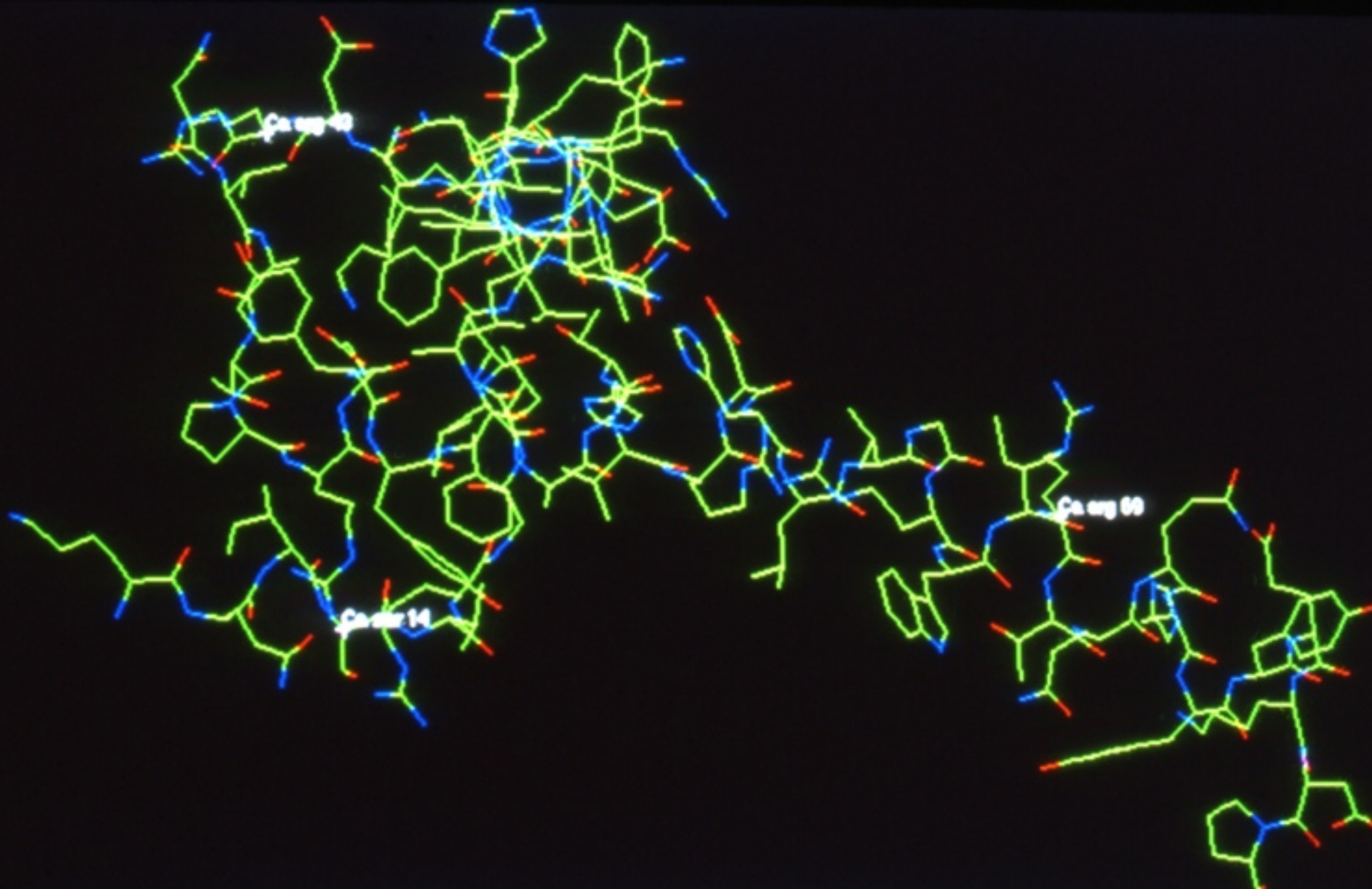
Steven Shapin
(Pasteurization)

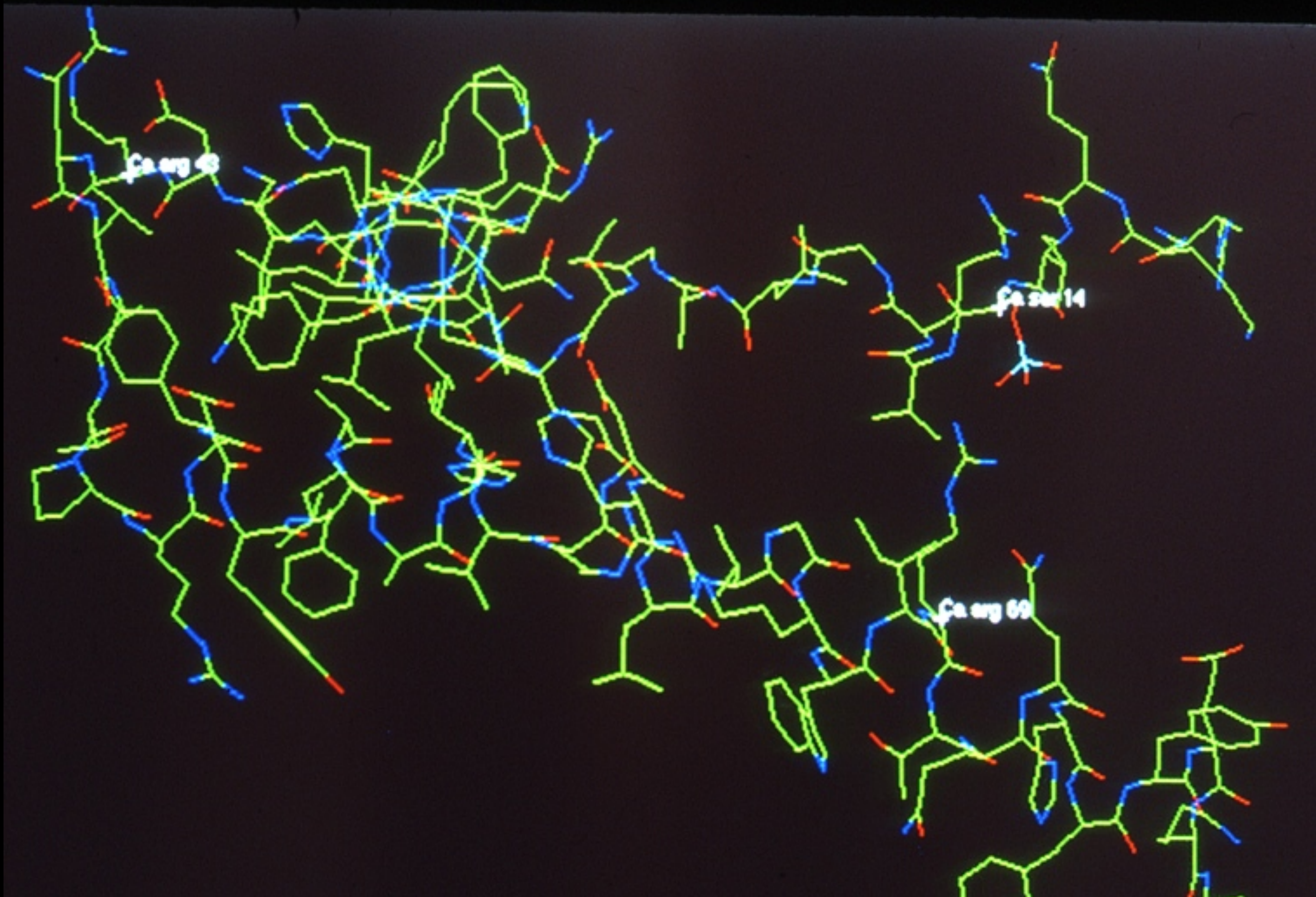
Steven M. Stanley
(Gaia anew)

Philip Kitcher
(process of science)

Desmond King-Hele
(Soviets in space)

Igor Aleksander
(mind-bending robots)





Ca arg 43
Ca ser 14
Ca arg 69

1 5 10

M **R** **K** S A **T***T **K** **K** V A S S   pea light harvesting complex II

S R P L S D Q E **K** **R** **K** Q I **S***V **R** G L A G   rabbit glycogen phosphorylase

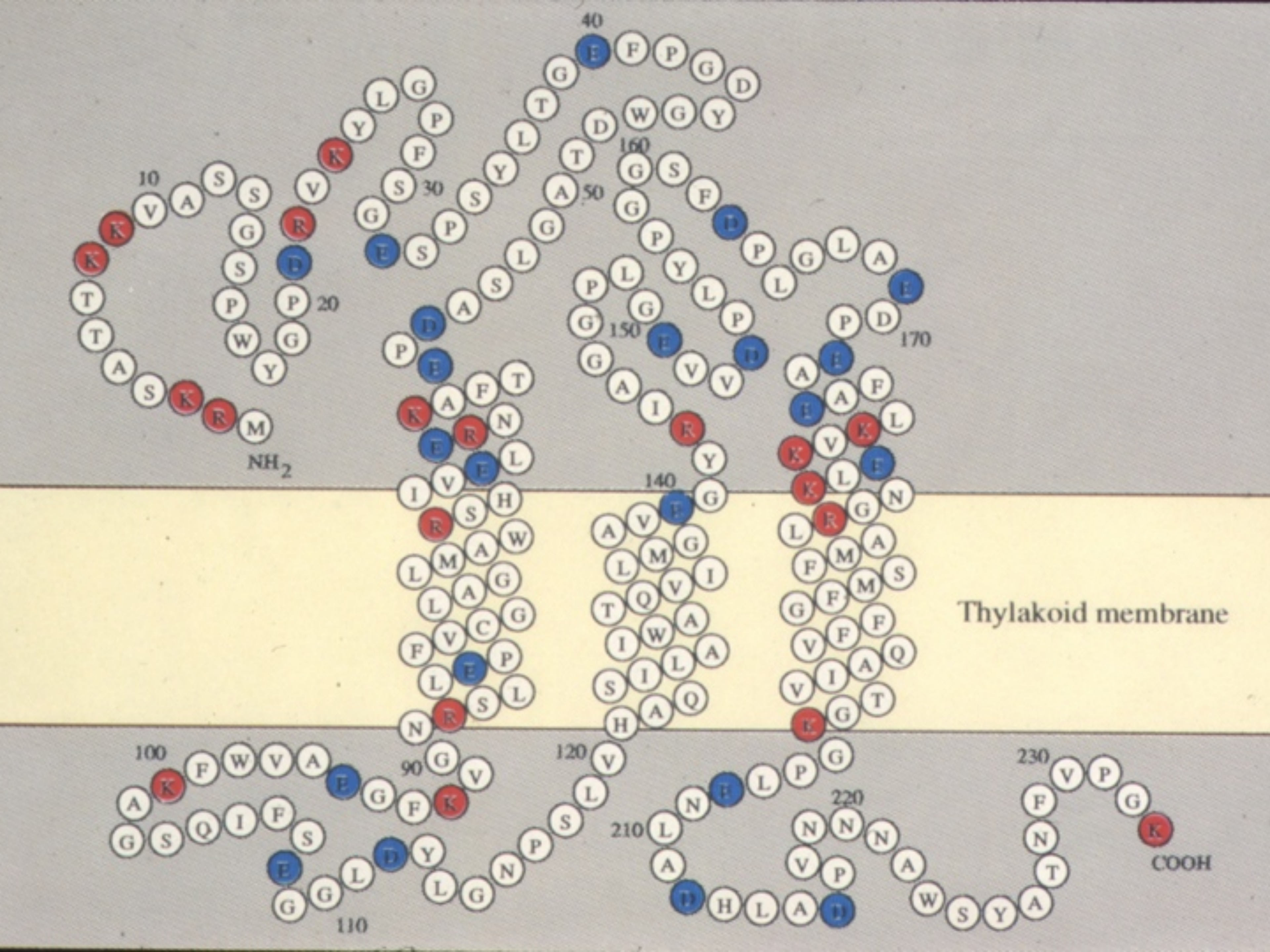
5 10 15 20

--------- *helix* ------

95 100 105 110 115 120 125 130 135 140

Y **R** V A I **K** G P L T T P V G G G I **R** **S***L N V A L **R** Q E L D L Y I C L **R** P V **R** Y Y Q G T P S P

E. coli isocitrate dehydrogenase



10
20
30
40
50
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100
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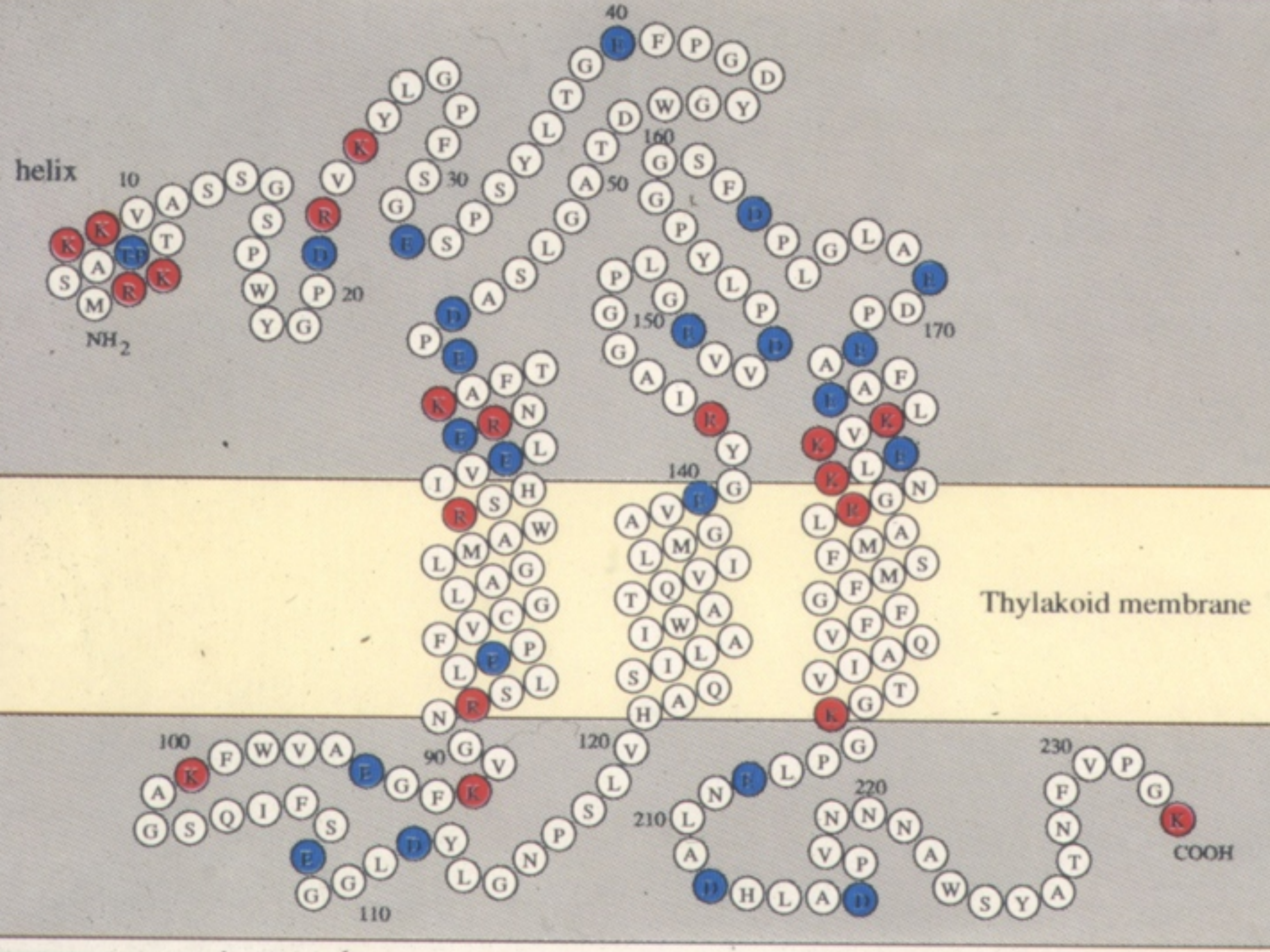
120
140
150
160
170
210
220
230
NH_2
COOH
Thylakoid membrane


helix
10
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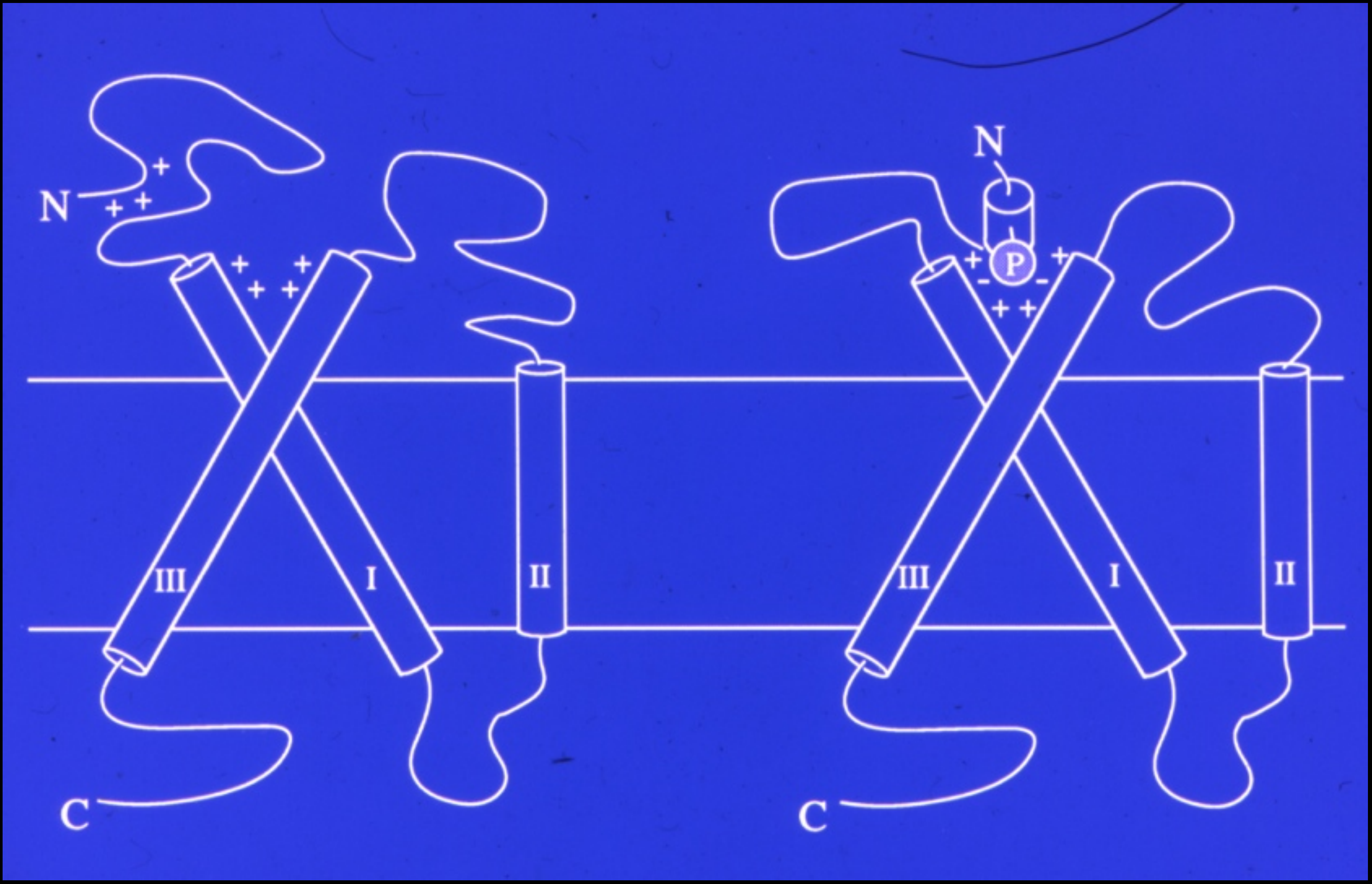
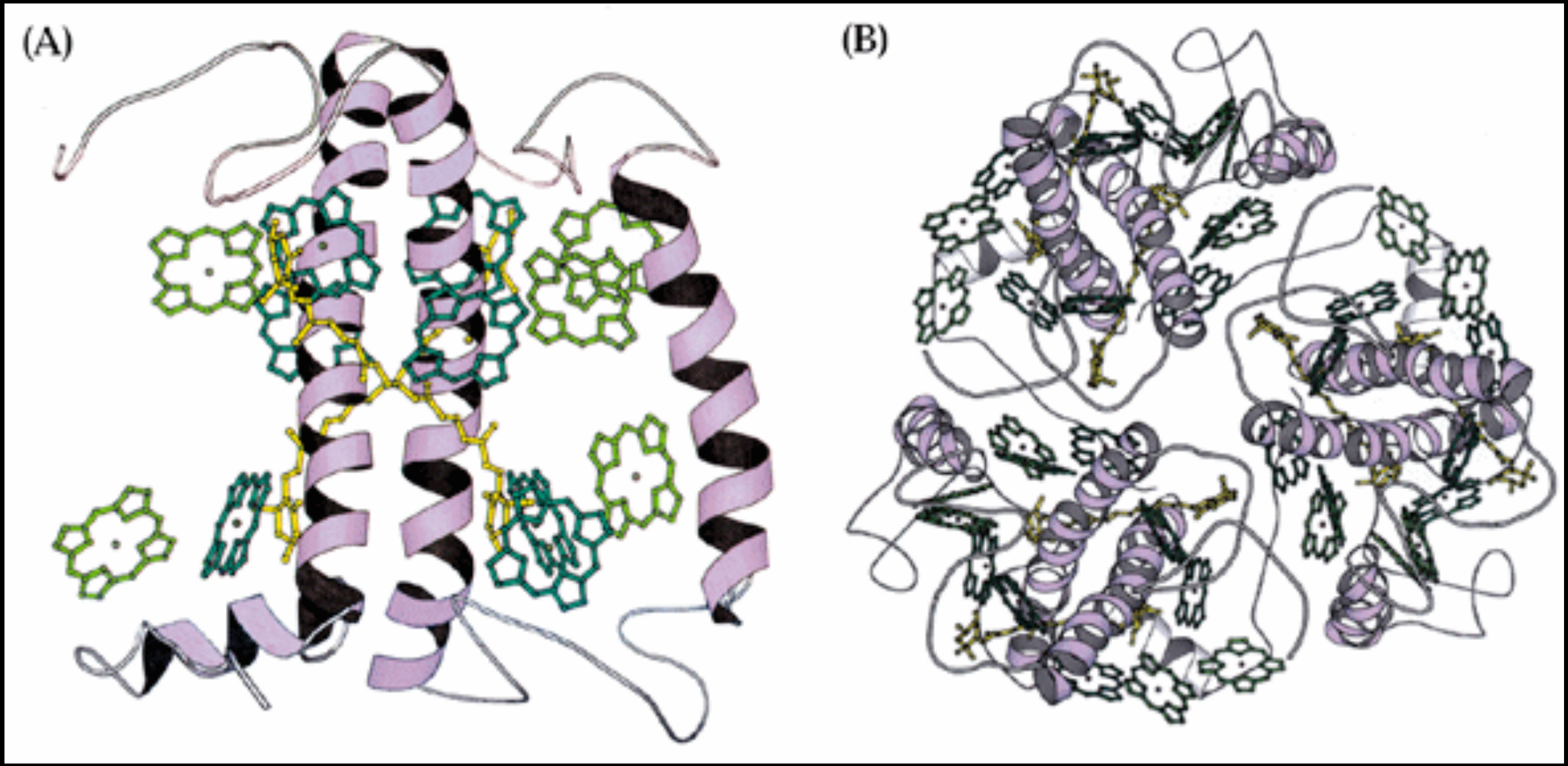
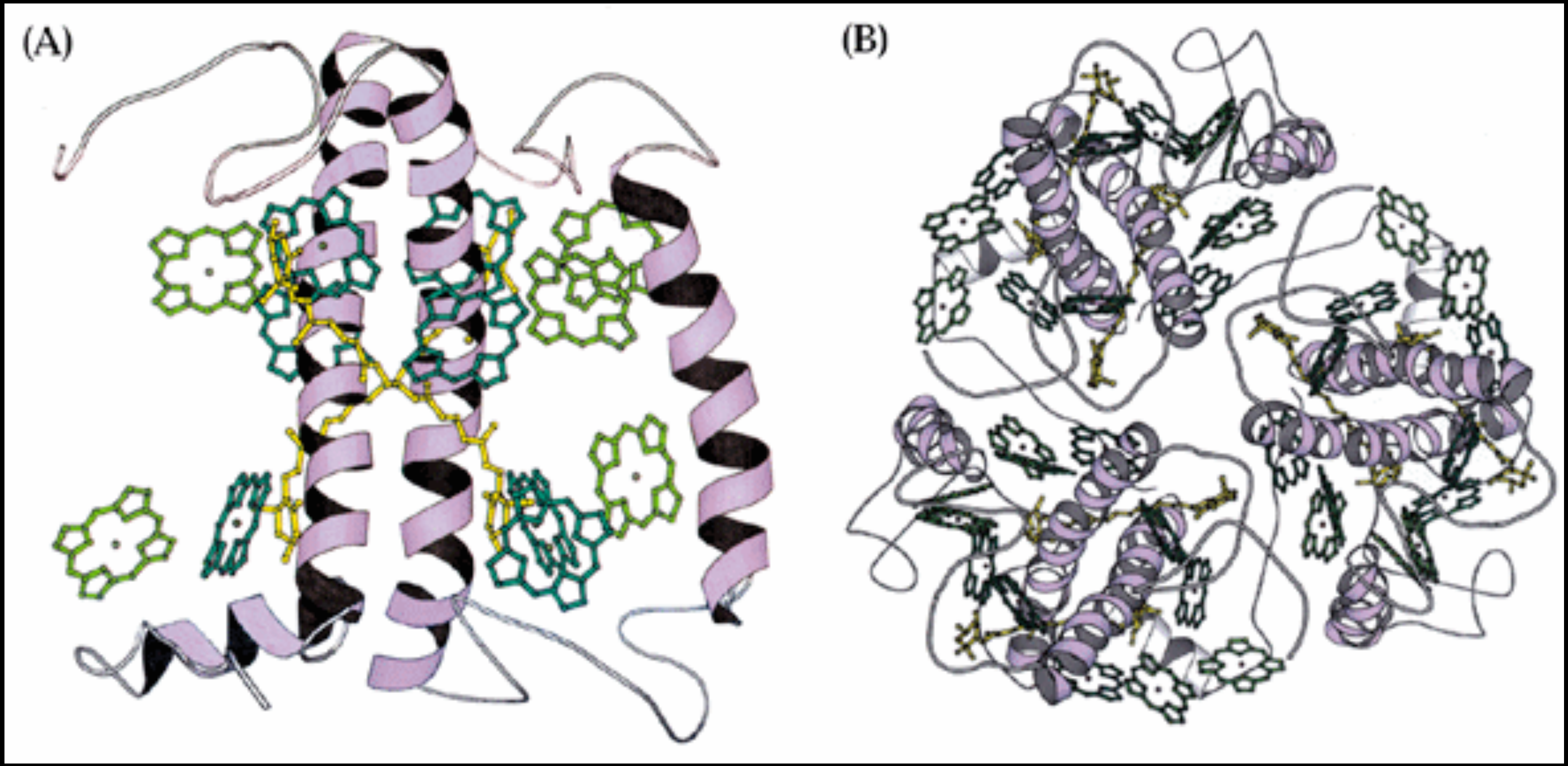
230
NH2
COOH
Thylakoid membrane


N
C
III
I
II
N
P
C
III
I
II

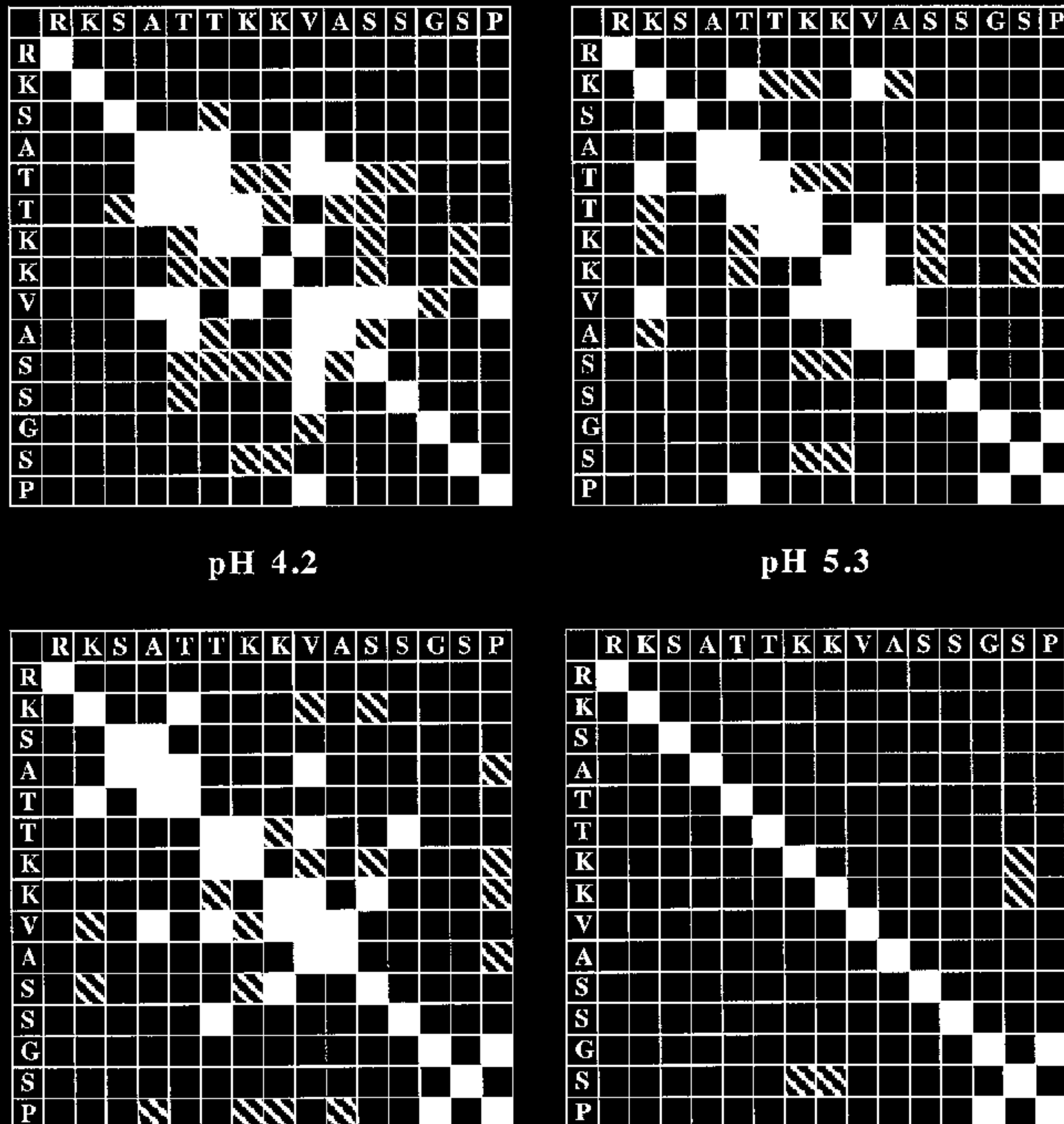


The light-harvesting complex of chloroplast photosystem II (LHC II)



The light-harvesting complex of chloroplast photosystem II (LHC II)

Kühlbrandt, W. et al. (1994) Nature. 367, 614-621



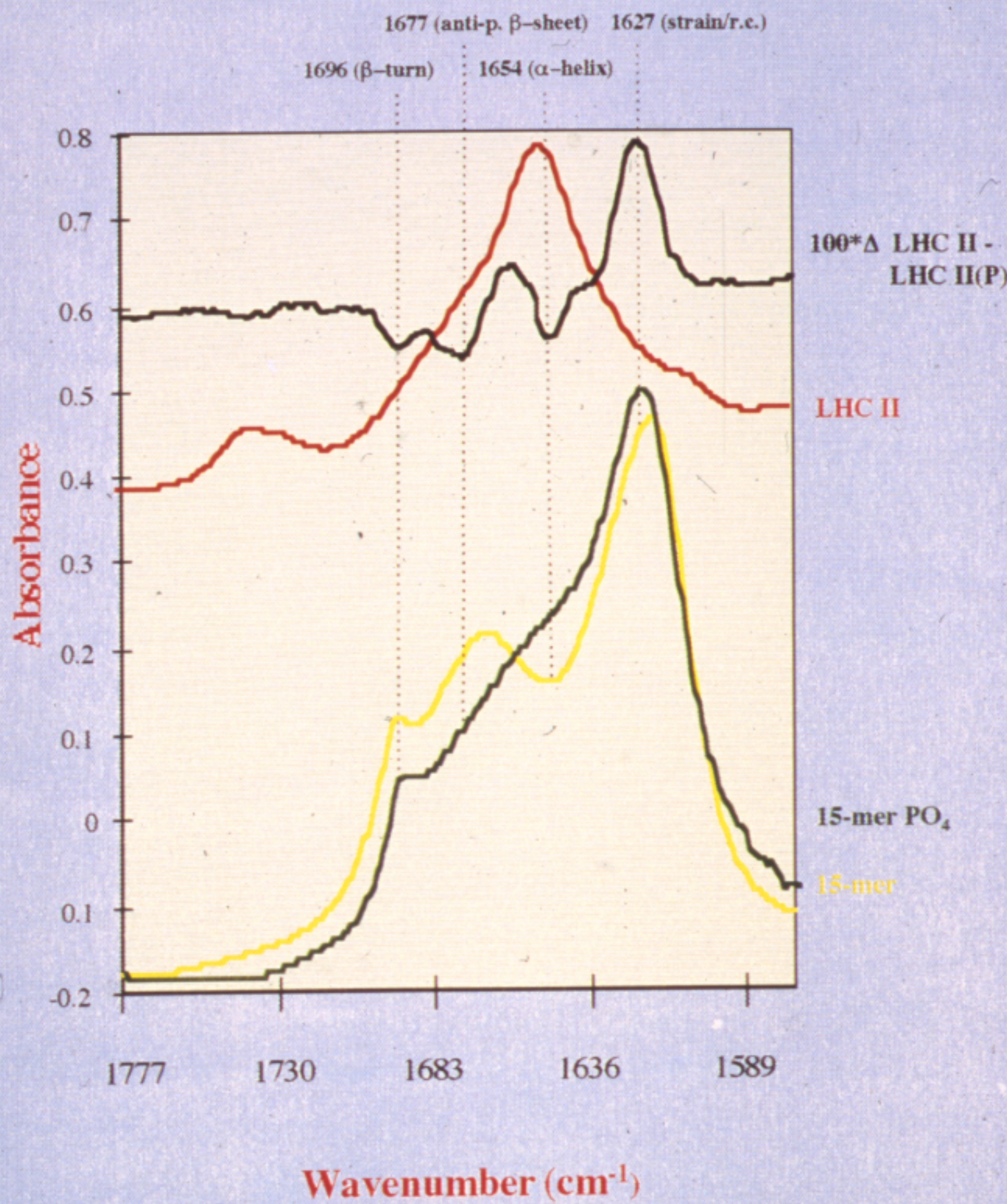
pH 4.2

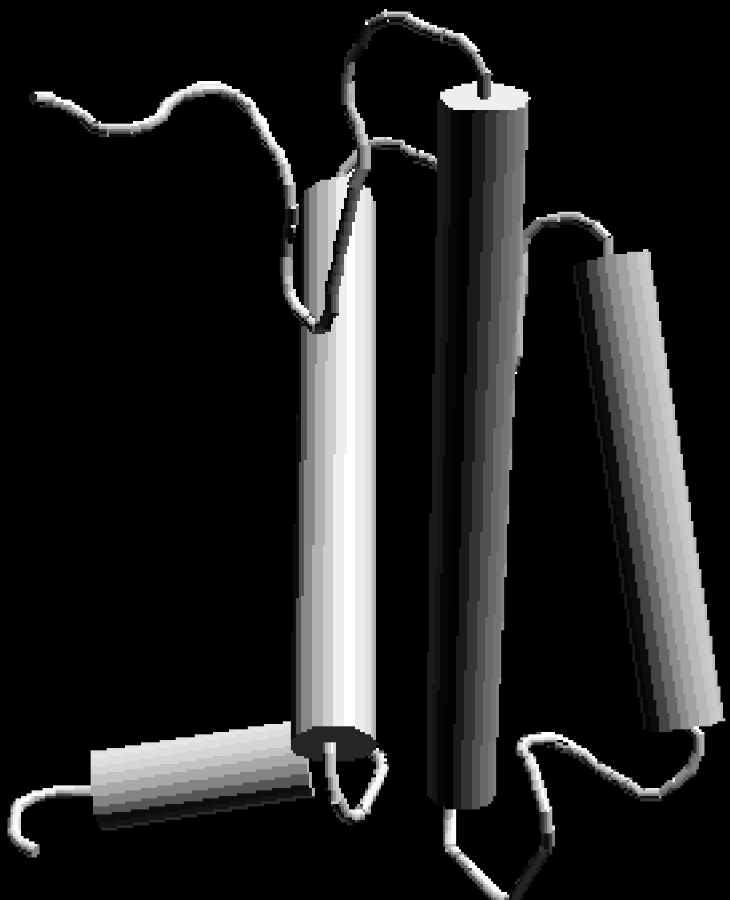
pH 5.3

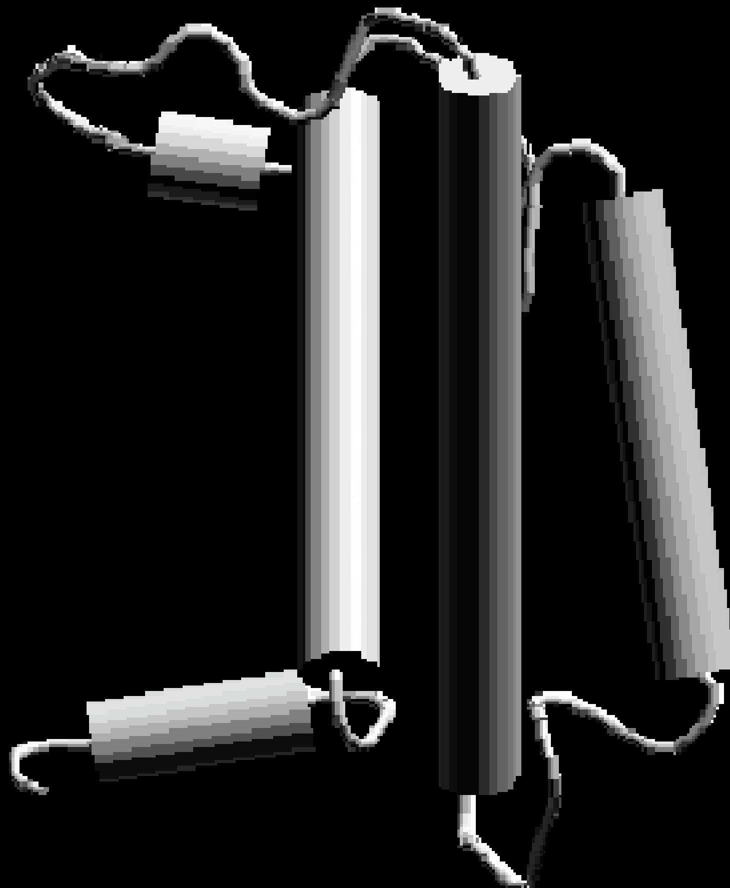
pH 6.2

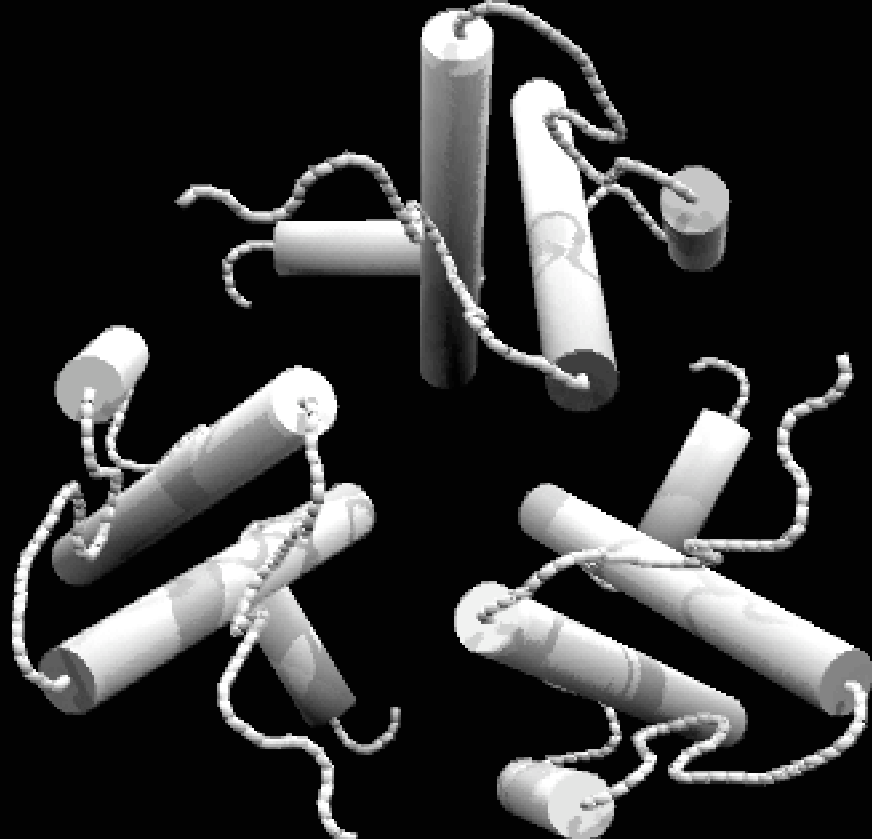
non-phosphorylated pH 5.3

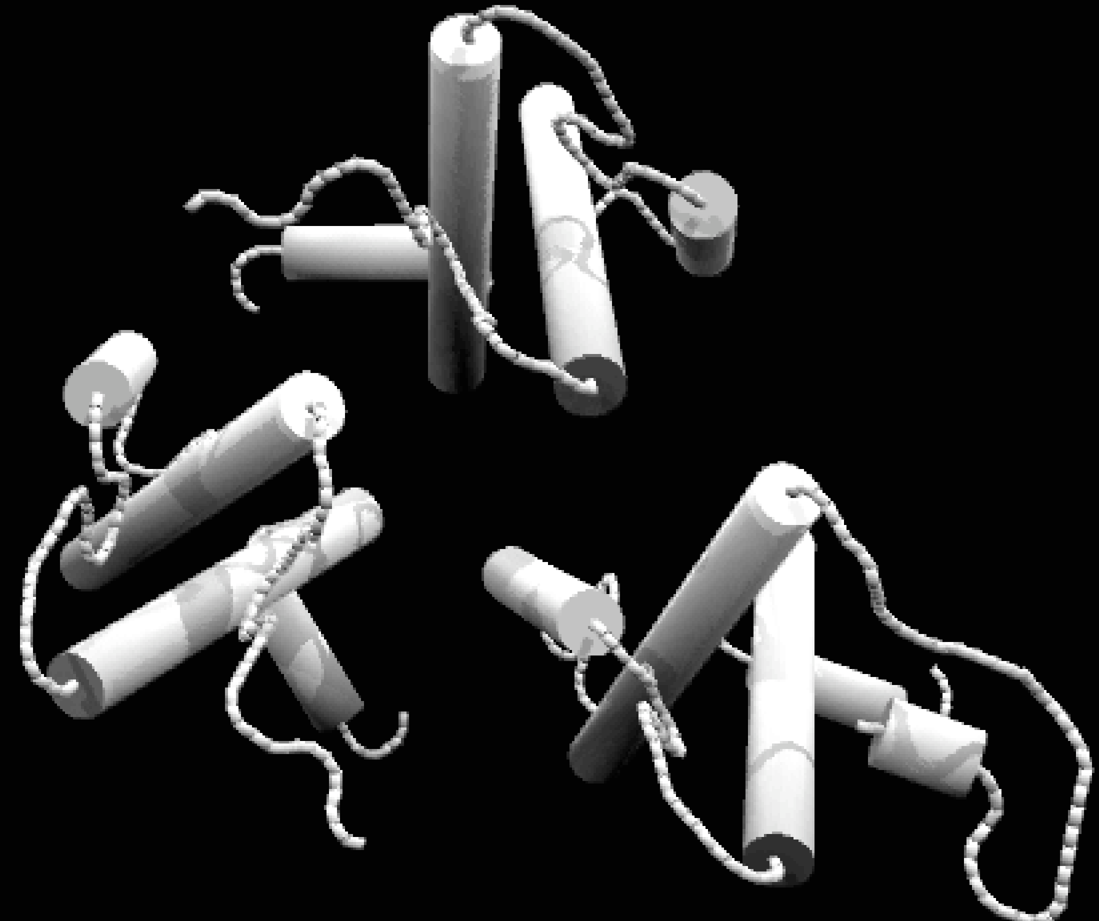
LHC II
FTIR-DATA
Amide I vibration (C=O stretch)

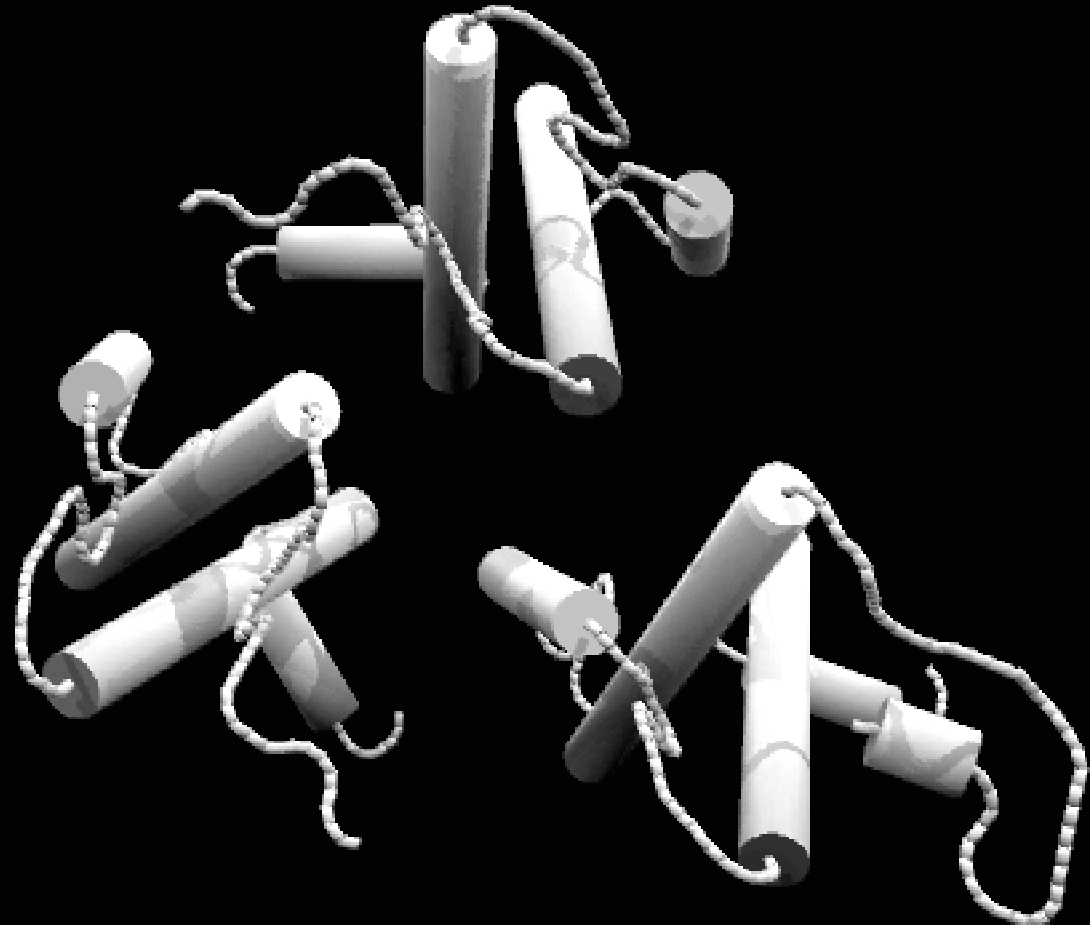












Nilsson, A. et al. (1997) JBC 272, 18350-18357

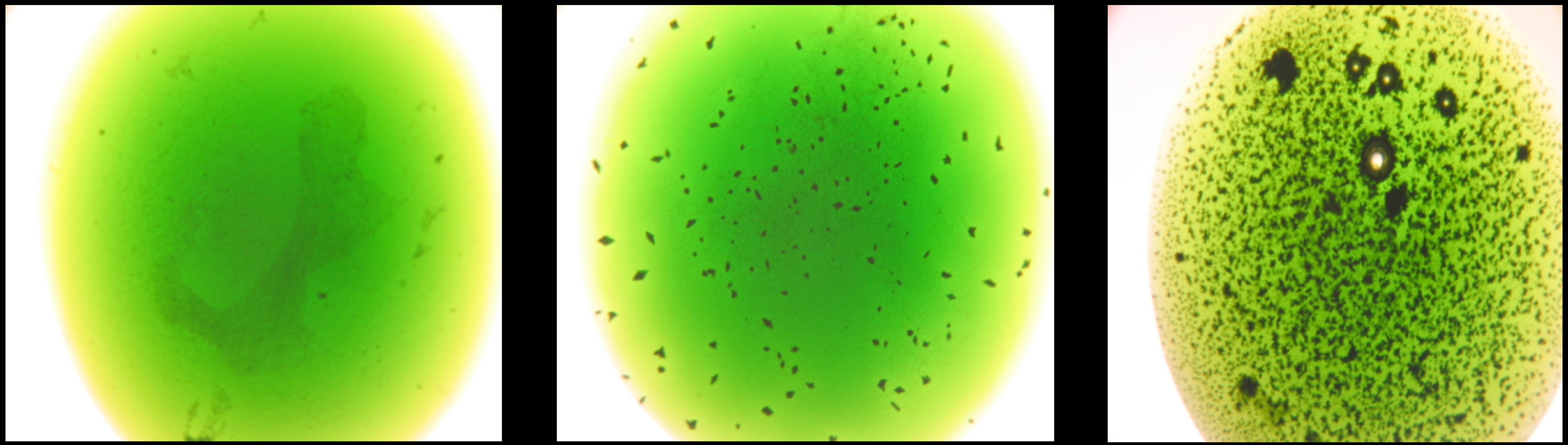


Figure 1, above, shows results from one of our optimisation strategies for pea LHC II crystallization using different concentrations of the precipitant PEG over a narrow range: 26 % gives no crystals; 28 % gives crystals; 30% gives mostly LHC II aggregates.

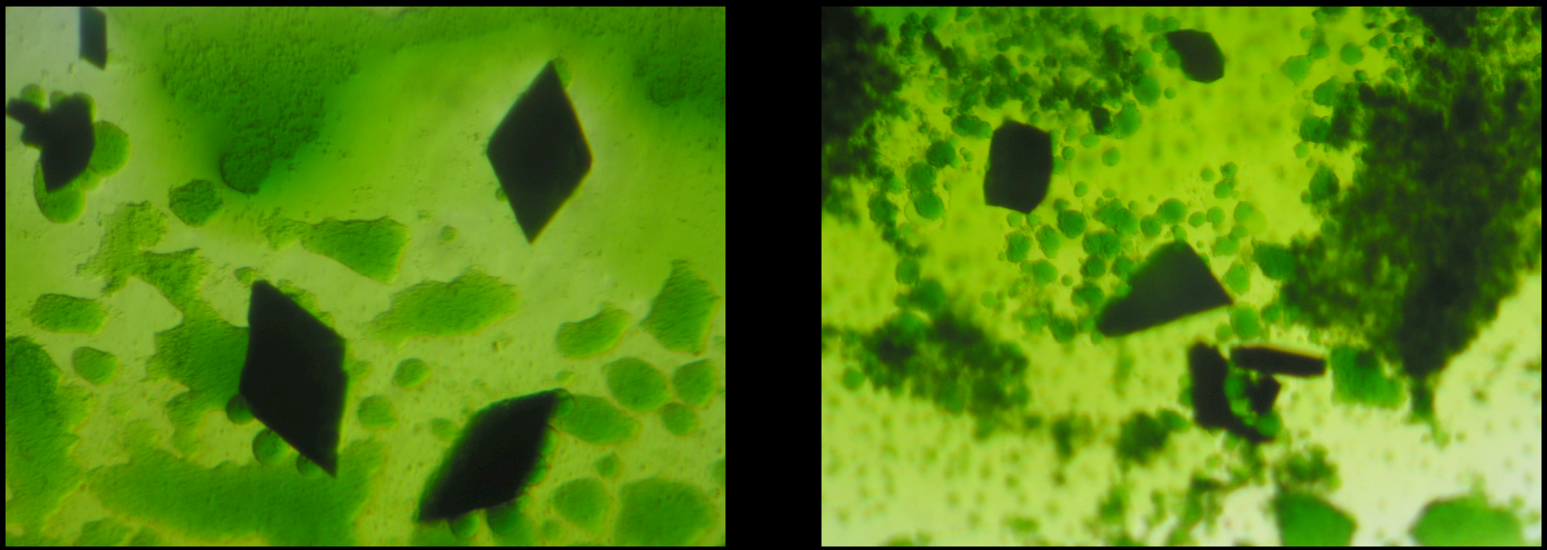
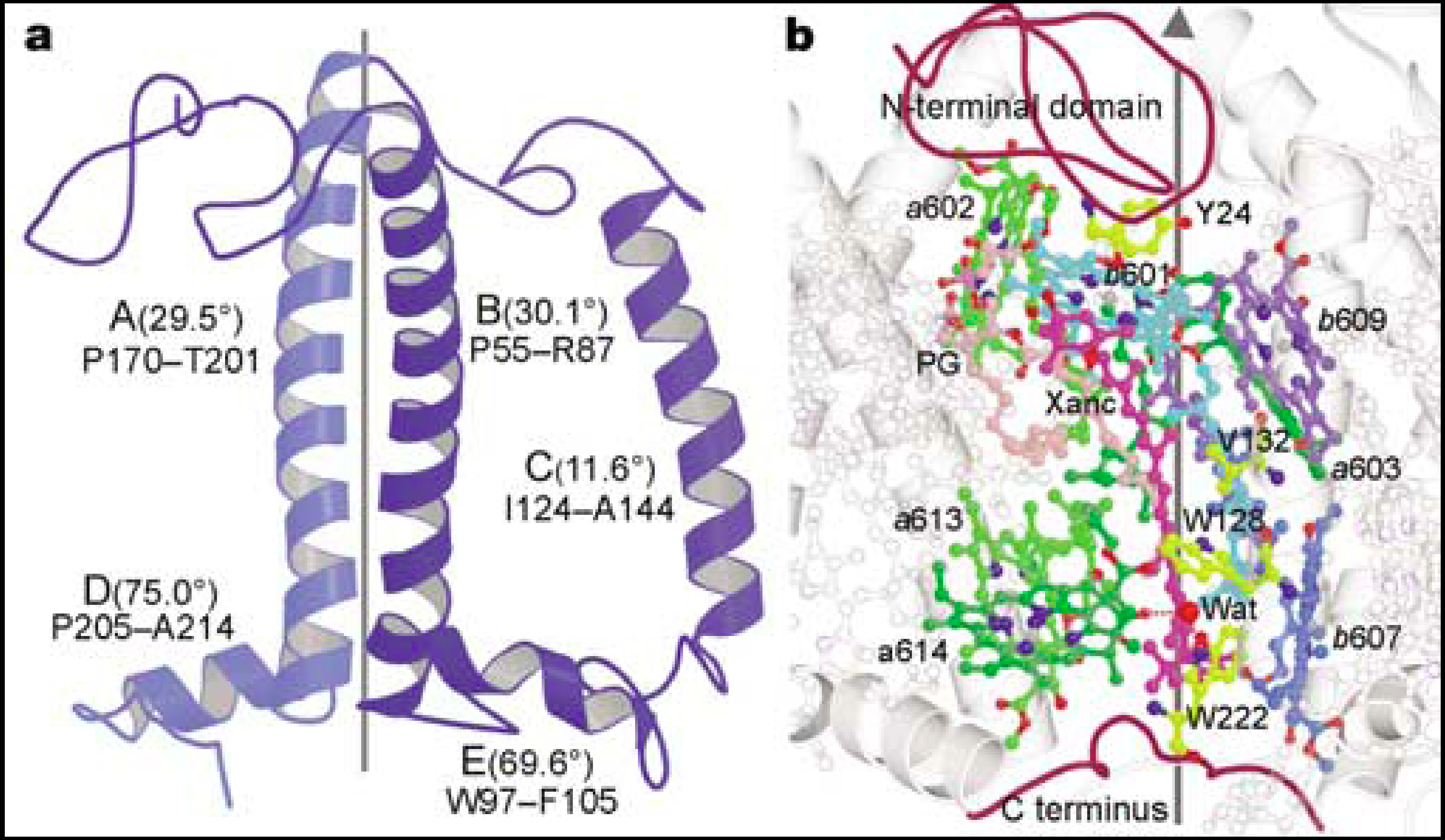


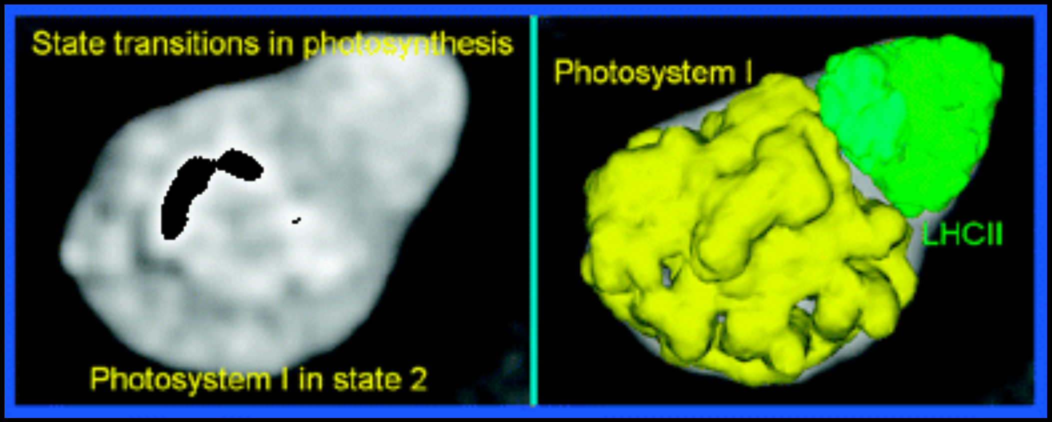
Figure 2. Our best LHC II crystals were approximately 100 µm-long lozenges. These crystals routinely diffracted to 5 Å with the best crystals diffracting to 3.7 Å. At the same time (early 2004) Lui et al published the 2.7 Å structure of spinach LHC II. Further crystal optimization was not attempted, and these results are unpublished. (Snijder, A., Forsberg, J and Allen, J. F. unpublished).


nature
Power plant
Structure of a spinach light-harvester
Recipe for a snowball Earth
Hungry for facts

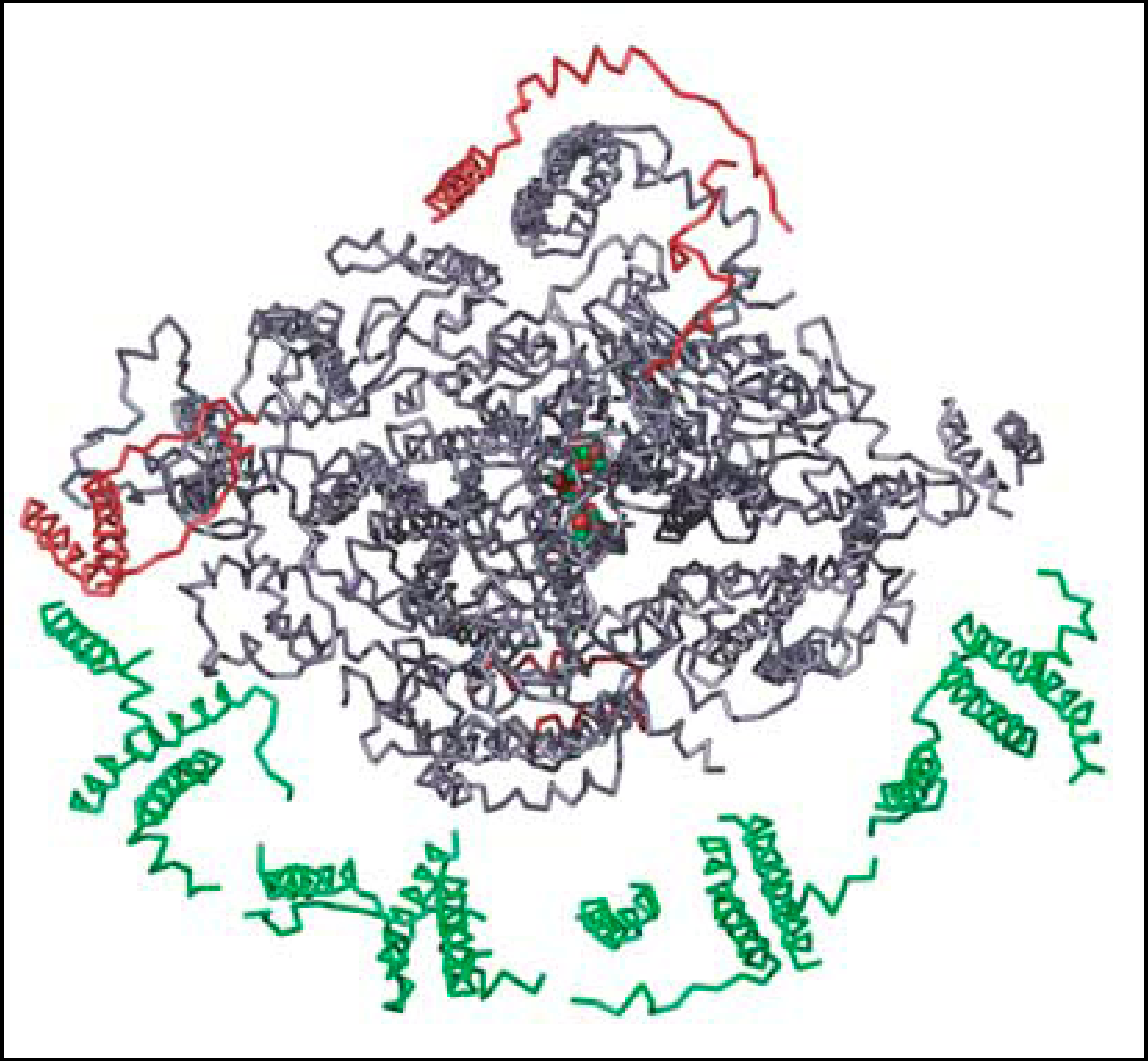


Structure of spinach LHC II at 2.7 Å resolution

Z. Liu *et al.*, (2004) *Nature* **428**, 287-292

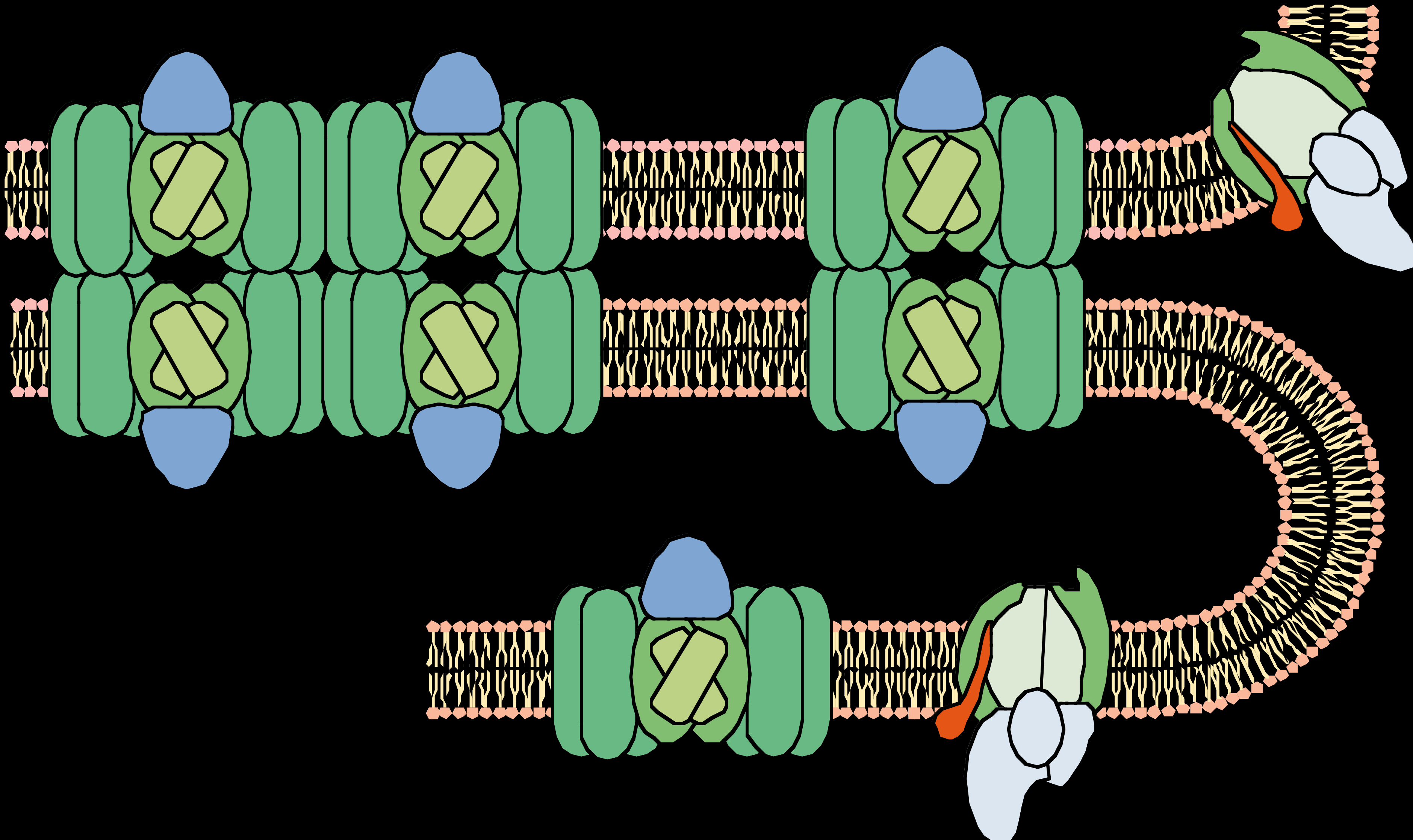


Kouril, R., Zygadlo, A., Arteni, A.A., de Wit, C.D., Dekker, J.P., Jensen, P.E., Scheller, H.V. and Boekema, E.J. (2005) Structural characterization of a complex of photosystem I and light-harvesting complex II of Arabidopsis thaliana. *Biochemistry* 44, 10935-40

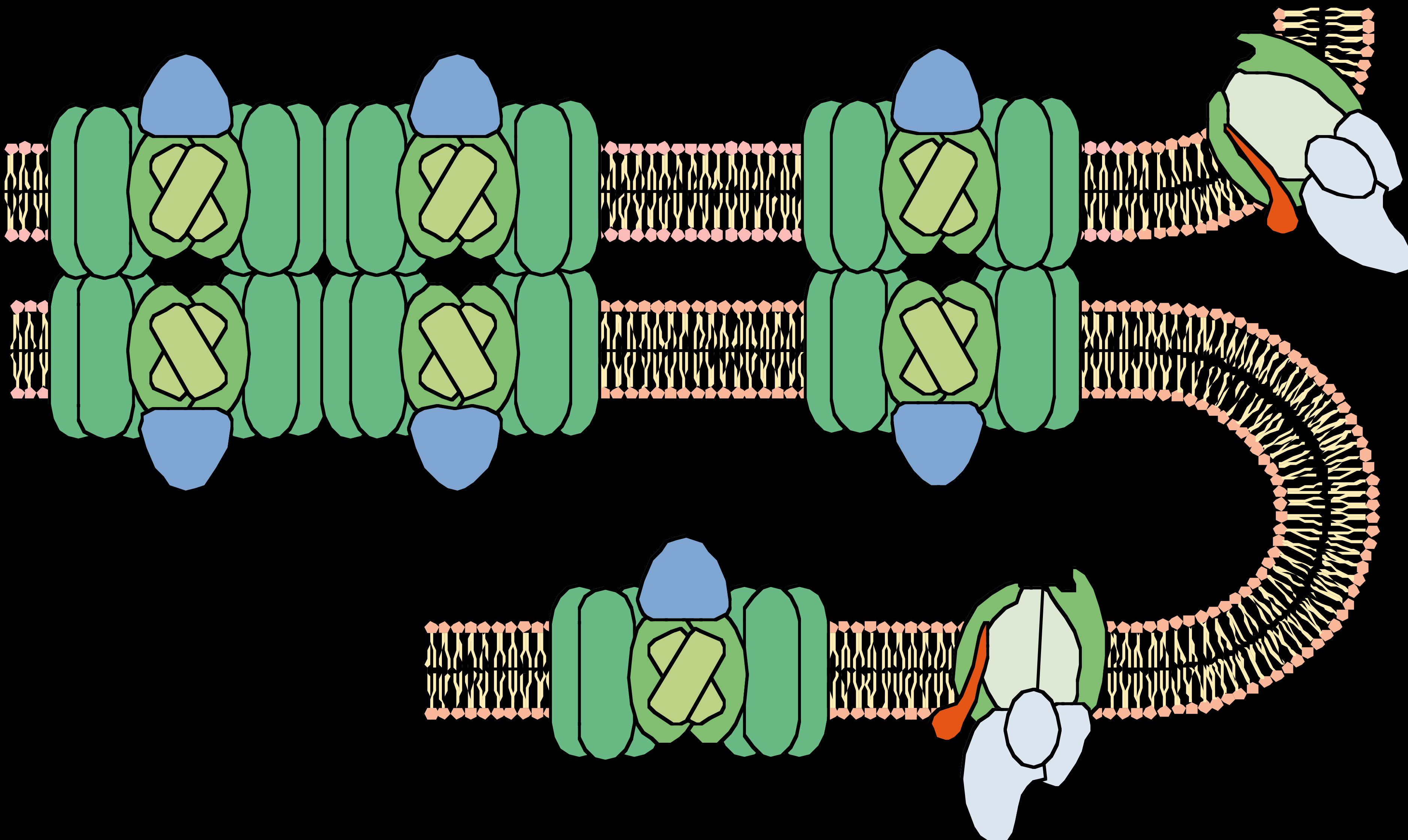


Structure of pea photosystem I at 4.4 Å resolution

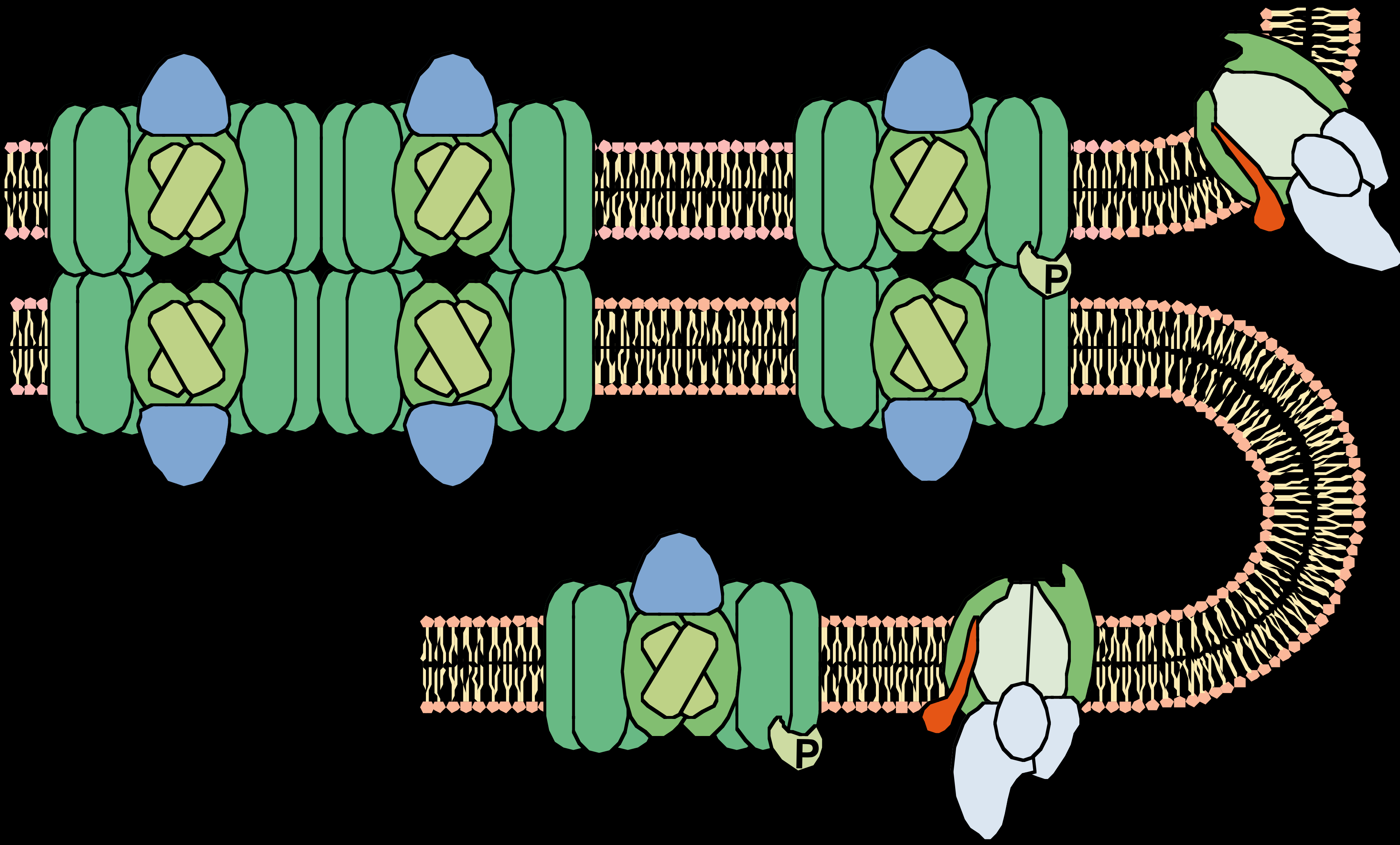
Ben-Shem, A., Frolow, F., Nelson N. (2003) *Nature* **426**, 630



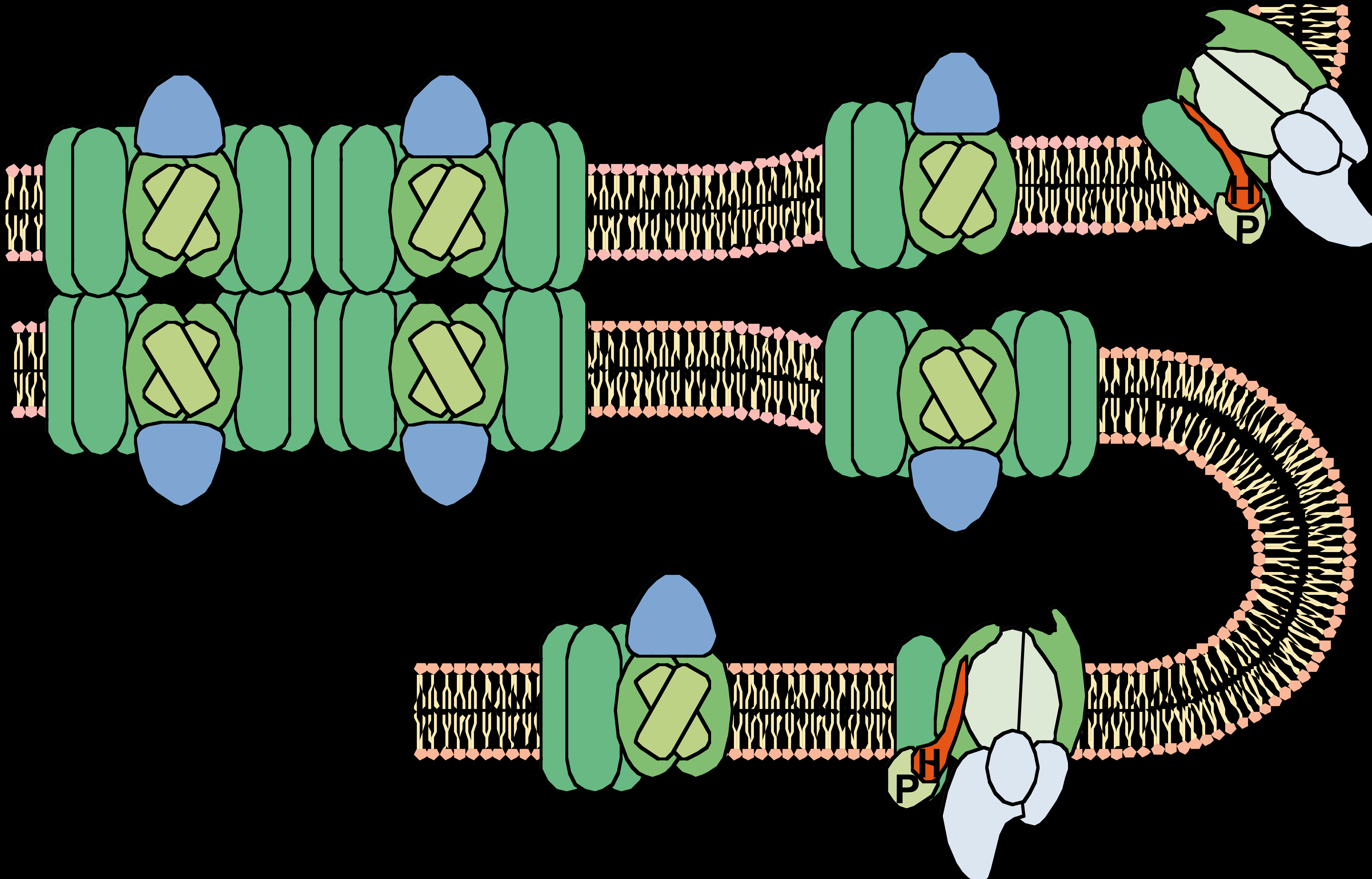
State 1

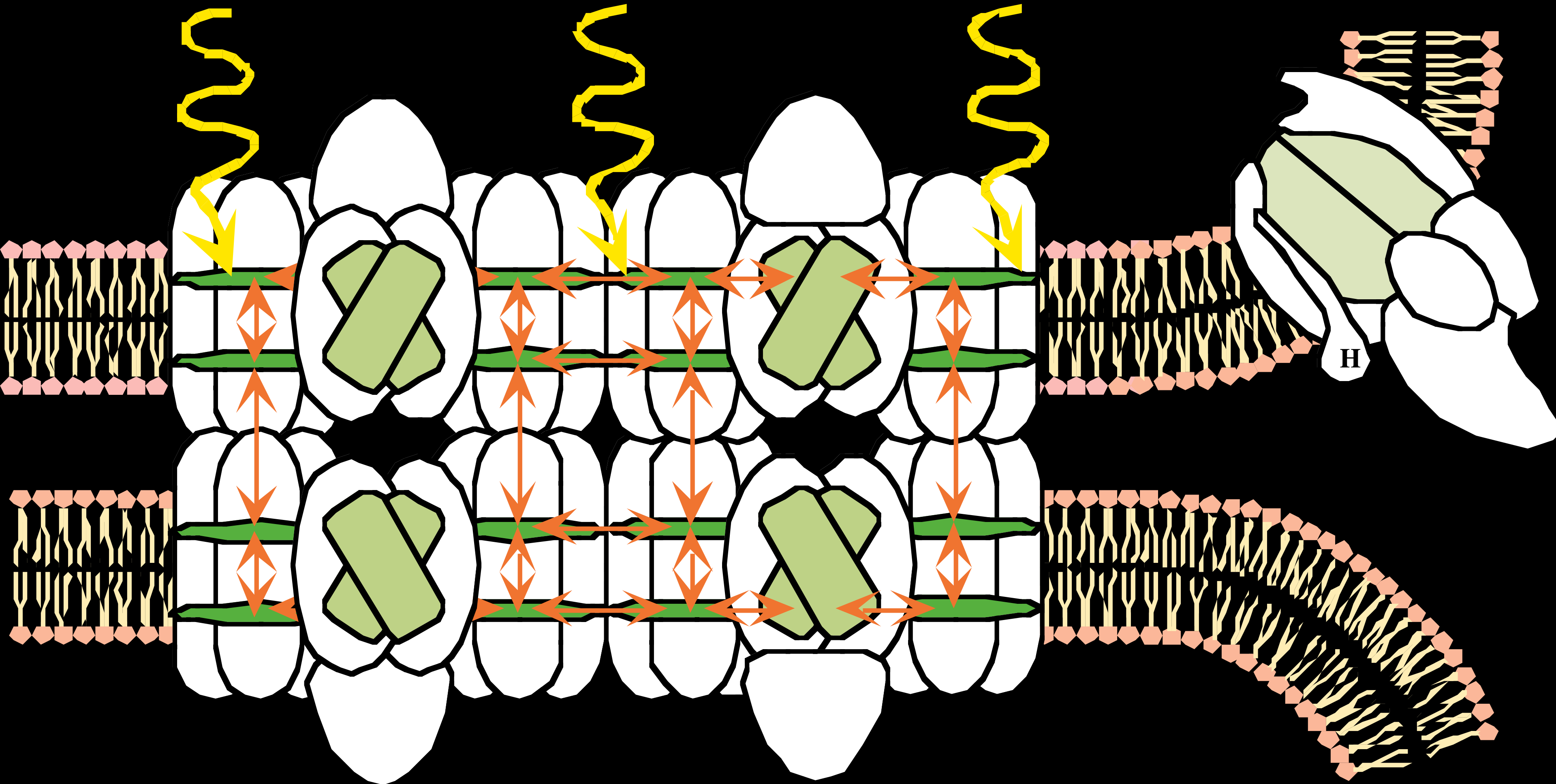


State 1

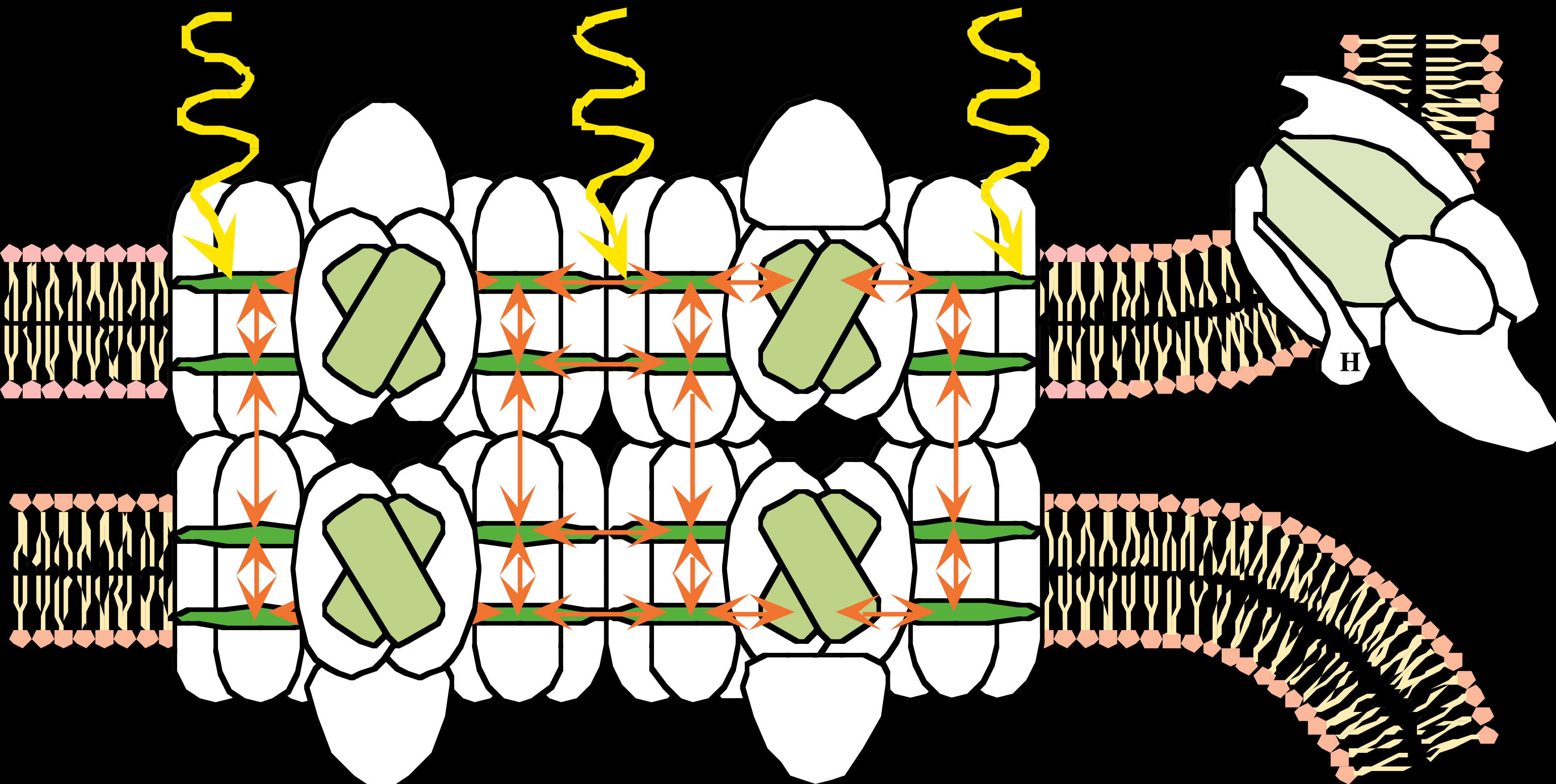


State 2

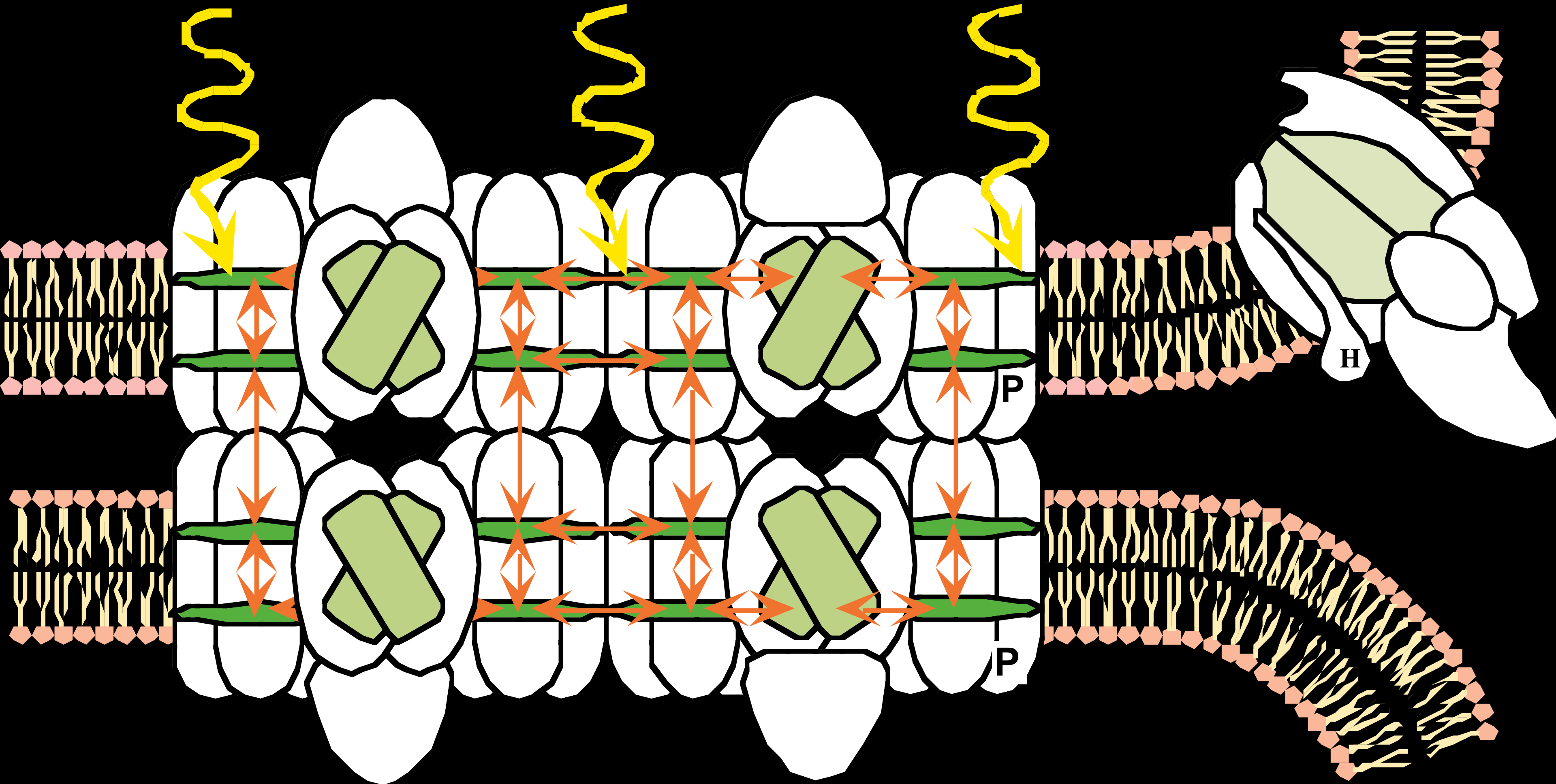



H

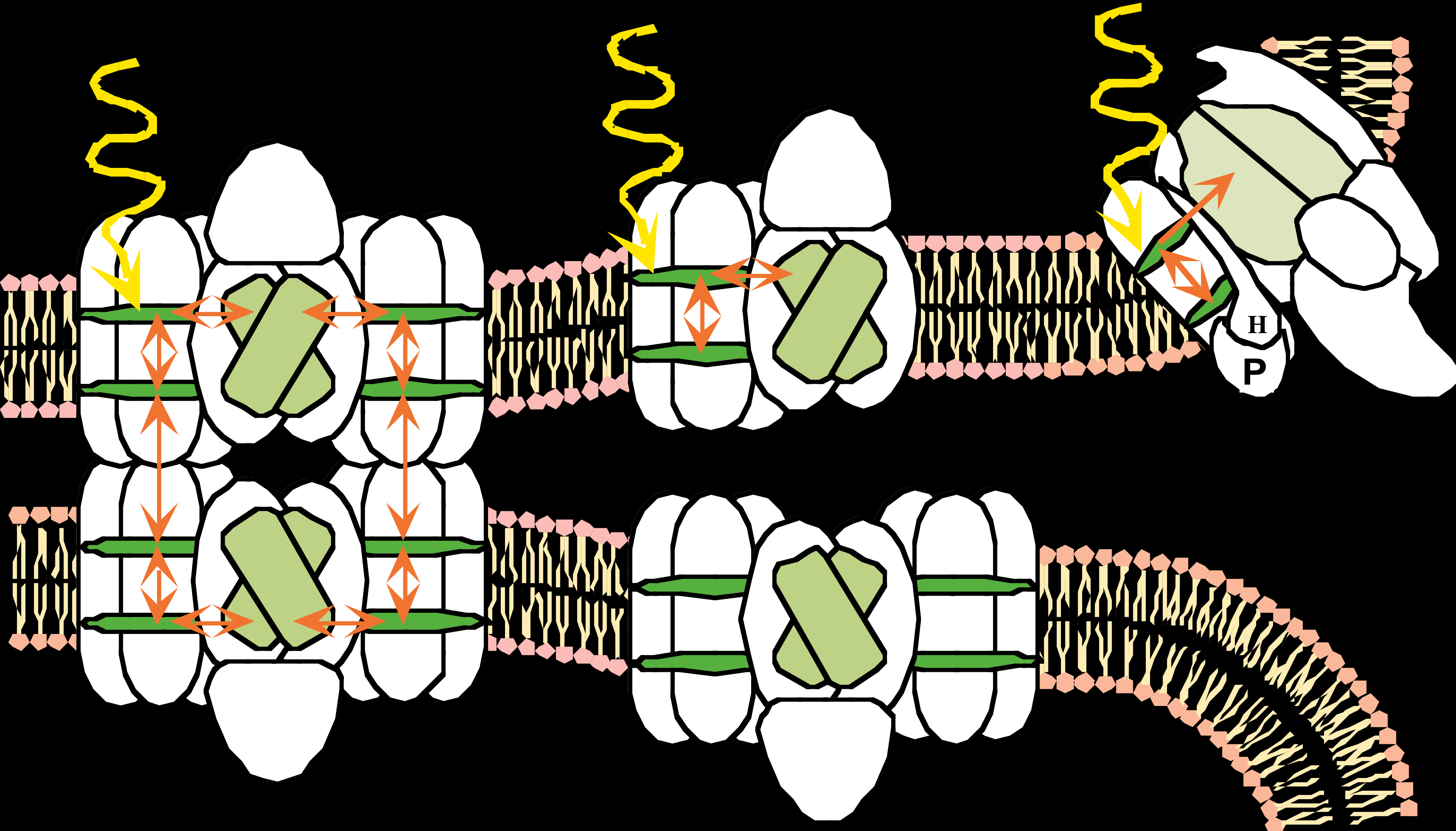
State 1



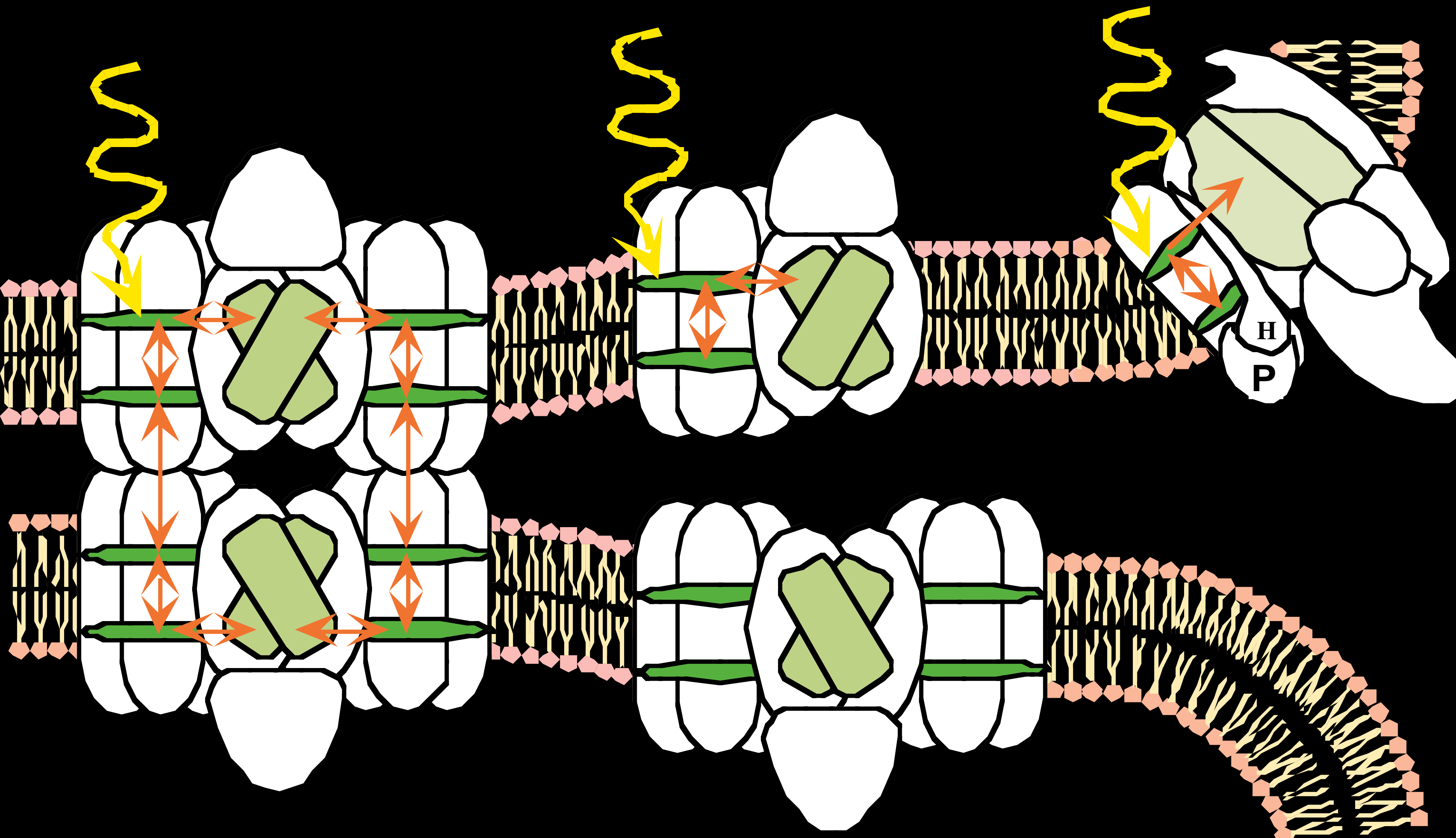
State 1



State 2



State 2



Allen, J. F. and Forsberg, J. (2001) Trends Plant Sci.6, 317-326


31. 7. 2001


31. 7. 2001


31. 7. 2001


Light 1
31. 7. 2001

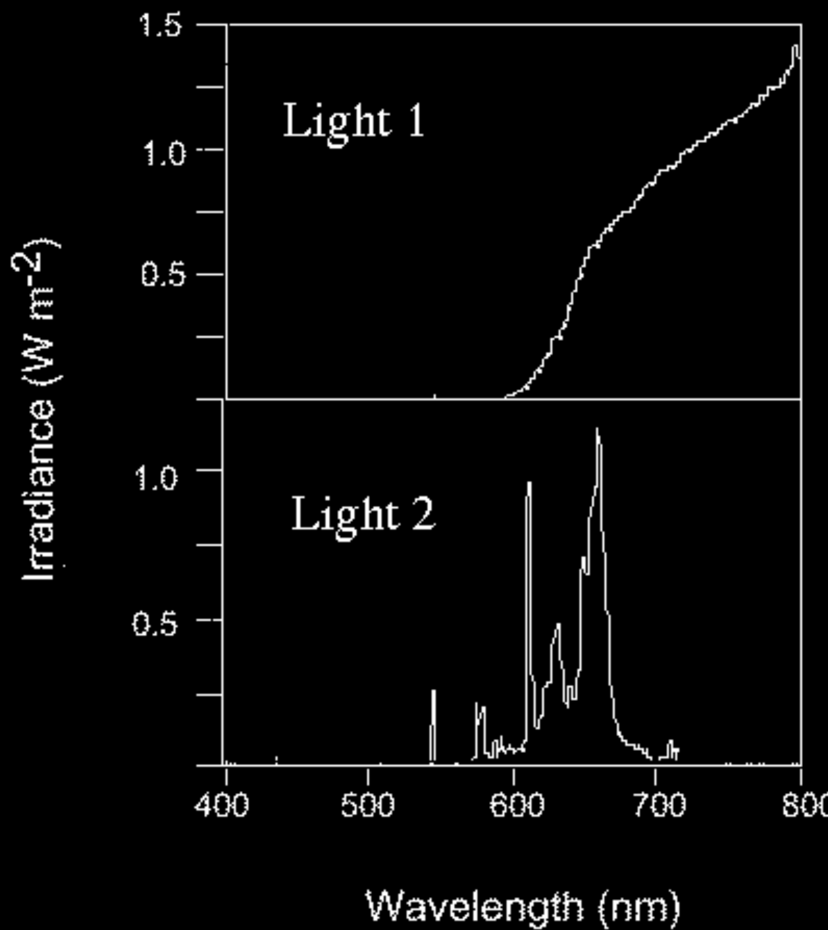

31. 7. 2001


Light 1
31. 7. 2001


Light 2
31. 7. 2001


Light 1
31. 7. 2001

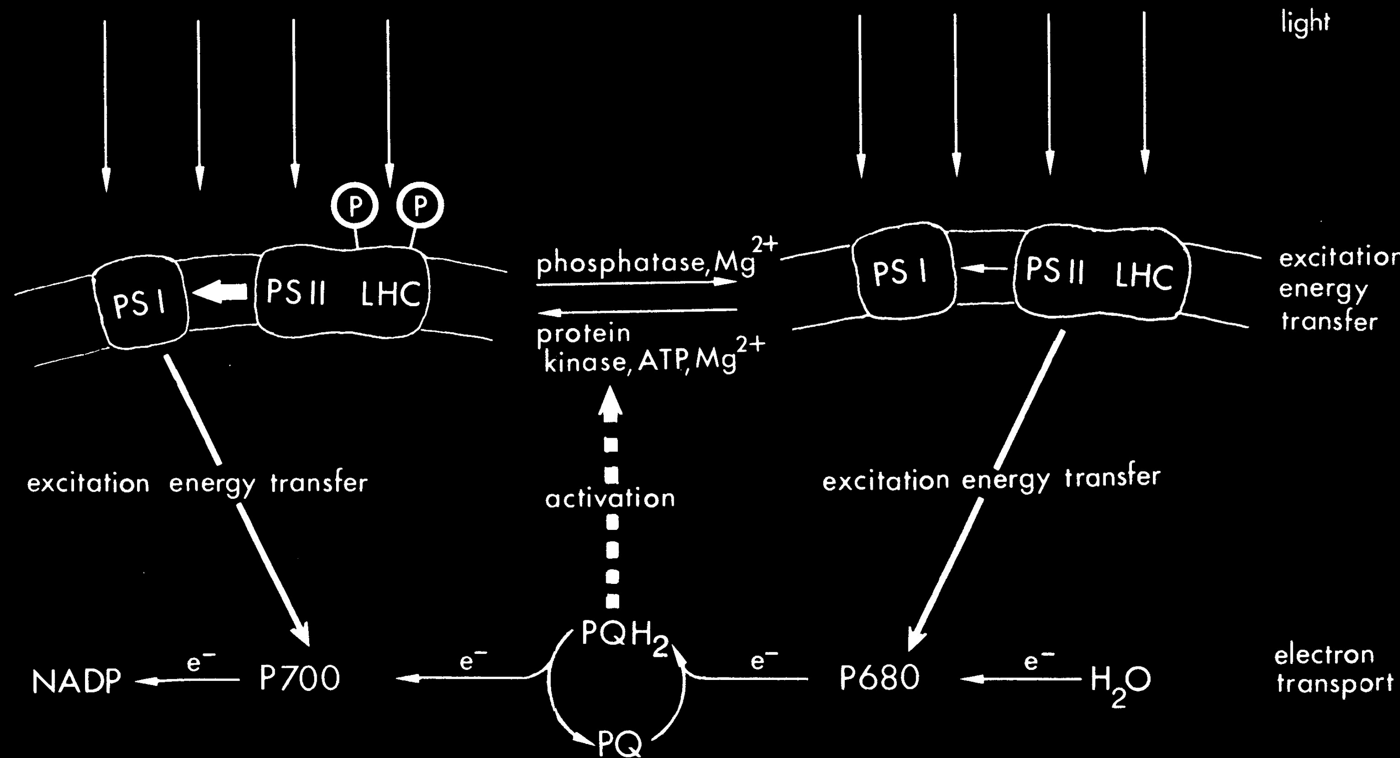

Light 2
31. 7. 2001


Light 1
Light 2
Irradiance (W m-2)
1.5
1.0
0.5
1.0
0.5
400
500
600
700
800
Wavelength (nm)

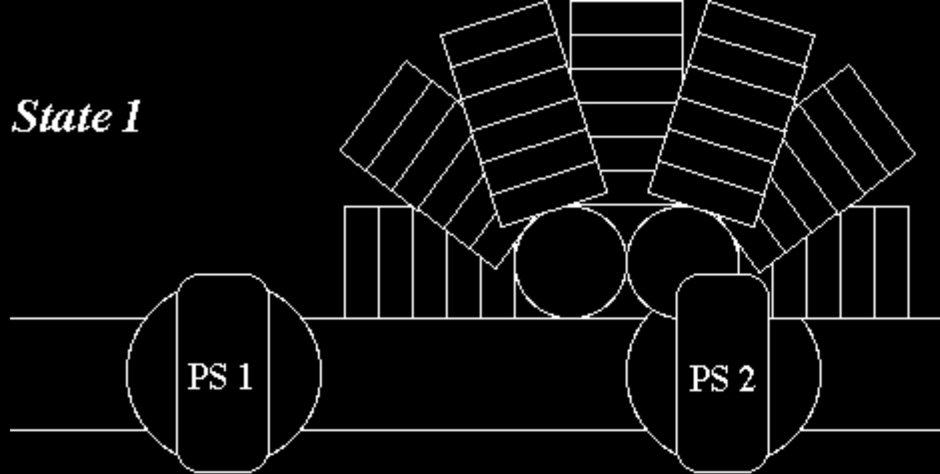
Impasse.

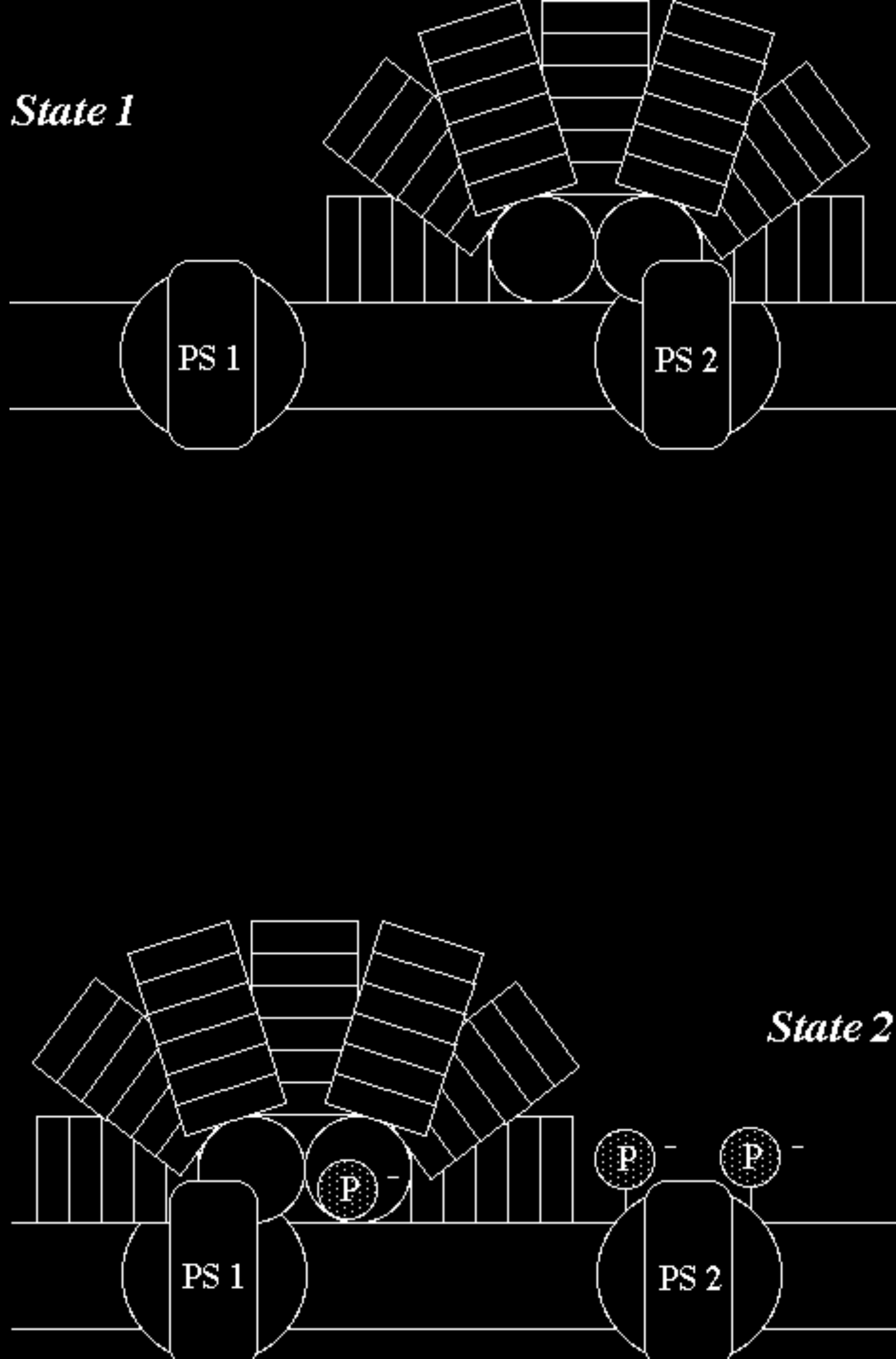
Slight change of subject….(brief)

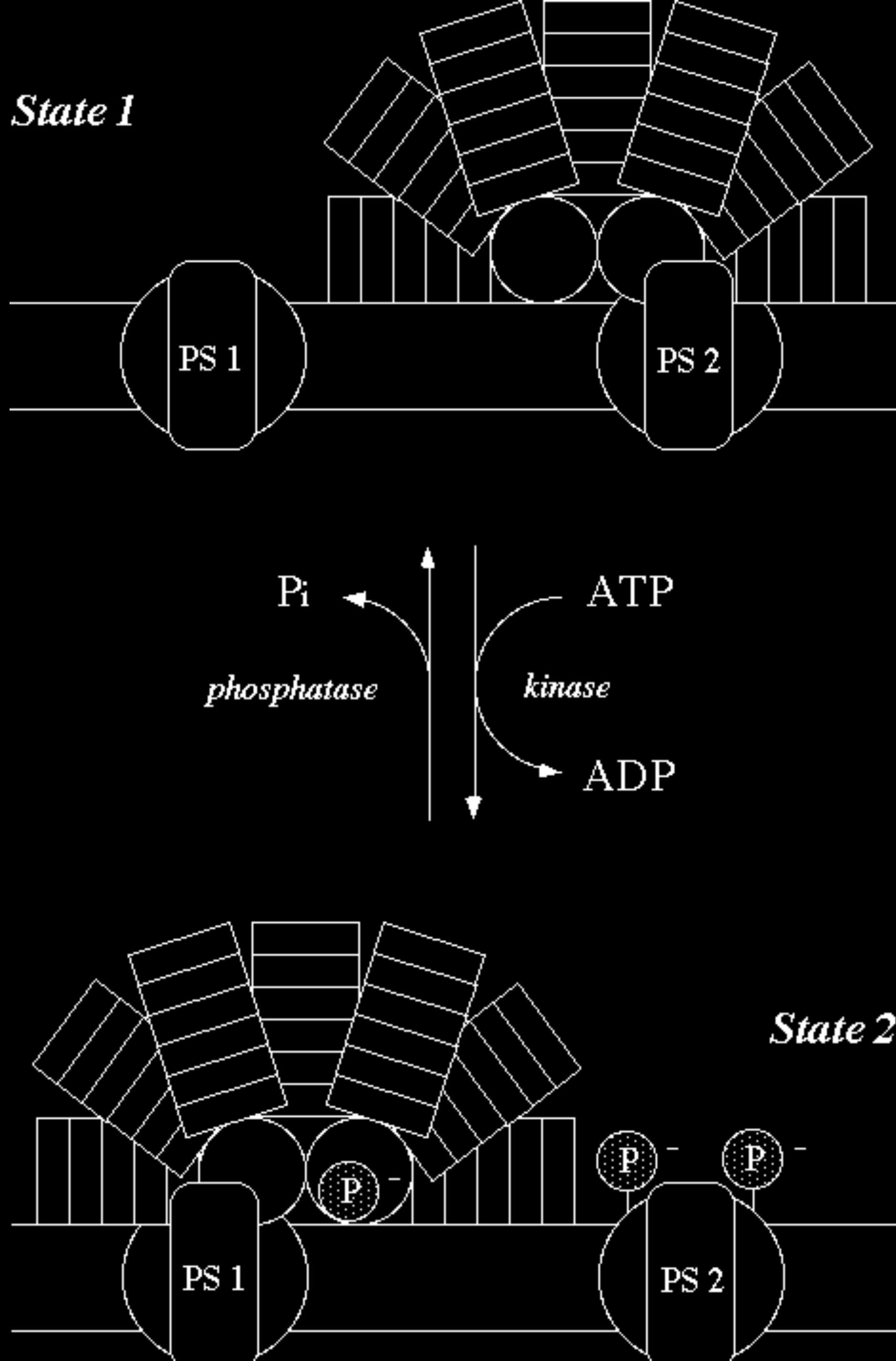
Postscript on two-component systems


light
PS I
PS II LHC
P
P
phosphatase, Mg2+
protein kinase, ATP, Mg2+
PS I
PS II LHC
excitation energy transfer
excitation energy transfer
activation
excitation energy transfer
NADP
e−
P700
e−
PQH2
PQ
e−
P680
e−
H2O
electron transport

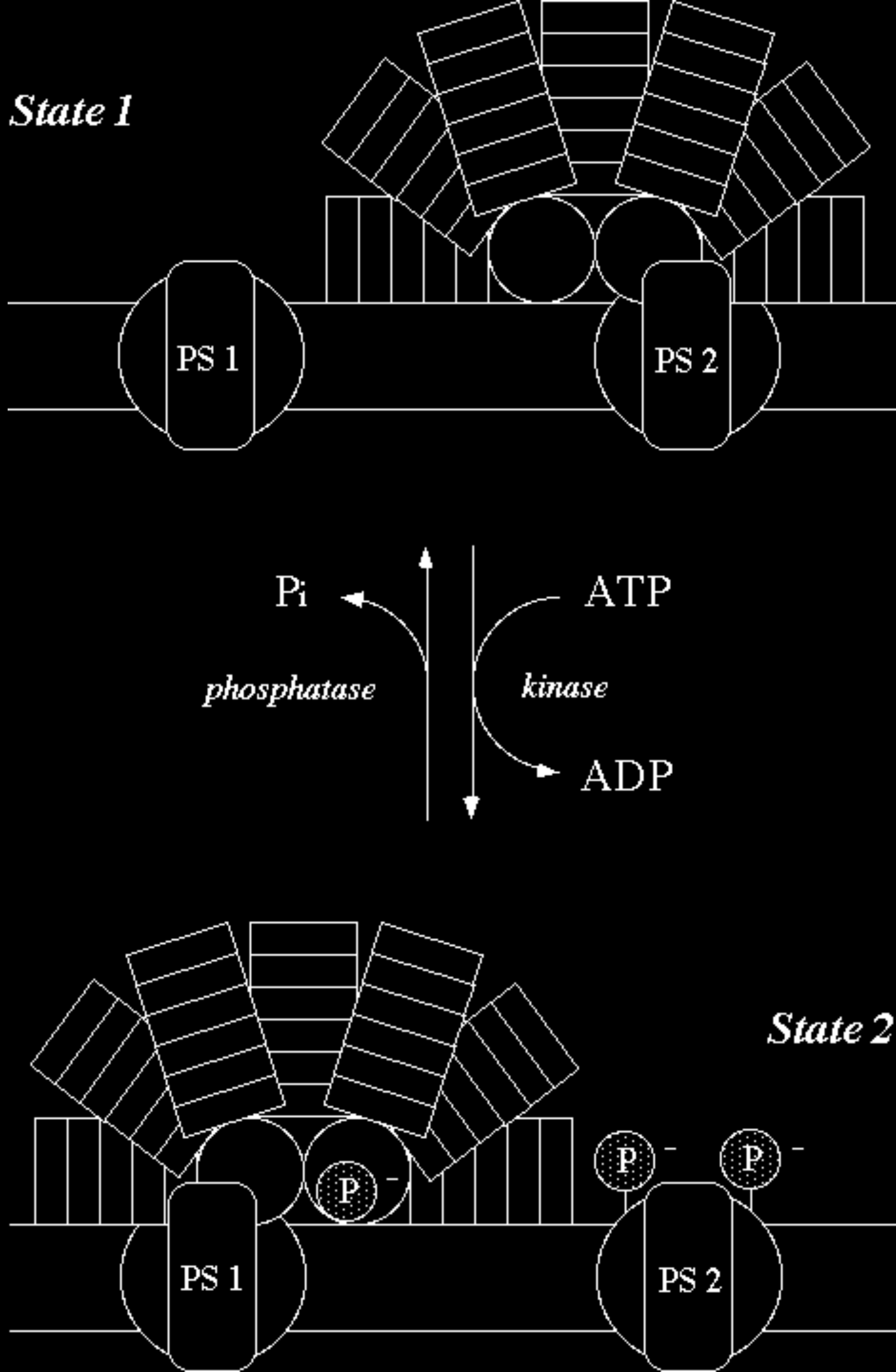
State 1




State 1
PS 1
PS 2
State 2
P
P
P
PS 1
PS 2



State 1
PS 1
PS 2
Pi
ATP
phosphatase
kinase
ADP
State 2
P –
P –
P –
PS 1
PS 2



Allen, J. F., Sanders, C. E. and Holmes, N. G. (1985) FEBS Lett. 193, 271-275

Volume 264, number 1, 25–28 FEBS 08384 May 1990

Modification of a glnB-like gene product by photosynthetic electron transport in the cyanobacterium *Synechococcus* 6301

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Department of Pure and Applied Biology and [+]Department of Biochemistry, The University of Leeds, Leeds LS2 9JT, UK

Received 26 February 1990

Covalent modification of a 13 kDa soluble-phase protein occurs during adaptation of cells of the cyanobacterium *Synechococcus* 6301 (mutant AN112) to light specifically absorbed by photosystem II. This adaptation is accompanied by functional changes indicative of altered excitation energy distribution between the photosystems. The 13 kDa protein is identified by solid-phase N-terminal sequencing as a protein related to P_{II}, the glnB gene product of *E. coli*. In *E. coli*, the P_{II} protein undergoes uridylylation and acts as a regulator of glutamine synthetase at both the post-translational and transcriptional levels. The implications of modification of a transcriptional regulator by photosynthetic electron transport are discussed.

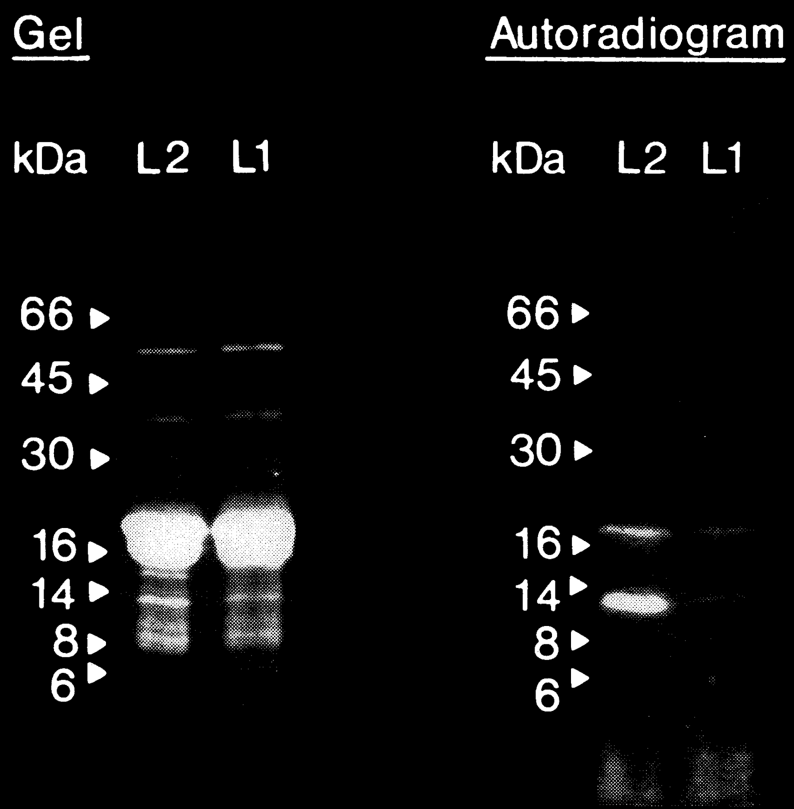
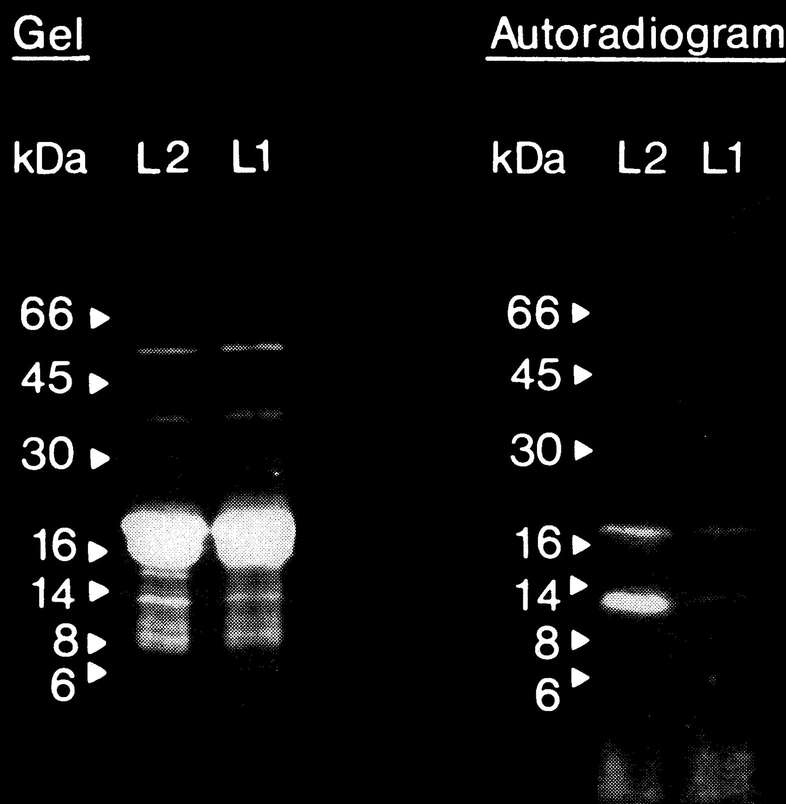


Fig. 1. SDS-PAGE analysis of whole cell polypeptides from *Synechococcus* 6301 (AN112) after incubation with [^{32}P]orthophosphate. L1 and L2 indicate SDS-PAGE tracks of sample derived from cells incubated under Light 1 and Light 2, respectively. Gel, stained gel; Autoradiogram, ^{32}P-labelling of the same gel. Positions and M_r of markers are indicated.



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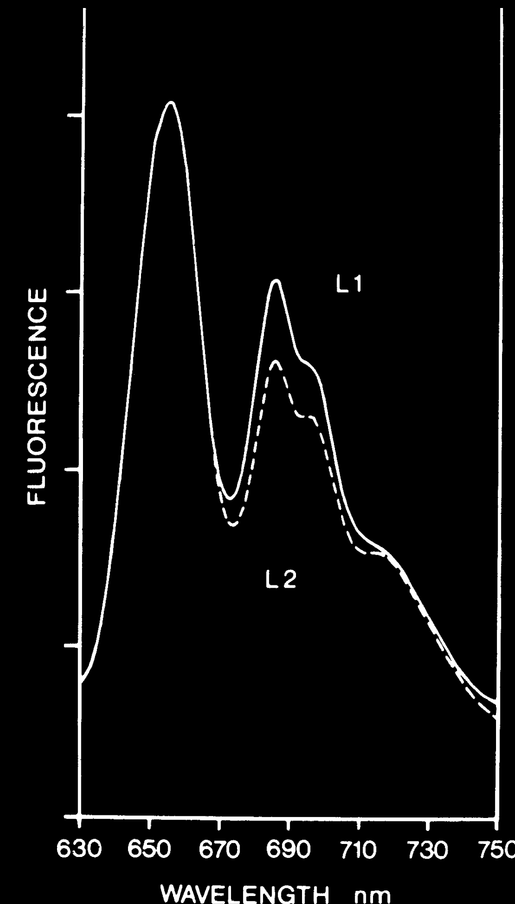

Fig. 2. Fluorescence emission spectra of *Synechococcus* 6301 (AN112) cells at 77 K. Excitation wavelength 600 nm. L1 and L2 indicate cells preilluminated as in Fig. 1. Spectra are normalised to phycocyanin emission at 650 nm.

```
MKXIEAIIRPFKLDEVKIALVNAGIVGMTV  Synechococcus 6301
MKKIDAIIKPFKLDDVRERLAEVGITGMTV  E. coli [18]
MKKIEAIIKPFKLDEVRSP-SGVGLQGITV  R. leguminosarum [19]

MKXIEAIIRPFKLDEVKIALVNAGIVGMTV  Synechococcus 6301
## #*###*#####*#*  # * ## ####  E. coli [18]
## #####*#######* *    #* #*##  R. leguminosarum [19]
```

Fig. 4. The sequence of 30 amino acid residues obtained for the purified 13 kDa protein from *Synechococcus* 6301 (AN112), together with the two sequences of greatest similarity from the OWL database. Amino acid identity is represented by # and a conservative substitution by *.

```
MKXIEAIIRPFKLDEVKIALVNAGIVGMTV  Synechococcus 6301
MKKIDAIIKPFKLDDVRERLAEVGITGMTV  E. coli [18]
MKKIEAIIKPFKLDEVRSP-SGVGLQGITV  R. leguminosarum [19]

MKXIEAIIRPFKLDEVKIALVNAGIVGMTV  Synechococcus 6301
## #*###*#####*#*  # * ## ####  E. coli [18]
## #####*#######* *    #* #*##  R. leguminosarum [19]
```

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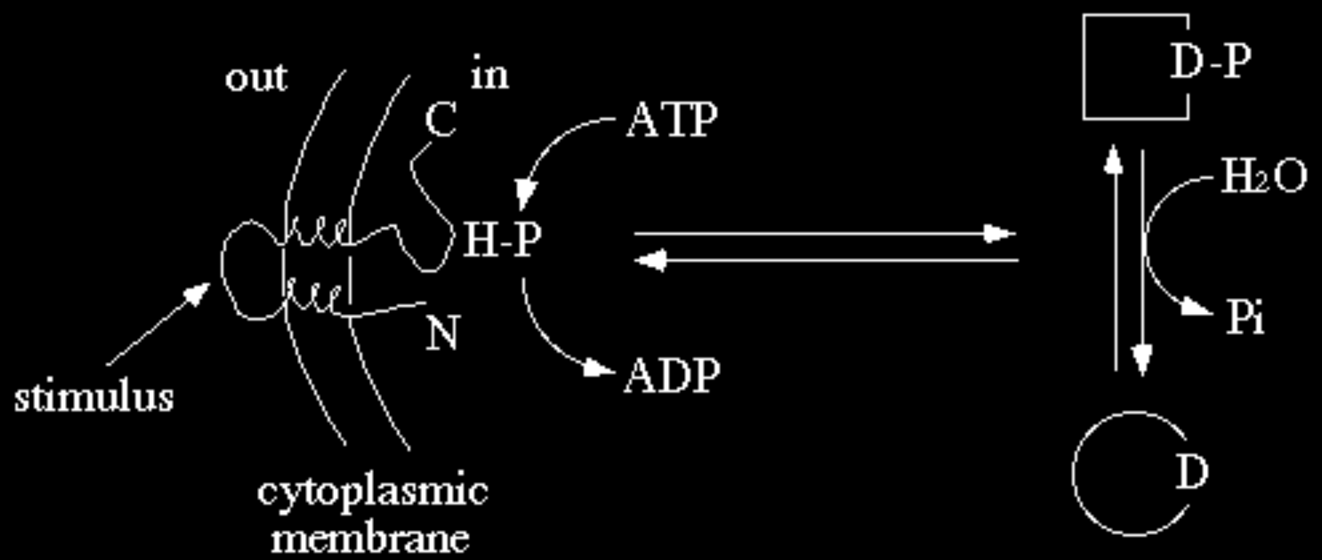
From the results described here, the possibility arises that post-translational modification during light-state transitions [4] and photosynthetic control of gene expression share common components and that both respond to environmental changes via perturbation of the redox poise of the photosynthetic electron transport chain. Such a two-component regulatory system for photosynthesis could involve components with structural features known to be conserved throughout a wide range of other biological processes [26].

Two-component regulatory systems



SENSOR

- phosphorylated
- protein kinase or phosphotransferase
- membrane protein (usually)
- responds to stimulus

EFFECTOR (RESPONSE-REGULATOR)

- phosphorylated
- DNA-binding
- transcriptional control

1. Specific redox sensors and effectors may act at specific redox potentials to regulate synthesis of specific complexes through transcription of specific groups of genes (e.g. *psa, psb, pet, puf, puc.*, *ndh, rbc*)

2. Chloroplast and mitochondrial DNA may have been retained in evolution to encode a sub-set of organelle proteins whose synthesis must be subject to redox control.

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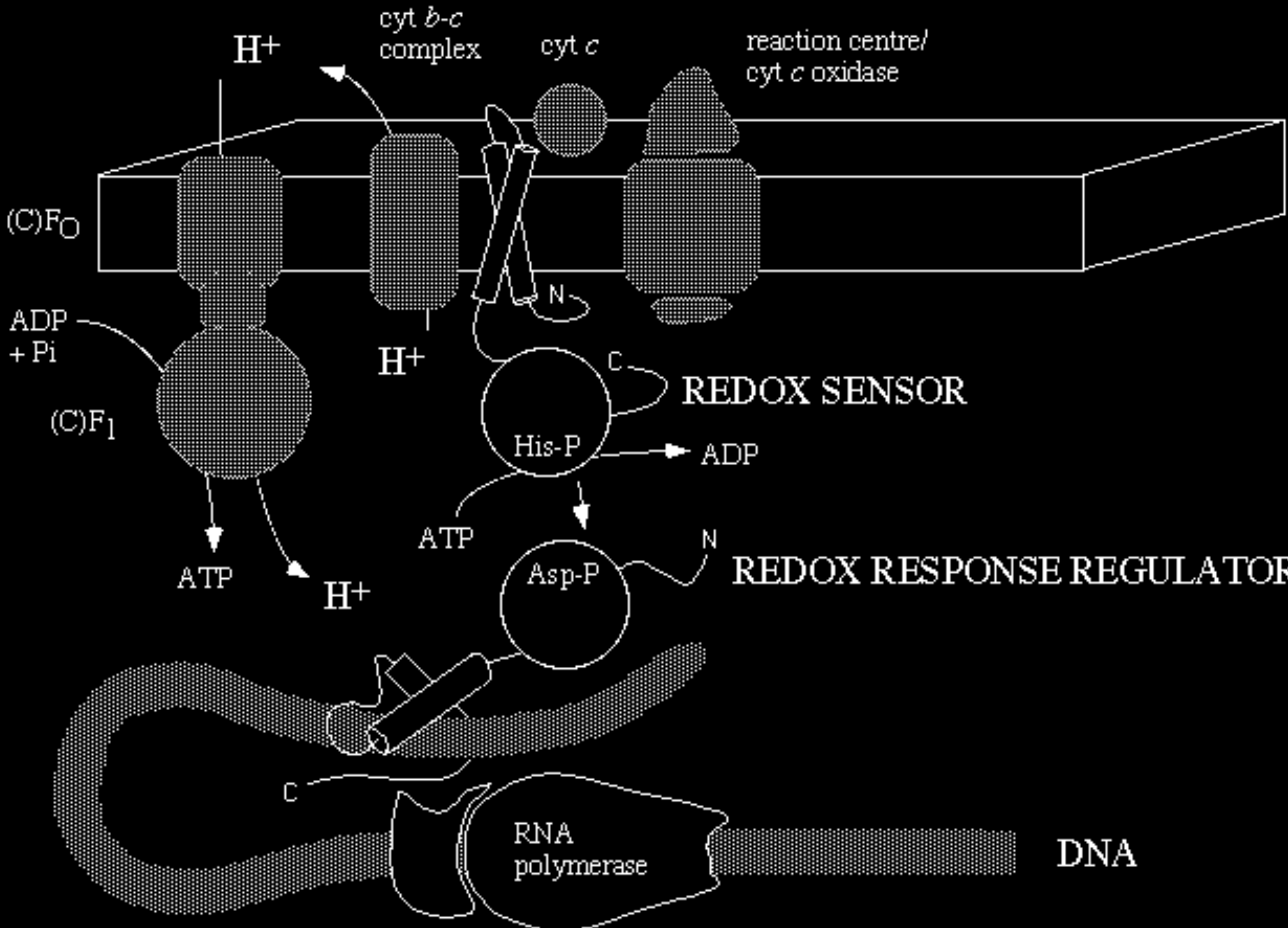
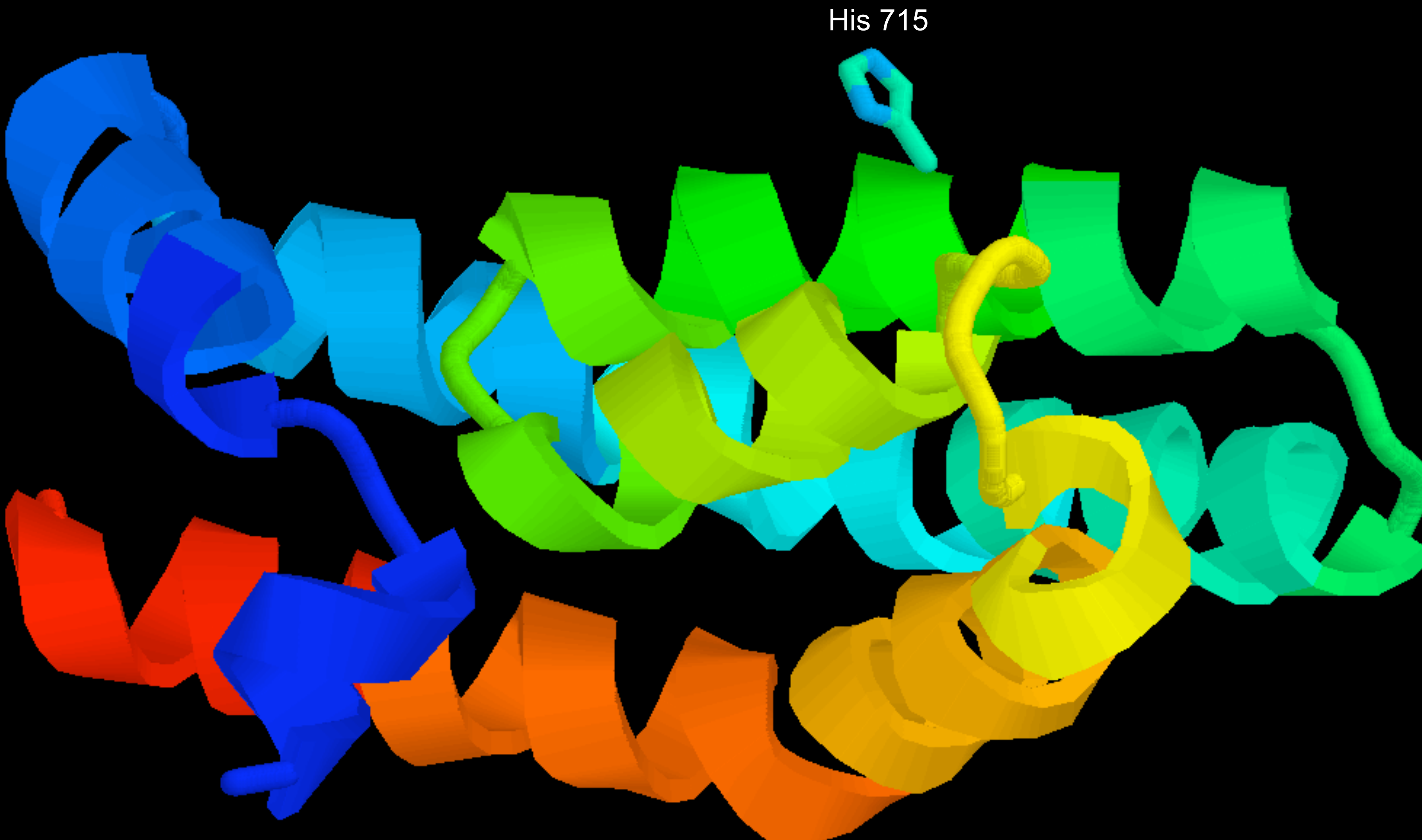
2. Chloroplast and mitochondrial DNA may have been retained in evolution to encode a sub-set of organelle proteins whose synthesis must be subject to redox control.

Allen, J. F. (1992) BBA 1098, 275-225



cyt b-c
complex
cyt c
reaction centre/
cyt c oxidase
H+
(C)F_O
N
ADP
+ Pi
H+
C
REDOX SENSOR
(C)F_1
His-P
ADP
ATP
N
Asp-P
REDOX RESPONSE REGULATOR
ATP
H+
C
RNA
polymerase
DNA

Redox sensor. Histidine-containing phosphotransfer domain of ArcB from E. coli

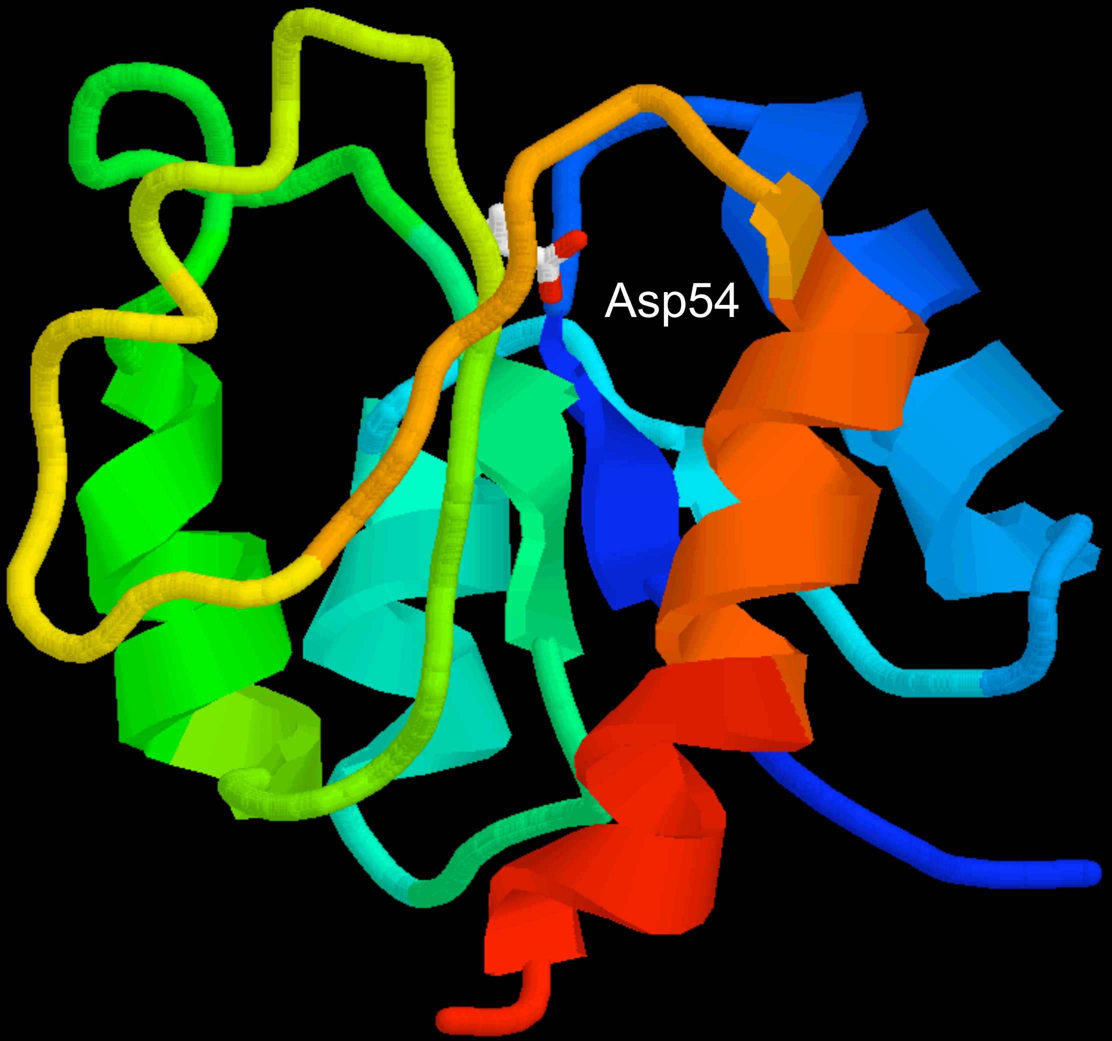


Kato, M., Mizuno, T., Shimizu, T. and Hakoshima, T. (1999) 2aob.pdb

Nitrogen response regulator NtrC

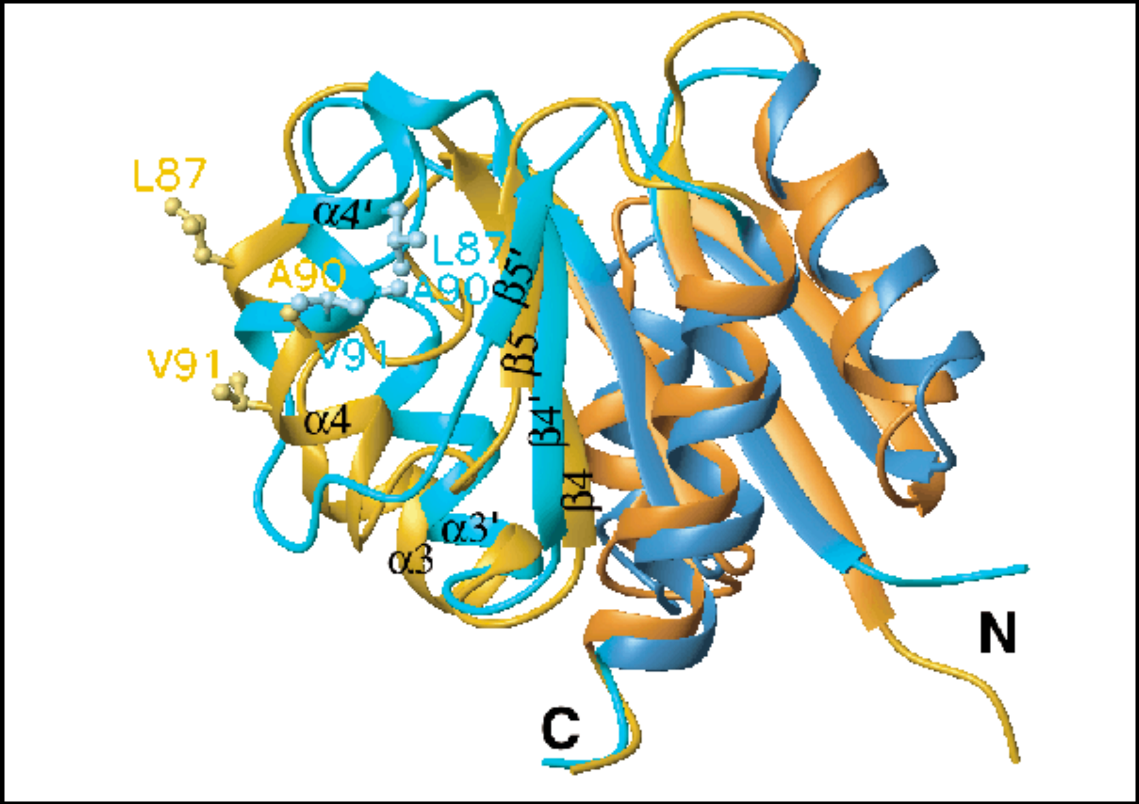
1dc7.pdb

Phospho-NtrC: 1dc8.pdb



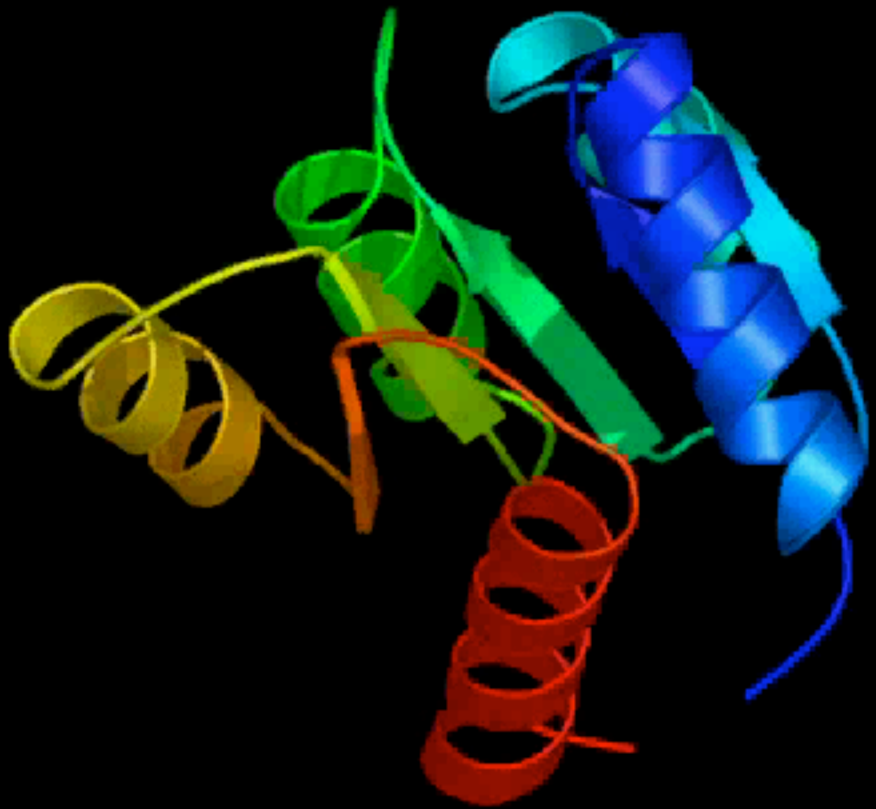
Structure of a transiently phosphorylated “switch” in bacterial signal transduction
Kern, D. et al. (1999) Nature 402, 894

Nitrogen response regulator NtrC



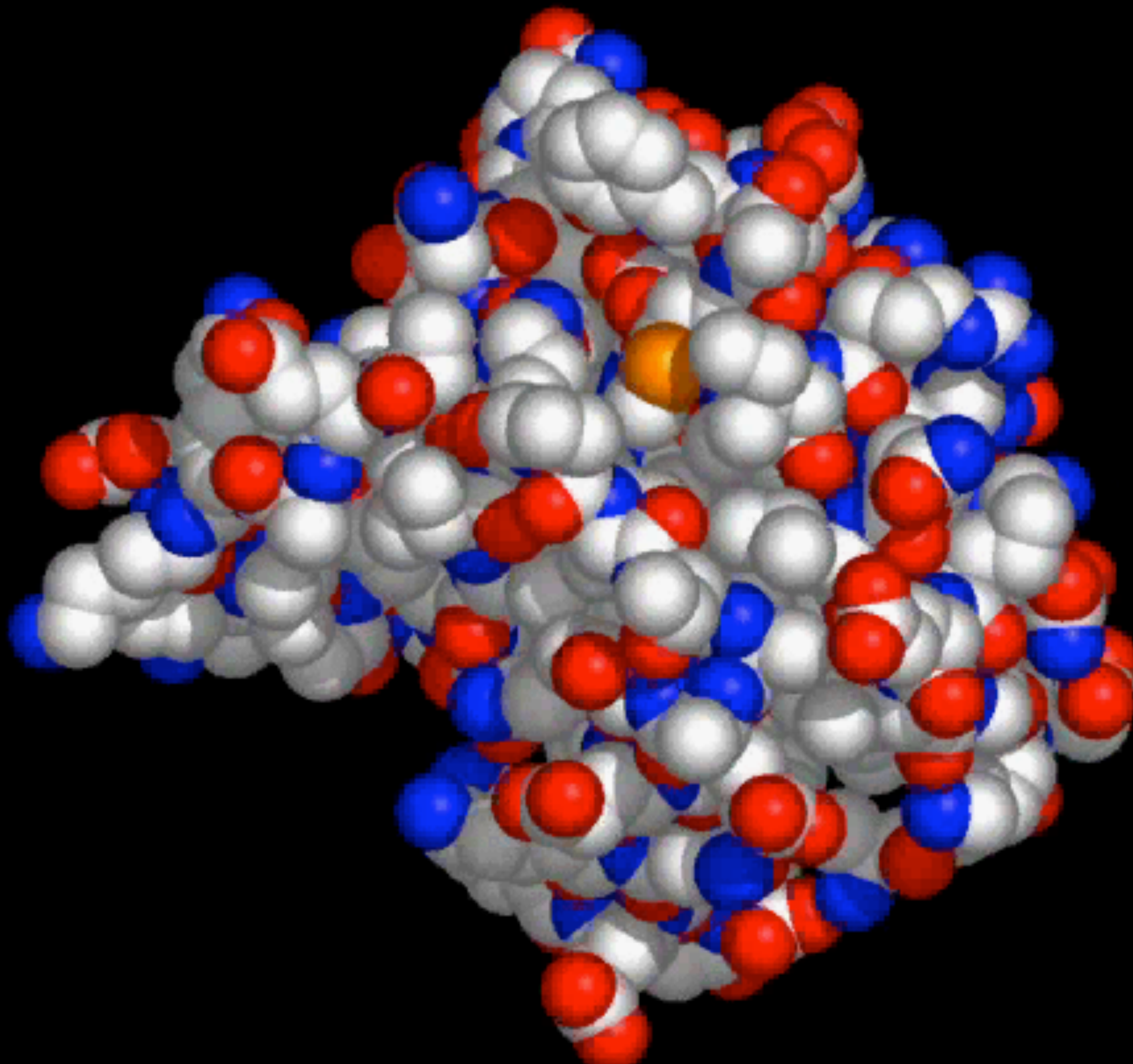
Structure of a transiently phosphorylated "switch" in bacterial signal transduction
Kern, D. et al. (1999) Nature 402, 894

Chemotaxis response regulator CheY



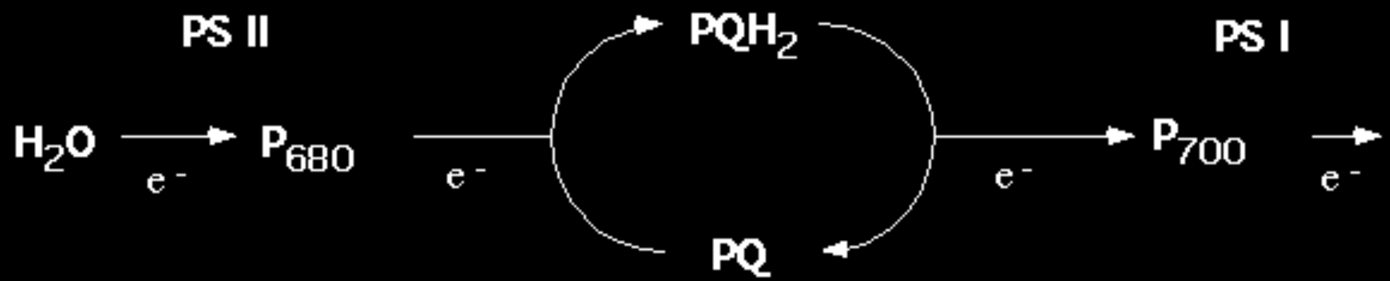
Database of Macromolecular Movements, Gerstein Lab, Yale University http://molmovdb.mbb.yale.edu/

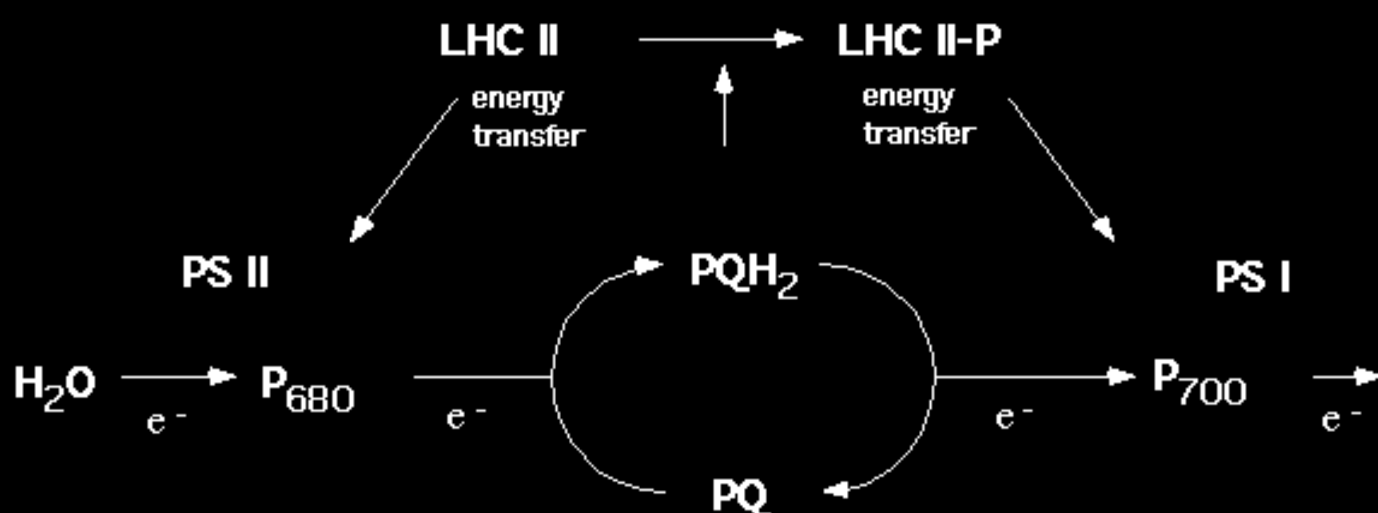
Chemotaxis response regulator CheY

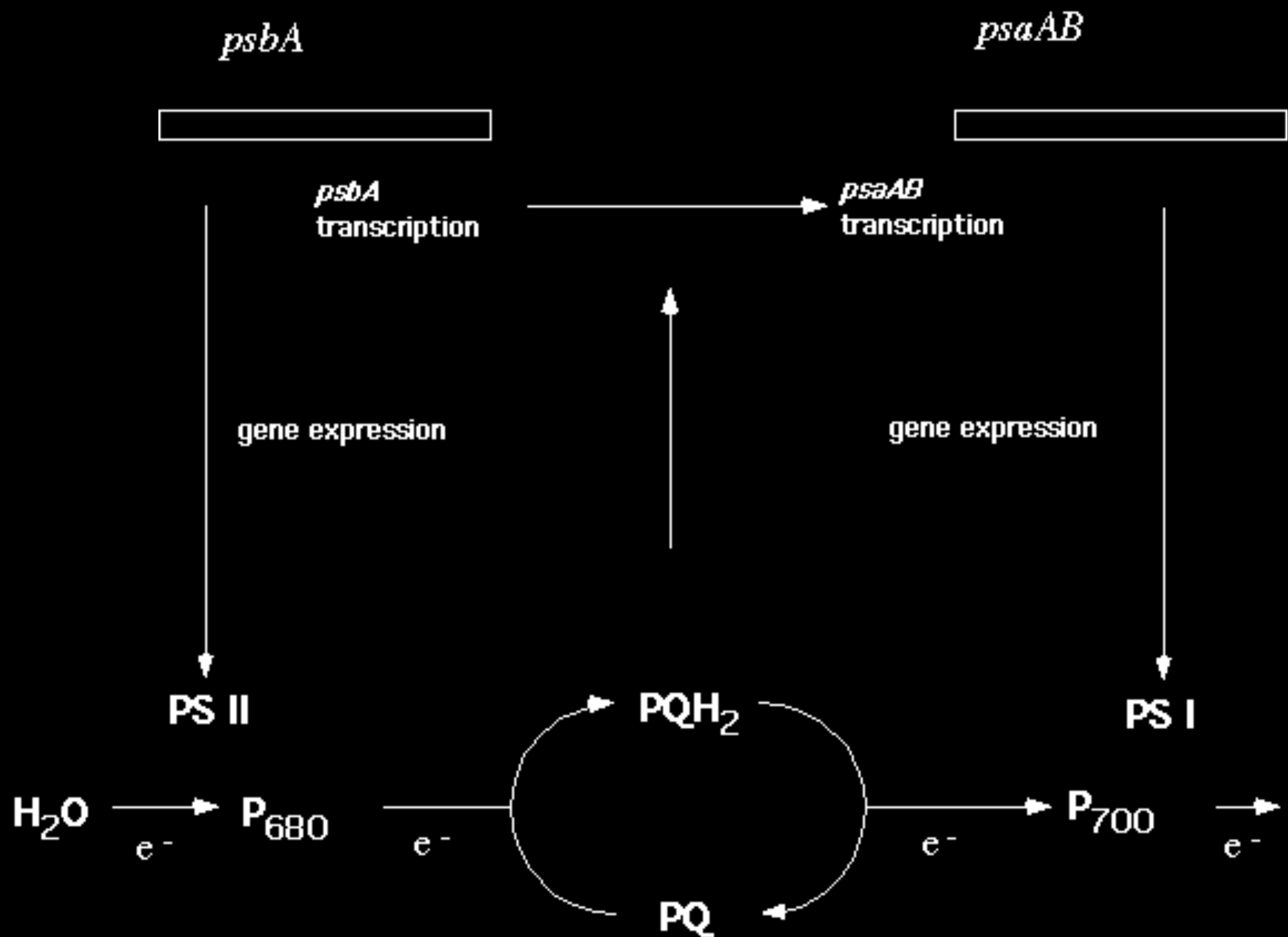


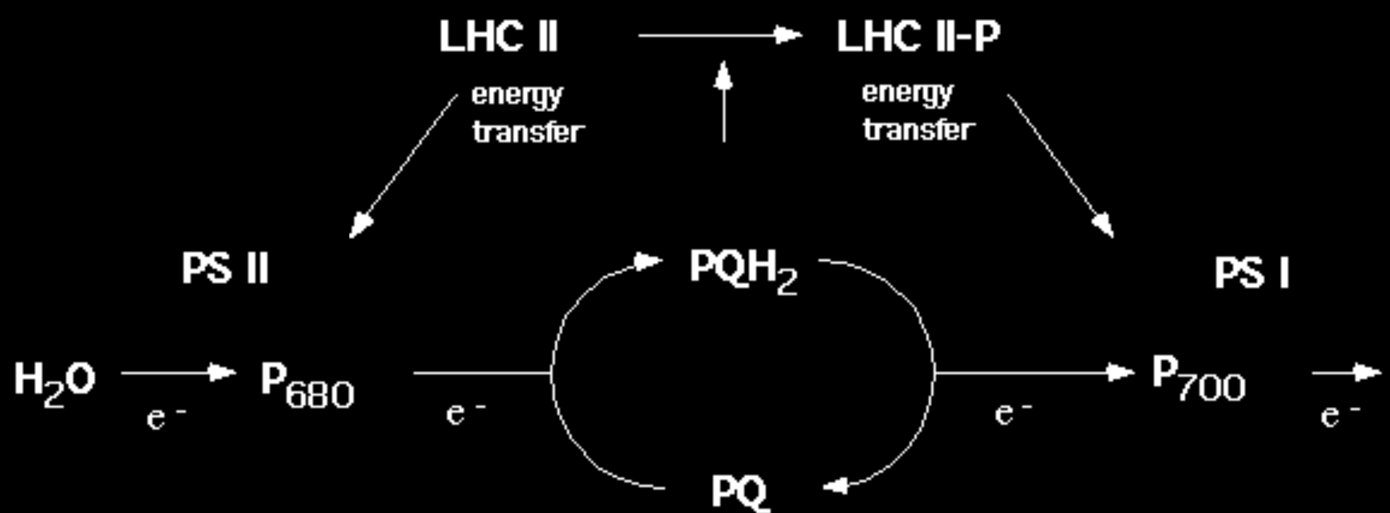
Database of Macromolecular Movements, Gerstein Lab, Yale University http://molmovdb.mbb.yale.edu/

Nitrogen response regulator NtrC

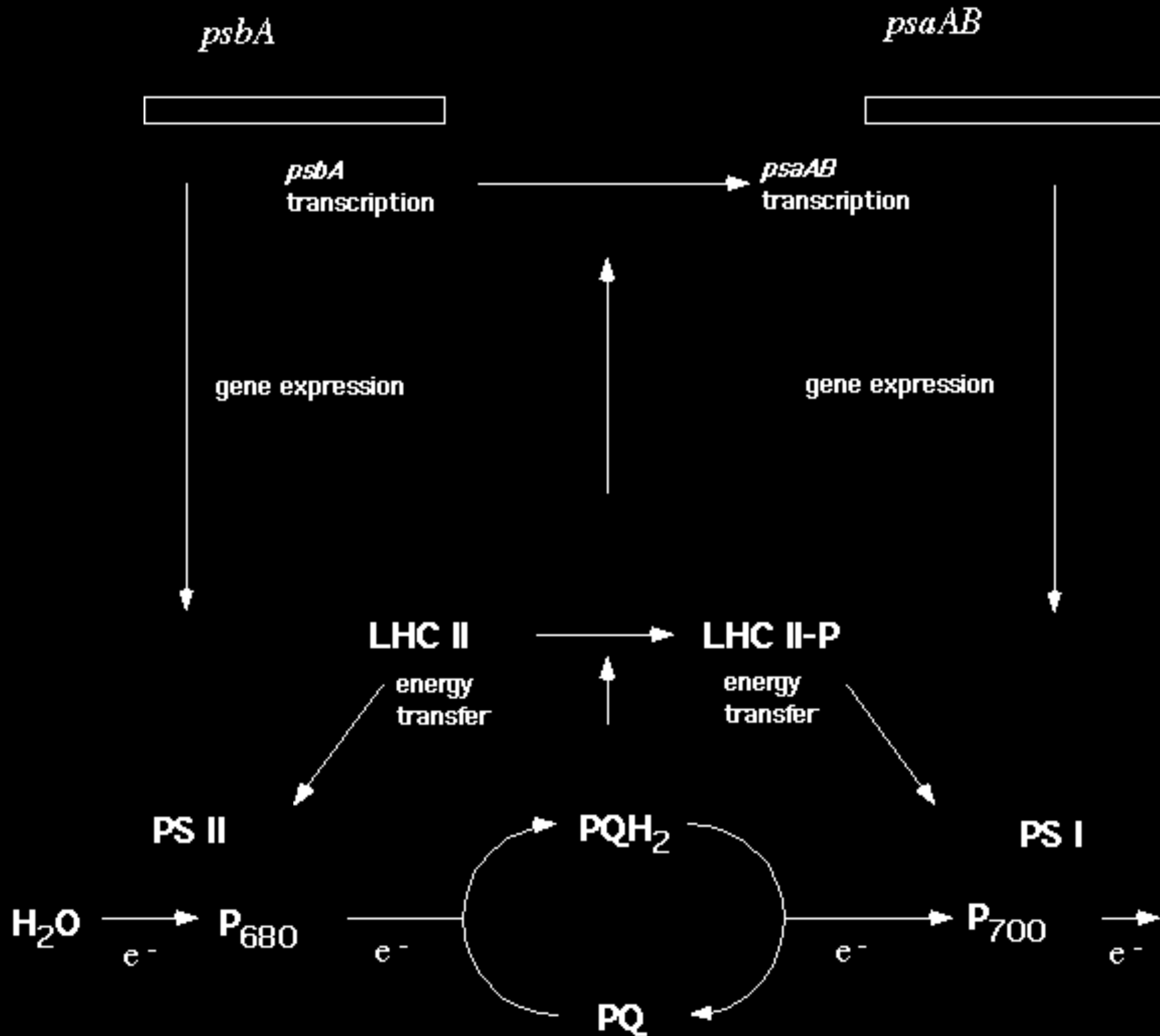

PS II
PQH2
PS I
H2O
e⁻
P680
e⁻
e⁻
P700
e⁻
PQ

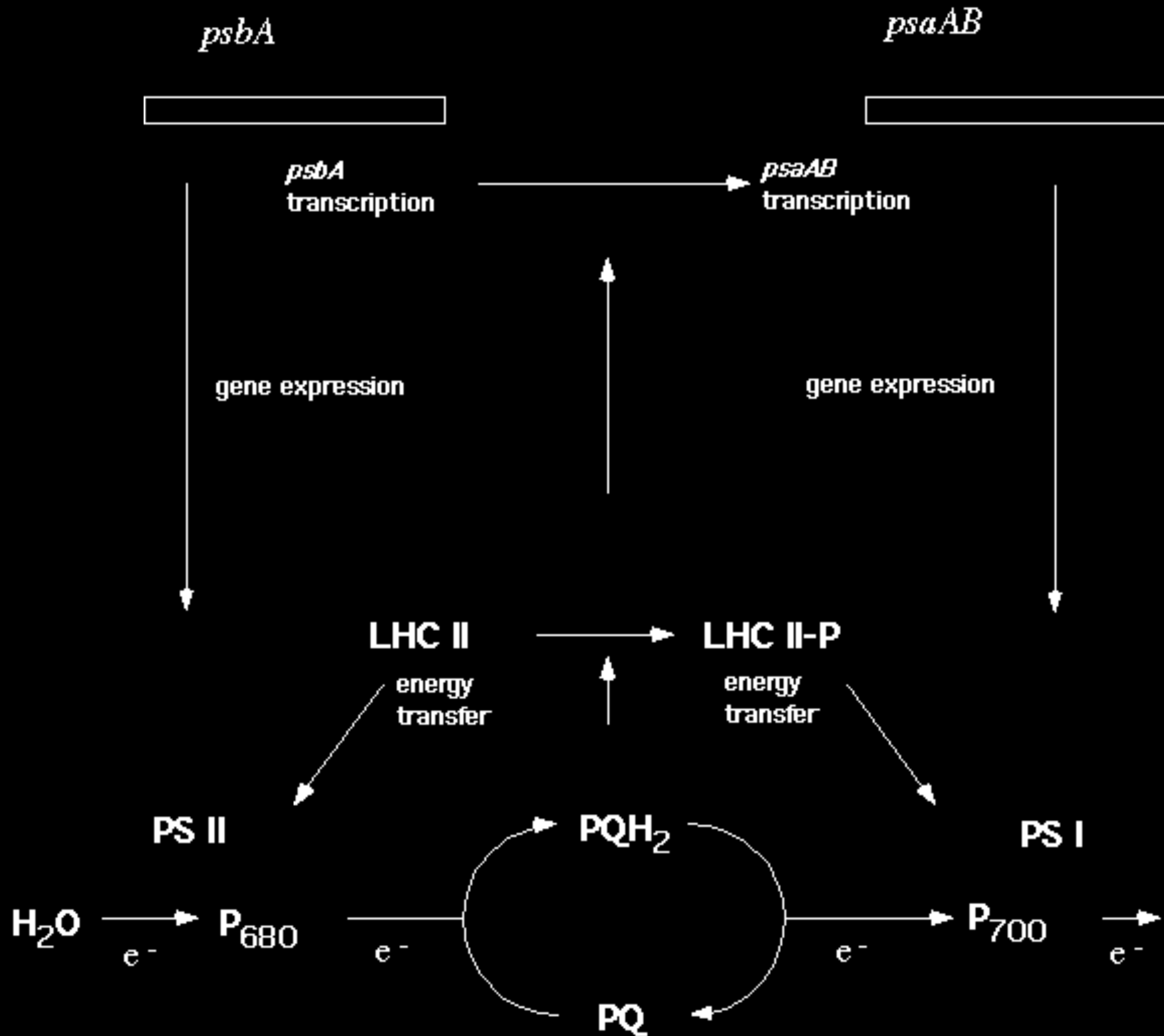

LHC II
LHC II-P
energy transfer
energy transfer
PS II
PS I
PQH2
H2O
P680
P700
e -
e -
e -
e -
PQ


psbA
psaAB
psbA
transcription
psaAB
transcription
gene expression
gene expression
PS II
PQH2
PS I
H2O
P680
P700
e-
e-
e-
e-
PQ



LHC II
LHC II-P
energy transfer
energy transfer
PS II
PS I
PQH2
H2O
P680
P700
e -
e -
e -
e -
PQ


psbA
psaAB
psbA transcription
psaAB transcription
gene expression
gene expression
LHC II
LHC II-P
energy transfer
energy transfer
PS II
PS I
PQH_2
H_2O
P_{680}
P_{700}
e^-
e^-
e^-
e^-
PQ



Allen, J. F. (1992) BBA 1098, 275-225

On December 7, 2004, Jack Myers wrote:

Gov: I have no muse that easily turns on. The following is the best thoughts I have:

"The book encompasses a tumultous period of photosynthetic research. For those who lived through the period it will be a reminder of old arguments now moot. For those who find this part of history newly displayed it will reveal the raggedness of science in the changing of paradigms."

The End. Thank you for your attention.