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Nucleotide sequence of the second *psb*G gene in *Synechocystis* 6803

Possible implications for *psb*G function as a NAD(P)H dehydrogenase subunit gene

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Nucleotide sequencing of the second *Synechocystis* 6803 *psb*G gene, *psb*G2 shows the predicted polypeptide to be 219 amino acids long. It is less similar to chloroplast *psb*G genes than is the *Synechocystis psb*G1 copy. Alignment with seven other *psb*G protein sequences, including that from the *Paramecium* mitochondrial genome reveals a central highly conserved region common to each. This is discussed as evidence supporting the proposal that the *psb*G polypeptide is a NAD(P)H dehydrogenase (complex I) subunit in cyanobacteria, chloroplasts and mitochondria.

Cyanobacterium; Gene, *psb*G; NADH dehydrogenase; Photosynthesis; Respiration; (*Synechocystis* 6803)

1. INTRODUCTION

The *psb*G gene shows a conserved location between the *ndh*C (or *ndh*3) and an open reading frame of around 158 residues (ORF158 in *Nicotiana tabacum*) in all the chloroplast genomes in which it has been studied [1–5]. Originally Steinmetz et al. identified the *psb*G gene product to be a photosystem II (PSII) component [6]. More recently Nixon et al. have concluded it is not a PSII component and suggested instead that the *psb*G polypeptide may be a subunit of an as yet ill-defined chloroplast NAD(P)H plastoquinone-oxidoreductase [7].

Steinmüller et al. have shown that there is a *psb*G copy located between *ndh*C and 'ORF158' analogues in the cyanobacterium *Synechocystis* 6803 [4]. Previously we have shown that there is a second *psb*G gene copy residing in a 5.7 kb *Hin*dIII fragment which appears unlinked to a *ndh*C copy [8]. To avoid confusion in the literature and following the nomenclature proposals of Houmard and Tandeau de Marsac [9], we now propose to call the copy sequenced by Steinmüller et al. *psb*G1 and this second copy, for which we report the sequence here, *psb*G2. (It should be noted that we had reversed these assignments in our preliminary observations when we were unaware of parallel work.)

A *psb*G-like open reading frame in the mitochondrial genome of the ciliate *Paramecium* has been sequenced [10]. We have aligned the predicted *Paramecium psb*G protein sequence with all the photosynthetic species' *psb*G sequences currently available, including *Synechocystis psb*G2. The high degree of homology across the central region of all the *psb*G sequences strongly suggests that the *Paramecium* gene encodes a functional product and supports the proposal that the *psb*G protein is a NAD(P)H dehydrogenase (complex I) subunit in cyanobacteria, chloroplasts and mitochondria.

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This nucleotide sequence data will appear in the EMBL/Genbank/DBJJ Nucleotide Sequence Databases under the accession number X17359

2. MATERIALS AND METHODS

The strain studies was glucose-tolerant *Synechocystis* 6803 (described in [11]) from which a partial *Sau*3A λEMBL3 genomic DNA library with an insert size of 15–20 kb was prepared (both were kind gifts from Dr. J.G.K. Williams). The low stringency hybridisation conditions and specific *Triticum aestivum psb*G, *ndh*C DNA probes we used in this investigation have been previously described [8]. A 1.1 kb *Eco*RI-*Sal*I *T. aestivum* restriction fragment containing the 3′ end of ORF158 [3] was also used as a DNA probe (courtesy of Dr. P.J. Nixon). The library screening and clone analysis used established techniques (essentially as [12]). Radiolabelling of probes with ^{32}p was performed by primer extension from random oligonucleotides [13]. Dideoxy DNA sequencing was performed by subcloning fragments into M13 and using the U.S. Biochemical Corp. Sequenase sequencing kit available from Cambridge BioScience. *Psb*G protein sequences were aligned using the CLUSTAL multiple sequence alignment program [14] available on-line through Seqnet. This was particularly useful for the initial multiple alignment (fig.3) and pairwise homology comparisons. Conservative amino acid substitutions had a score of

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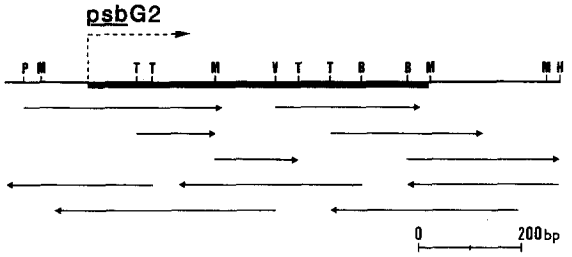

Fig.1. Sequencing strategy for the 1.05 kb *Pst*I-*Hin*cII fragment containing *psb*G2. The solid arrows indicate the direction and extent of sequencing for each M13 clone. The solid box shows the *psb*G2 coding region and the dotted arrow, the direction of predicted transcription. Restriction enzyme sites are denoted by single letters: B, *Bgl*II; H, *Hin*cII; M, *Mbo*I; P, *Pst*I; T, *Taq*I; V, *Pvu*II.

eight or over on a Dayhoff [15] matrix using this program. DNA and protein sequences were analysed using the PC/Gene microcomputer software marketed by Genofit.

3. RESULTS

The *Synechocystis* 6803 library was screened with the *T. aestivum psb*G probe using the low stringency hybridisation conditions. After two rounds of screening thirteen candidate λEMBL3 clones had been isolated. Four of these were examined further by hybridisation of extracted *Hin*dIII-restricted DNA with the *psb*G probe. Each was found to contain the 5.7 kb *Hin*dIII fragment identified in Southern blots to genomic *Synechocystis* 6803 DNA [8]. Using a variety of restriction enzymes the region of homology to the *T. aestivum psb*G probe was further localised to a 1.05 kb *Pst*I-*Hin*cII fragment within the 5.7 kb *Hin*dIII fragment. DNA sequencing (see fig.1) confirmed this was a second *psb*G gene with a sequence different to *psb*G1.

The deduced amino acid sequence sequence of *psb*G2 is 219aa long (fig.2), appearing shortened at both amino- and carboxy-termini compared to *psb*G1 (see fig.3). Initiation of translation is presumed to occur at the ATG codon shown in fig.2 which is preceded by a candidate Shine Dalgarno-like sequence [16]. If the amino-terminal methionine is post-translationally removed then the predicted mass of the gene product is 24.4 kDa. We can recognise no definite consensus upstream DNA promoter or downstream termination sequences, though these features have not been particularly well characterised in *Synechocystis* 6803.

The characterised λEMBL3 library clones were probes at low stringency with the radioactively labelled *T. aestivum ndh*C and ORF158 sequences. No positive signals were observed and it was concluded that *psb*G2 is not linked to *ndh*C or 'ORF158' gene copies within a

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AACTCGTGGGCCGGTTCCTGCCCTTGCCCTGCAGTCTTCTGTAGGAGCTTGAGCCATGGT    60
CATACCCGTGATCGCTACGGCATTCCTGCTTTAACAGGGCCGTCAATCGCGACGGTCTAA   120
                          S.D.
CTTACTCATAGACCATAGACCGCTTTAAGAGGTTTAACCATGTCCACCAGCACCCATGCC   180
                                  M  S  T  S  T  H  A

CTCACCCTTCAAAATCCCATCCAGGCACCCCAGGTGACAAAAGAATTGTCTGAGAACGTT   240
 L  T  L  Q  N  P  I  Q  A  P  Q  V  T  K  E  L  S  E  N  V

ATTCTCACCTGCCTCGACGACATCTACAATTGGGCCCGGCTCTCGACCCTGTACCCAATG   300
 I  L  T  C  L  D  D  I  Y  N  W  A  R  L  S  T  L  Y  P  M

ATGTTTGGCACCGCCTGCTGCTTTATGGAGTTCATGGCGGCTTTTGGTCCCCGCTTTGAC   360
 M  F  G  T  A  C  C  F  M  E  F  M  A  A  F  G  P  R  F  D

CTAGAGCGGTTTGGTTCCATCCCCAGGGCAACCCCCCGCCAGGCCGATCTGATGATTACC   420
 L  E  R  F  G  S  I  P  R  A  T  P  R  Q  A  D  L  M  I  T

GCTGGCACCATCACCATGAAATACGCTCCGGCTTTGGTGCAACTCTACGAACAAATTCCG   480
 A  G  T  I  T  M  K  Y  A  P  A  L  V  Q  L  Y  E  Q  I  P

GAGCCGAAATATGTCATCGCTATGGGGGCTTGTACGATTACAGCTGGTATGTTTAGTGCC   540
 E  P  K  Y  V  I  A  M  G  A  C  T  I  T  A  G  M  F  S  A

GATTCCCCCACCGCAGTTCGGGGGGTCGATAAGCTGATTCCGGTAGATGTCTACATTCCG   600
 D  S  P  T  A  V  R  G  V  D  K  L  I  P  V  D  V  Y  I  P

GGCTGCCCGCCGCGACCGGAAGCAGTCATCGACGGCATCATCAAACTCCGCAAGAAAGTT   660
 G  C  P  P  R  P  E  A  V  I  D  G  I  I  K  L  R  K  K  V

GCAGGCGAAAGCCGGCAAGACTACACCGAAGATCTGCAAACTCACAGATTCCATGCCGTG   720
 A  G  E  S  R  Q  D  Y  T  E  D  L  Q  T  H  R  F  H  A  V

CGGCACCGGATGAAGCCGGTATCCCCGATTTTGACGGGCCAATATCTTCGGCATCATGAA   780
 R  H  R  M  K  P  V  S  P  I  L  T  G  Q  Y  L  R  H  H  E

GATCTCACTCCGCACCATGACCCTTTACTCATCAAATAATCATGATCTAAGACGAATGAA   840
 D  L  T  P  H  H  D  P  L  L  I  K  -

ACGGCTGACGAGTCCGCCGCTGAATGGTTACTACTGCTGGACGGGATAGCATATCTCCAC   900
TATTCGGCCAATGGGACTGTAACGGGACAGTACGAGTTTGCAGAAACGGTTCGCCATTCG   960
TGGTGGTTAAAGGCATAGTGACTATCTCTGTTTGCCGCAGACCATTGAGTTCCCCTGGAT  1020
GTTGAACCGCCAAAAAGAGGGTTTTTTGATCCTGACTGAAGACCGGCCCTGTC         1073
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Fig.2. Nucleotide and predicted amino acid sequence of *psb*G2. Underlined is the candidate Shine-Dalgarno sequence (S.D.).

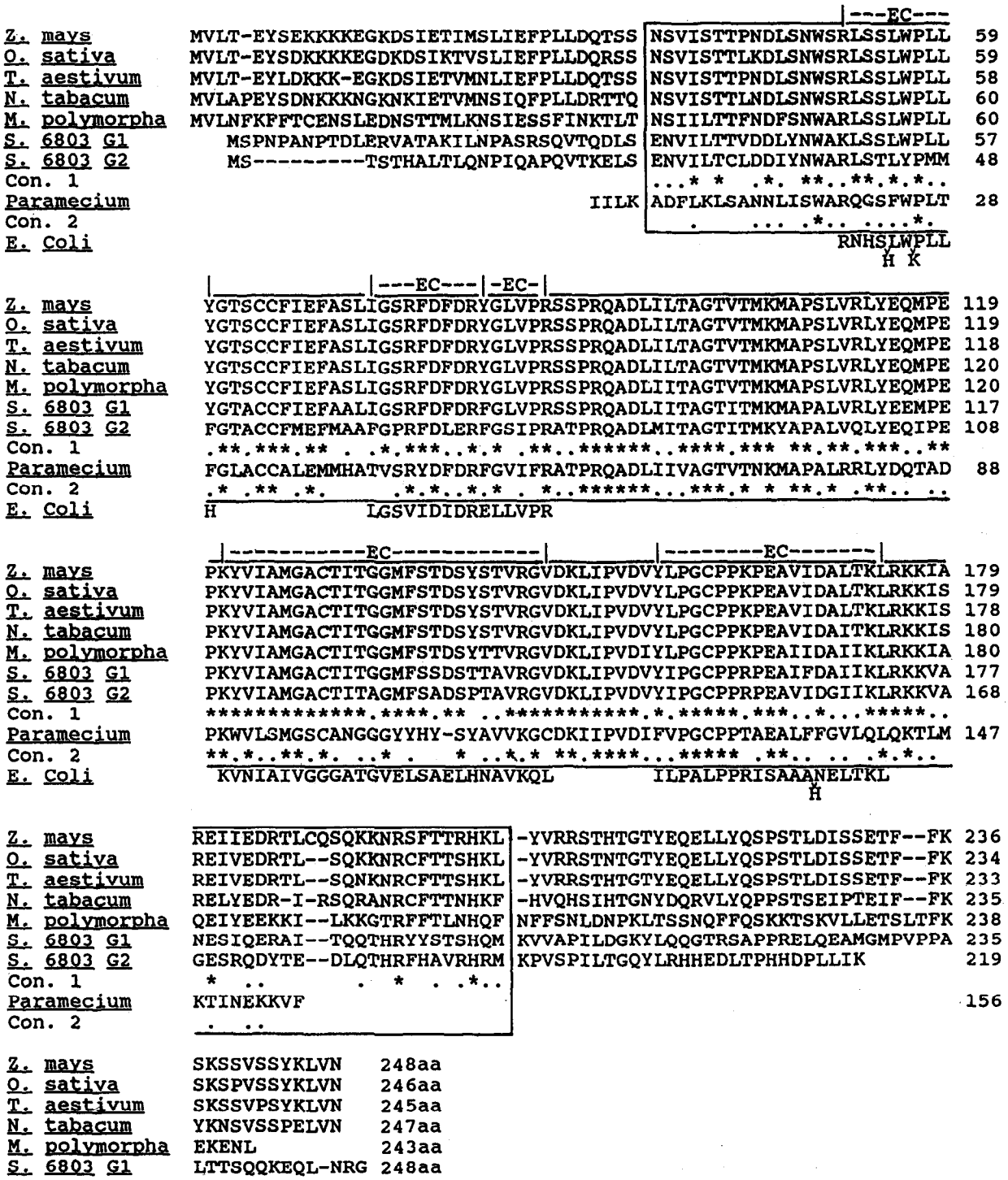

Fig.3. Alignment of predicted *psb*G polypeptide sequences. The initial alignment used CLUSTAL (Gap fixed = 10; Gap vary = 10) with final manual editing of N- and C-terminal portions. The central region, conserved across all sequences has been boxed. Con. 1 is the consensus match across the photosynthetic species sequences within the boxed area. The Con.2 match includes the *Paramecium* sequence. '*' denotes identical amino acid; '-' denotes a conservative substitution. The regions of potential homology to *E. coli* NADH dehydrogenase noted by Nixon et al. [7] are marked and the corresponding *E. coli* sequence [17] is placed below the alignment. Sequences were obtained from: *Z. mays* [6]; *Oryza sativa* [5]; *N. tabacum* [2]; *T. aestivum* [7]; *Marchantia polymorpha* [1]; *Synechocystis* 6803 *psb*G1 [4]; *Paramecium* [10].

distance of 8 kb upstream or downstream in the *Synechocystis* 6803 genome.

Fig.3 shows the alignment of *psb*G2 with the other deduced *psb*G protein sequences. From this *psb*G2 shows 63.9% identity (89.0% conservation) with *psb*G1 over its 219 residue span. Underneath the cyanobacterial and plastid *psb*G sequences a first consensus line (Con. 1) shows the identical and conserved residue posi-

Table 1

Pairwise identity comparisons for the central conserved region of the deduced *psb*G polypeptides. The number of identical residues within the central boxed region of fig.3 is expressed as a percentage of all the positions in this area (169 residues for comparisons with the *Z. mays* sequence; 167 residues for all other pairwise comparisons.) Species codes are: *Z. mays*, Z.m.; *O. sativa*, O.s.; *T. aestivum*, T.a.; *N. tabacum*, N.t.; *M. polymorpha*, M.p.; *Synechocystis psb*G1, *psb*G2, G1 and G2 respectively

	Z.m.	O.s.	T.a.	N.t.	M.p.	G1	G2
Z.m.	x						
O.s.	95.3	x					
T.a.	95.9	98.2	x				
N.t.	91.7	94.0	94.0	x			
M.p.	82.2	83.2	83.2	85.0	x		
G1	74.6	74.3	74.3	74.3	76.6	x	
G2	61.5	61.7	61.1	61.7	62.9	73.1	x

tions. This was only calculated for the boxed region as outside this central area there is no real consensus across all photosynthetic species. Over this boxed region of similarity the deduced *psb*G1 protein sequence shows greater similarity to plastid *psb*G sequences than does that for *psb*G2 (table 1). Furthermore the *psb*G1 sequence is as similar to the plastid homologues in this region as it is to the *psb*G2 sequence.

Even with this degree of divergence between the two *Synechocystis psb*G copies, certain primary structure features are very similar. There is little variation in the GC content of the *psb*G coding regions. This is 53.3% for *psb*G1 and 54.3% for *psb*G2 whilst the overall GC content of the *Synechocystis* 6803 genome is 47.5% [9]. Comparisons of amino acid composition and codon usage (data not shown) do not reveal dramatic differences which might suggest why *Synechocystis* 6803 harbours two *psb*G copies.

Hydropathicity plots for *psb*G1 and *psb*G2 are also very similar (fig.4). The use of three different methods for predicting transmembrane helices (the PC/Gene versions of Rao and Argos [19]; Eisenberg et al. [20]; and Klein et al. [21]) yields ambiguous results. It is probably that the *psb*G polypeptide is a peripheral protein (as suggested that Ohyama et al. [22]). However, if it does cross the membrane the most likely span has been marked in fig.4. This region might otherwise serve to anchor the protein in the membrane.

The *Paramecium psb*G gene sequence has also been included at the bottom of the alignment in fig.3. The lower consensus line (Con.2) includes its contributions. There is high identity between the *Paramecium* and photosynthetic species sequences (table 2) (over 10% higher than the matches between *M. polymorpha ndh*1-6 and the corresponding human mitochondrial *ND*1-6 genes [23]). On the assumption that *psb*G encodes a functional product in *Paramecium* mitochondria (see section 4), then an overall comparison of conserved positions may give useful pointers for important amino acids in the *psb*G polypeptide. Of particular in-

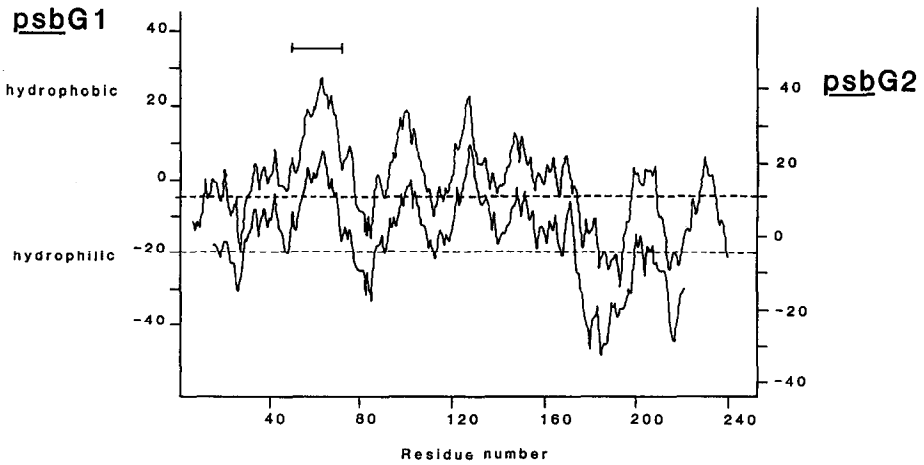

Fig.4. Hydropathicity plots of *Synechocystis* 6803 *psb*G1 and *psb*G2 generated by the PC Gene software version of the method of Kyte and Doolittle [18]. For ease of comparison the plots are shown displaced, *psb*G1 above *psb*G2. Hydropathic index is plotted against *psb*G1 residue number with the *psb*G2 plot positioned relative to *psb*G1 according to the sequence alignment of fig.3. A window size of fifteen amino acids was used. Hydropathic index values above the dotted line (centred at −5 for each plot) indicate a hydrophobic nature, those below a hydrophilic nature. The region most likely to be membrane-associated is marked with the horizontal bar (see text).

Table 2

Percentage of identical amino acids between *Paramecium* (P.) and the photosynthetic organisms deduced *psb*G polypeptide sequences. The values are calculated over the length of the *Paramecium* sequence alignment in fig.3 (157 residues). The numbers in parentheses are the percentage similarities including conservative replacements. Species codes are as table 1

	Z.M.	O.S.	T.A.	N.T.	M.P.	G1	G2
P.	44.6 (82.8)	43.9 (81.5)	44.6 (82.8)	43.9 (81.5)	47.1 (82.8)	44.6 (80.9)	42.0 (79.0)

terest are the four conserved cysteines at positions 64, 65, 129 and 160 (numbering according to the *Z. mays* sequence, see fig.3). The *psb*G polypeptide might potentially, if it is another *ndh* gene, be an iron-sulphur protein. However, the spacing of these cysteines does not conform to a 4Fe-4S consensus motif [24] or the less rigidly defined 2Fe-2S sequences [25,26]. Still, at least two could possibly form a disulphide bridge and therefore be important structurally. Also distinctive are the large number of basic residues (R-76, R-81, R-87, R-91, K-105, K-121, K-149, K-176), seven glycines and eight prolines that are conserved across all eight sequences. H-202 is present in all the photosynthetic *psb*G genes though, as it is at the periphery of the conserved block, it may be of marginal significance.

Finally, the regions of local homology between the *E. coli* NADH dehydrogenase [17] and *psb*G sequences that Nixon et al. highlighted [7] as having possible evolutionary significance have also been included in fig.3. The results are inconclusive though it can be seen that by and large the regions conserved best across all eight *psb*G sequences (denoted * in Con.2) are not those which were matched to the *E. coli* sequence segments.

4. DISCUSSION

The existence of more than one *psb*G copy in *Synechocystis* 6803 is not without precedent. Gene families encoding the D1 and D2 photosystem two reaction centre polypeptides, phycobiliproteins and linker proteins, gas vesicle proteins, and nitrogenase reductase have all been identified in various cyanobacteria (for listing, see [9]).

*Psb*G1 is transcribed in *Synechocystis* 6803 [4]. Being flanked by *ndh*C and ORF159 and with its higher degree of sequence homology *psb*G1 seems to resemble more closely plastid *psb*G copies than does *psb*G2. Work is currently in progress to determine whether psbG2 encodes a functional product. At present the degree and nature of the sequence divergence between *psb*G1 and *psb*G2 is open to two possible interpretations. Either (i) *psb*G2 is not transcribed under any conditions, or (ii) it encodes a product which may or may not function distinctly from the *psb*G1 polypeptide. In *Anacystis nidulans* UTEX 625 we have only detected one *psb*G gene using the same probe and stringency of hybridiation that readily identifies both *psb*G copies in *Synechocystis* [8]. As this appears flanked by *ndh*C it seems likely that the *psb*G2 copy is absent in *A. nidulans* UTEX 625 and thus by extension, might be a redundant copy in *Synechocystis* 6803. Against this, as fig.3 shows, most of the residues differing in *psb*G2 from the *psb*G1/plastid *psb*G consensus are conservative replacements. Also, although the *psb*G2 N- and C-termini appear shortened it has retained the central gene region well-conserved in *psb*G1 and the chloroplast copies. These observations would not necessarily be expected if the evolution of *psb*G2 was under no selective pressure.

The function of the *psb*G product is presumably similar in cyanobacteria and chloroplasts. The conclusion that it is probably a subunit of an as yet ill-defined thylakoid membrane NAD(P)H-plastoquinone oxidoreductase [7] is persuasive, irrespective of whether or not the local sequence homologies Nixon et al. highlighted between *psb*G and the *E. coli* NADH dehydrogenase are significant. Indirect evidence for the existence of a chloroplast NAD(P)H-plastoquinone oxidoreductase comes from chloroplast DNA sequence data. To date published data suggests that eight transcribed open reading frames (*ndh*1, *ndh*2, *ndh*3, *ndh*4, *ndh*41, *ndh*5, *ndh*6 and *frx*B according to the *M. polymorpha* terminology [23,27,28]) and one open reading frame, ORF392, from which transcripts have not yet been studied [29] encode thylakoid counterparts of mitochondrial NADH dehydrogenase (complex I) subunits. Recent sequencing of the gene encoding the 30kDa polypeptide of the iron-protein fraction of bovine mitochondrial complex I has revealed it has extensive homology to 'ORF158'. This means the chloroplast *psb*G and *Synechosystis psb*G1 genes are cotranscribed with two *ndh* genes (J.E. Walker, personal communication). Biochemical evidence for respiratory activity (chlororespiration, [30]) in the chloroplast thylakoid membrane has mainly come from studies on *Chlamydomonas reinhardtii* [30–32]. Recently though, chlororespiration in *N. tabacum* and *Pisum sativum* chloroplasts, involving a cyanide-sensitive terminal oxidase activity has been reported [33].

In cyanobacteria the respiratory and photosynthetic electron transport chains are known to share components within the thylakoid membrane, namely the

cytochrome b6/f complex and the soluble carriers cytochrome c-553 and/or plastocyanin. Electrons are passed through these to either P700 or the terminal oxidase (for a review see [34]). In *Anabaena variabilis* ferredoxin-NADP+ oxidoreductase acts as a specific NADPH dehydrogenase, at least in the dark [35]. A separate thylakoid membrane enzyme consisting of two principal subunits functions as a NADH dehydrogenase [36]. Both activities channel electrons to the cytochrome b6/f complex via a quinone, most likely plastoquinone. However, the discovery of *ndh*C and ORF159, open reading frames similar to *ndh*E and at least the N-terminal portion of *ndh*D (L. McIntosh, personal communication) and, we argue, *psb*G in *Synechocystis* 6803 suggests, as in the chloroplast, that another multisubunit NAD(P)H-plastoquinone oxidoreductase may be present in at least certain cyanobacteria.

In this context we suspect the presence of a *psb*G copy in the *Paramecium* mitochondrial genome (even though transcription data is not yet available) represents the discovery of another mitochondrial complex one subunit in a mitochondrial genome. This is indeed the case for the nearby ORF400 in the *Paramecium* mitochondrial genome [10]. Such an interpretation is consistent with the observations that the *Paramecium psb*G gene shows typical *Paramecium* mitochondrial gene organisation [10], yet has high homology to the region well-conserved across cyanobacterial and chloroplast *psb*G sequences. Undoubtedly it remains critical to these conclusions to identify the *psb*G product within mitochondrial NADH dehydrogenase and/or demonstrate its function within the thylakoid membrane.

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