Structure and Expression of the Chlorobium vibrioforme hemB Gene and Characterization of its Encoded Enzyme, Porphobilinogen Synthase*

(Received for publication, December 26, 1995, and in revised form, January 23, 1996)

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Plasmids containing DNA from the green photosynthetic bacterium Chlorobium vibrioforme complement a heme-requiring Escherichia coli hemB mutant that is deficient in porphobilinogen (PBG) synthase activity. PBG synthase activity was detected in extracted of complemented cells but not in that of cells transformed with control plasmid. The sequence of the C. vibrioforme hemB gene predicts a HemB protein that contains 328 amino acids, has a molecular weight of 36,407, and is 53% identical to the homologous proteins of Synechocystis sp. PCC 6301 and Rhodobacter capsulatus. The response of C. vibrioforme PBG synthase to divalent metals is unlike that of any previously described PBG synthase; Mg2+ stimulates but is not required for activity, and Zn2+ neither stimulates nor is required. This response correlates with predicted sequences of two putative variable metal binding regions of C. vibrioforme HemB. The C. vibrioforme hemB open reading frame begins 1585 bases downstream from the end of the hemD open reading frame and is transcribed in the same direction as hemA, hemC, and hemD. However, hemB is not part of the same transcription unit as these genes, and the hemB transcript is approximately the same size as the hemB gene alone. Between hemD and hemB there is an intervening open reading frame that is oriented in the opposite direction and encodes a protein with a predicted amino acid sequence significantly similar to that of inositol monophosphatase, an enzyme that is not involved in tetrapyrrole biosynthesis. The gene order within hem gene clusters is highly conserved in phylogenetically diverse prokaryotic organisms. This conservation suggests that there are functional constraints on the relative order of the hem genes.

Biosynthesis of porphyrins and related compounds proceeds via a common set of intermediates from ALA,1 the first universal precursor, through the first cyclic tetrapyrole, uroporphyrinogen III, at which point the pathway splits into two branches, one leading to reduced products such as siroheme and vitamin B12 and the other leading to oxidized end products, including hemes, bilins, chlorophylls, and bacteriochlorophylls (Fig. 1). There are two routes to ALA, one that involves the condensation of glycine and succinyl-coenzyme A and occurs exclusively in α-proteobacteria and nonphototrophic eukaryotes and the other more common pathway that begins with glutamyl-tRNA (Beale, 1995).

Although the early biosynthetic steps from ALA onward are identical in all species examined, there are some interesting differences in the properties of certain enzymes from different sources. For example, PBG synthase (also known as ALA dehydratase) obtained from different species has different metal requirements for activity (Jaffe, 1993, 1995). Another difference is that in some species, the cysG gene product, siroheme synthase, catalyzes three sequential steps in the conversion of uroporphyrinogen III to siroheme, whereas in other species, a different enzyme, S-adenosyl-L-methionine: uroporphyrinogen III methyltransferase, catalyzes only the first step, forming precorrin-2 (Spencer et al., 1993; Warren et al., 1994). Interestingly, the amino acid sequence of the methyltransferase is similar to that of the C-terminal portion of siroheme synthase (Spencer et al., 1993).

Genes for the enzymes catalyzing the early steps of tetrapyrrole biosynthesis have been cloned and sequenced from several prokaryotic species. Often, two or more of the genes are arranged in a cluster in the genome, and in some cases the clustered genes comprise a common transcription unit (Hansson et al., 1991; Jordan et al., 1988). There is wide variation among species in the identity and number of clustered hem genes, and this variation may have both regulatory significance and evolutionary implications.

Chlorobium vibrioforme is a strictly anaerobic green phototrophic bacterium. Green bacteria have been very useful for comparative and evolutionary studies of photosynthesis and related processes because they are only distantly related to other photosynthetic organisms; their photosynthetic reaction center and light harvesting apparatus are completely different from those of the other group of phototrophic anaerobes, the purple bacteria, and their mode of carbon fixation is totally unlike that of purple bacteria, cyanobacteria, or plants (Blankenship et al., 1995; Feller and Hauska, 1995; Sirevåg, 1995). Previous studies of C. vibrioforme provided the first information about the structure of tetrapyrrole biosynthetic enzymes and their genes in any strict anaerobe. C. vibrioforme has a gene cluster that contains three hem genes, hemA, hemC, and hemD, which encode glutamyl-tRNA reductase, hydroxymethylbilane synthase, and uroporphyrinogen III synthase, respectively (Majumdar et al., 1991; Moberg and Avissar, 1994). These three genes appear to comprise an operon that yields a transcript of sufficient size to encompass all three open reading frames (Majumdar et al., 1991).

We now communicate the sequence of the C. vibrioforme hemB gene, describe its positional relationship to and expression from the hemACD genes, and report on some catalytic properties of its encoded enzyme, PBG synthase.
Chlorobium Porphobilinogen Synthase

EXPERIMENTAL PROCEDURES

C. vibrioforme Cell Culture—C. vibrioforme f. thiosulfatophilum NC1B 8327 was obtained from J. G. Ormerod (University of Oslo) and grown at 30°C in the medium described by Rieble et al. (1989) in complexly filled 60- or 2400-ml bottles. Light was supplied by incandescent lamps at an intensity of 50–100 microeinsteins m−2 s−1. Cell growth was monitored by measuring the A640.

Cloning and Sequence Analysis of C. vibrioforme PBG Synthase—Encoding DNA—Esherichia coli RP523, a hemB strain (Li et al., 1988), and C600, the hemin-permeable parental strain, were obtained from B. J. Bachmann (E. coli Genetic Stock Center, Yale University, New Haven, CT). Recombinant plasmid pYA1 containing 5.8 kilobases of Sau3A1-digested C. vibrioforme genomic DNA inserted into the BamHI site of pBluescript SK(+) vector (Stratagene, La Jolla, CA) was constructed as described previously (Avissar and Beale, 1990). Plasmid pYA4 containing 2.8 kilobases of C. vibrioforme genomic DNA was derived from pYA1 by digestion with SalI and ligation with SalI-digested pBluescript SK(+) vector.

DNA sequencing of the 2.8-kilobase insert of pYA4 was done in both directions using an fmol DNA sequencing kit (Promega, Madison, Wisc.) according to the manufacturer’s protocol. Sequence information was compiled with the MacVector DNA sequence analysis program (Eastman Kodak Co.).

Analysis of the hemB Transcript—C. vibrioforme cells were harvested in the mid-exponential growth phase (A600 = 0.5–0.6) by centrifugation at 5000 × g for 15 min at 4°C. Total cellular RNA was isolated using the TRI reagent (Molecular Research Center, Inc., Cincinnati, Ohio) according to the manufacturer’s protocol. Glyoxal-denatured total cellular RNA (8 µg) was separated on 0.9% (w/v) agarose gels in duplicate. One set, including an RNA marker (Life Technologies, Inc.), lane was stained with ethidium bromide to confirm the RNA integrity and to determine the size of the transcript. The other set was transferred to a Nytran nylon membrane (Schleicher & Schuell) in 20 × SSPE. The blot was UV cross-linked and probed in 50% (v/v) formamide/5 × SSPE/2 × Denhardt’s reagent/5% (w/v) SDS/50 µg/ml salmon sperm DNA at 45°C and washed in 2 × SSPE/0.1% (w/v) SDS at 50°C followed by a final wash in 0.2 × SSPE/0.1% (w/v) SDS at 55°C.

As a probe for Northern hybridizations, a 827-bp fragment of pYA4 containing most of the C. vibrioforme hemB coding region was prepared by polymerase chain reaction using the oligonucleotides 5′-GCATCGC-CCGAGAAG-3′ and 5′-TCACCATGCGCTTATCG-3′ for the sense and antisense primers, respectively. The 827-bp fragment was purified by electrophoresis in low melting point agarose followed by elution and phenol extraction and labeled with [32P]dATP by the nick translation method using a kit obtained from Life Technologies, Inc.

PBG Synthase Enzyme Assay—E. coli and C. vibrioforme cells were harvested in the mid-exponential growth phase by centrifugation for 15 min at 5000 × g and resuspended in extraction buffer consisting of 100 mM Bis-Tris-Propane-HCl, pH 8.5, 10 mM β-mercaptoethanol, and 0.004% (w/v) phenylmethylsulfonyl fluoride at a concentration of 1 g of packed cells/2 ml of buffer. 1 g of 5-µm diameter glass beads was added per g of packed cells, and the cells were broken by sonication (ten 15-s bursts separated by 45-s cooling periods). Cell debris and glass powder were removed by centrifugation for 10 min at 10,000 × g. The pellet was washed once with an equal volume of extraction buffer and centrifuged, and the supernatants were combined. The C. vibrioforme extract was purified further by centrifugation for 60 min at 285,000 × g, and the soluble proteins in the supernatant were separated from small molecules by chromatography through a Sephadex G-25 column that had been pre-equilibrated with extraction buffer. Extracts were stored as 1-ml aliquots at −80°C until use.

The standard incubation medium contained 100 mM Bis-Tris-Propane-HCl, pH 8.5, 1 mM β-mercaptoethanol, 10 mM ALA, 50 mM KCl, 10 mM MgCl2, and cell extract (additions and variations are described under “Results and Discussion”). Incubation was for 15 or 30 min at 32°C in a total volume of 0.5 ml. Incubations were stopped by the addition of 0.5 ml of modified Ehrlich-Hg reagent (Urata and Granick, 1963) and mixing. The mixture was clarified by centrifugation for 2 min in the microcentrifuge, and the absorbance was recorded at 555 nm between 5 and 15 min after the addition of the modified Ehrlich-Hg reagent. The PBG concentration was calculated using a molar absorption value of 68,000 (Urata and Granick, 1963).

Table I

| Strain | Without hemin | With hemin |
|-------|---------------|------------|
| C600  | +             | +          |
| RP523 | -             | +          |
| RP523pBluescript SK(+) | - | + |
| RP523pYA1 | + | + |
| RP523pYA3 | - | + |
| RP523pYA4 | + | + |

RESULTS AND DISCUSSION

Cloning of C. vibrioforme hemB—It was previously shown that pYA1 contains 5.8 kilobase pairs of C. vibrioforme genomic DNA that is capable of complementing heme-dependent E. coli strains that are deficient in glutamyl-tRNA reductase (hemA) and uroporphyrinogen III synthase (hemD), and a Salmonella typhimurium strain that is deficient in hydroxymethylbilane synthase (hemC) (Majumdar et al., 1991; Moberg and Avissar, 1994). pYA1 was subcloned into approximately equal size
halves, pYA2 and pYA4 (Avissar and Beale, 1990). pYA2 was able to complement an E. coli hemA strain, and partial sequencing showed that it contains an open reading frame encoding the entire C. vibrioforme hemA gene (Majumdar et al., 1991). Further sequencing revealed that hemA, hemC, and hemD form a compact cluster in the C. vibrioforme genome (Majumdar et al., 1991). We now report that both pYA1 and its subclone pYA4 complement a heme-requiring E. coli strain RP523 (Li et al., 1988) (Table I). In contrast, neither the pBluescript SK(+) vector nor pYA3, a subclone of pYA1 that contains C. vibrioforme hemA and part of hemC, was able to complement RP523.

To verify that the complementation was caused by the expression of hemB, complemented RP523 cells were examined for the presence of PBG synthase activity. This verification was necessary because in some cases pseudo-complementation can be caused by overexpression of other hem genes. For example, overexpression of C. vibrioforme hemA in an E. coli hemL strain leads to heme-independent growth. This pseudo-complementation presumably results from nonenzymatic con-

**Table I**

| Strain         | Additions to growth medium | PBG formation |
|---------------|---------------------------|--------------|
| C600          | none                      | 0.49         |
| RP523/pBluescript SK(+) | ampicillin + hemin        | 0.00         |
| RP523/pYA4    | ampicillin                | 0.76         |
| RP523/pYA4    | ampicillin + hemin        | 0.75         |

**Table II**

| Strain Additions to growth medium | PBG formation |
|----------------------------------|--------------|
| C600 none                        | 0.49         |
| RP523/pBluescript SK(+) ampicillin + hemin | 0.00         |
| RP523/pYA4 ampicillin            | 0.76         |
| RP523/pYA4 ampicillin + hemin    | 0.75         |

FIG. 2. Nucleotide sequence of a 2872-bp cloned C. vibrioforme genomic DNA insert in pYA4, the deduced peptide sequence for the C-terminal 60 amino acids of the hemD gene product, and the deduced peptide sequence for the complete 328-amino acid hemB gene product. Stop codons are indicated by asterisks. For hemB, the −10 (Pribnow box) consensus sequence is indicated by asterisks, and a potential −35 region consensus sequence is indicated by double underlining. For hemD, putative metal binding sites B (residues 122−140) and C (residues 228−238) and the active site lysine (residue 253) are indicated with single underlining. Putative rho-independent transcription termination sequences downstream from the ends of hemD and hemB are shown in bold letters with the palindromic regions indicated by arrowheads. The GenBank accession number is U38348.

D. Majumdar and J. H. Wyche, unpublished results (GenBank accession number M96364).

Y. J. Avissar, unpublished results.
had PBG synthase levels comparable with those of the human.

In contrast, extracts of RP523 cells that were complemented with the pBluescript SK(+) vector were devoid of PBG synthase activity. Because it was necessary to add heme to the medium of uncomplemented RP523 cells to obtain growth, it was possible that the absence of PBG synthase in RP523 cell extract was due to repression of its formation or inhibition of its activity caused by the added heme. Therefore, PBG synthase activity was determined in extracts of RP523 cells that were transformed with pYA4 but grown in the presence of added heme. These cells had levels of PBG synthase activity equal to that of complemented cells grown without added heme. We therefore conclude that the complete absence of PBG synthase activity in uncomplemented RP523 cells is not caused by the heme added to the medium and that the activity in RP523 cells complemented by pYA4 is attributable to the expression of C. vibrioforme hemB in the transformed cells.

In the previous complementation studies with C. vibrioforme hemA, hemC, and hemD (Avissar and Beale, 1990; Moberg and Avissar, 1994), there was some uncertainty about whether the transcription of these genes in E. coli cells was directed by promoter elements on the C. vibrioforme DNA or from the lac promoter on the pBluescript SK(+) vector. For hemB, the size of the transcript (see below) indicates that transcription begins well within the inserted DNA, approximately 1750 bp from the beginning of the inserted C. vibrioforme DNA (Fig. 2). Furthermore, there is a transcription stop signal between the end of the hemD gene and the beginning of the hemB gene. Therefore, it is likely that the C. vibrioforme promoter for the hemB gene can function in E. coli sufficiently well to cause complementation and produce measurable PBG synthase activity in cell extracts.

Sequence of C. vibrioforme hemB—The sequence of the C. vibrioforme DNA in pYA4 indicates that its size is 2872 bp and that it contains the 3' portion of the hemD gene encoding the C-terminal 60 amino acids of uroporphyrinogen III synthase and a downstream open reading frame encoding the complete hemB gene product, PBG synthase (Fig. 2). The partial hemD sequence is identical to that of the hemD sequence reported previously.2 The beginning of the hemB open reading frame is separated from the end of the hemD open reading frame by 1585 bp. Potential −10 (Pribnow box) and −35 region consensus sequences are present upstream of the beginning of the hemB open reading frame. However, a recognizable translation initiation (Shine-Dalgarno) sequence was not found. It should be noted that a Shine-Dalgarno sequence also could not be identified for the C. vibrioforme hemA gene (Majumdar et al., 1991).

The deduced C. vibrioforme HemB sequence is significantly similar to all published PBG synthase sequences. The most similar sequence in the GenBank database is that of Synechocystis (Syn.) sp. PCC 6301 PBG synthase (GenBank accession number X70434), and the least similar PBG synthase sequence in the GenBank database, that of the human enzyme (GenBank accession number M13928).

version of glutamate-1-semialdehyde to ALA, which can occur at high glutamate-1-semialdehyde concentrations (Hoober et al., 1988).

Extracts of RP523 cells that were complemented with pYA4 had PBG synthase levels comparable with those of the hemB parental strain C600 (Table II). In contrast, extracts of RP523 cells that were complemented with the pBluescript SK(+) vector were devoid of PBG synthase activity. Because it was necessary to add heme to the medium of uncomplemented RP523 cells to obtain growth, it was possible that the absence of PBG synthase in RP523 cell extract was due to repression of its formation or inhibition of its activity caused by the added heme. Therefore, PBG synthase activity was determined in extracts of RP523 cells that were transformed with pYA4 but grown in the presence of added heme. These cells had levels of

FIG. 3. Comparison of the deduced amino acid sequence of C. vibrioforme (C. vib.) hemB with the most similar sequence in the GenBank database, that of Synechocystis (Syn.) sp. PCC 6301 PBG synthase (GenBank accession number X70434), and the least similar PBG synthase sequence in the GenBank database, that of the human enzyme (GenBank accession number M13928).

FIG. 4. pH dependence of C. vibrioforme PBG synthase activity. Gel-filtered C. vibrioforme extract was incubated for 15 min at 32°C in 0.5 ml of medium containing 100 mM Bis-Tris-Propane (buffered to the indicated pH with HCl), 1 mM β-mercaptoethanol, 10 mM ALA, 50 mM KCl, 10 mM MgCl₂, and cell extract (43 μg of protein).
bation medium are inhibited by EDTA, which presumably re-
moves the comparatively loosely bound metal atoms at the 
second site. Among the PBG synthases that require Zn\(^{2+}\)
in the incubation medium, some (e.g. that from E. coli) but not all 
are stimulated approximately 2-fold by Mg\(^{2+}\), which is pro-
posed to bind at a third site on the protein. Finally, a fourth 
class of PBG synthase, represented by the enzyme from Rho-
dobacter capsulatus, neither requires nor is stimulated by 
micromolar concentrations of either Zn\(^{2+}\) or Mg\(^{2+}\) (Nandi and 
Shemin, 1973).

C. vibrioforme PBG synthase has a broad pH optimum 
centered at pH 8.5 (Fig. 4). The C. vibrioforme enzyme appears 
to represent a new class of PBG synthase with respect to the 
effects of divalent metals. The gel-filtered enzyme does not 
require the addition of either Zn\(^{2+}\) or Mg\(^{2+}\) for activity, but it 
is stimulated approximately 2–3-fold (depending on the incu-
bation pH) by Mg\(^{2+}\) (Table III). Zn\(^{2+}\) is inhibitory. K\(^{+}\) is some-
what stimulatory in the absence of Mg\(^{2+}\), especially at the 
higher incubation pH, but K\(^{+}\) does not stimulate in incubations 
containing Mg\(^{2+}\). The absence of inhibition by EDTA rein-
forces the conclusion that activity does not require Zn\(^{2+}\) or 
Mg\(^{2+}\) in the incubation medium.

In one model that attempts to relate protein structural fea-
tures to divalent metal effects, PBG synthase is proposed to 
have three metal binding sites (Jaffe, 1993, 1995). Site A, 
which is proposed to bind Zn\(^{2+}\) very tightly in all PBG syn-
thases, has not been identified. Site B (Fig. 5) in the Zn\(^{2+}\)-
requiring enzymes has several cysteine and histidine residues, 
which are replaced by carboxyl-containing residues in the 
Mg\(^{2+}\)-requiring enzymes. Site C has several carboxyl-
containing residues in the Zn\(^{2+}\)-requiring enzymes that are 
stimulated by Mg\(^{2+}\), and these residues are absent from the 
enzymes that are not stimulated by Mg\(^{2+}\). For the Mg\(^{2+}\)-
requiring enzymes, it is difficult to determine experimentally 
whether Mg\(^{2+}\) additionally stimulates by binding at site C.

The responses of C. vibrioforme PBG synthase to divalent 
metals correlate well with the structures of the putative metal 
binding sites B and C (Fig. 5). Site B of the C. vibrioforme 
enzyme most closely resembles that of R. capsulatus PBG 
synthase, an enzyme that has no requirements for divalent 
metals in the incubation medium. However, site C of the C. vibrio-
forme enzyme more closely resembles those of Zn\(^{2+}\)-requiring 
PBG synthases that are stimulated by Mg\(^{2+}\). In summary,
these results for C. vibriiforme PBG synthase provide strong support for the model identifying metal binding sites B and C. 

PBG synthase from some bacteria has been reported to be allosterically inhibited by heme, a tetrapyrrole end product (Nandi et al., 1968). The effect of heme on C. vibriiforme PBG synthase activity was tested in incubations done at pH 8.5 in the presence of 50 mM K+ and 10 mM Mg2+. In this experiment, heme was added to the incubation mixture from a concentrated stock solution in dimethyl sulfoxide, and all incubations contained the same dimethyl sulfoxide concentration (2%, v/v). PBG synthase activity was not inhibited even by 100 μM heme, the highest concentration tested (data not shown).

Expression of C. vibriiforme hemB—A Northern blot of C. vibriiforme RNA probed with a hemB-specific probe reveals a single 1.0-kilobase band (Fig. 6). Because this hemB transcript corresponds in size to the hemB gene, this result indicates that hemB mRNA is not a part of a larger, multigene transcript. This result is consistent with the absence of significant open reading frames between the end of the hemD gene and the beginning of the hemB gene, a distance of 1585 bp, and the presence of rho-independent transcription terminators closely downstream from both hemD and hemB (Fig. 2). In contrast, transcription terminators are not present between hemD and hemC or between hemC and hemD, and these three genes appear to be co-transcribed (Majumdar et al., 1991).

Location of C. vibriiforme hemB Relative to Other hem Genes—The sequence of pYA4 indicates that hemB is located 1585 bp away from the end of hemD and is transcribed in the same direction as the genes in the hemACD cluster (Fig. 2). However, the distance between hemD and hemB suggests that although the genes are clustered on the C. vibriiforme chromosome, they are unlikely to be part of the same operon. Moreover, between hemD and hemB there is a 786-bp open reading frame oriented in the opposite direction. This open reading frame encodes a protein that has a high degree of similarity to inositol monophosphatase (Matsuhisa et al., 1995; McAllister et al., 1992), an enzyme that is unrelated to tetrapyrrole biosynthesis (Fig. 7). The putative C. vibriiforme inositol monophosphatase is 28.9 and 27.8% identical to the human and E. coli enzymes, respectively. The significance of the location of this gene between two hem genes in C. vibriiforme is unknown.

The clustering of hem genes is common in bacteria (Fig. 8) and may have regulatory as well as evolutionary implications. For example, the widespread close clustering and cotranscription of hemC and hemD probably ensures the presence of the hemD product, uroporphyrinogen III synthase, whenever the hemC product, hydroxymethylbilane synthase, is present. The activity of uroporphyrinogen III synthase is necessary to direct the conversion of hydroxymethylbilane to the physiologically relevant product uroporphyrinogen III and prevent its spontaneous conversion to uroporphyrinogen I, a nonphysiological dead-end product. Extreme regulatory coordination is found in
The extent of sequenced regions is indicated by horizontal lines, open reading frames of identified and putative genes are indicated by boxes, and the deduced directions of transcription are indicated by arrows. For ease of comparison, the sequences are arbitrarily aligned at the beginning of the hemC open reading frame, except in the case of the Synechocystis sp. PCC 6301 cluster, which does not contain hemC. In this case, the end of the cobA open reading frame is aligned with the end of the cysG open reading frames of C. josui and Mycobacterium leprae to indicate that the CofA sequence is similar to the C-terminal end of the CysG sequence. The GenBank accession numbers are: C. vibrioforme (M96364, U83384), B. subtilis (M57676), E. coli (X12614), Pseudomonas aeruginosa (M74844), Synechocystis sp. PCC 6301 (X70434), C. josui (D28503), M. leprae (U00018).

Acknowledgments—We thank B. J. Bachmann and J. G. Ormerod for supplying strains and D. L. Bolliwer, E. K. Jaffe, G. L. Matters, M. O’Connor, and J. Park for helpful advice and discussions.

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