Acinetobacter calcoaceticus Genes Involved in Biosynthesis of the Coenzyme Pyrrolo-Quinoline-Quinone: Nucleotide Sequence and Expression in Escherichia coli K-12

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Synthesis of the coenzyme pyrrolo-quinoline-quinone (PQQ) from Acinetobacter calcoaceticus requires the products of at least four different genes. In this paper we present the nucleotide sequence of a 5,085-base-pair DNA fragment containing these four genes. Within the DNA fragment three reading frames are present, coding for proteins of M_r 10,800, 29,700, and 43,600 and corresponding to three of the PQQ genes. In the DNA region where the fourth PQQ gene was mapped the largest possible reading frame encodes for a polypeptide of only 24 amino acids. Still, the expression of this region is essential for the biosynthesis of PQQ. A possible role for this DNA region is discussed. Sandwiched between two PQQ genes an additional reading frame is present, coding for a protein of M_r 33,600. This gene, which is probably transcribed in the same operon as three of the PQQ genes, seems not required for PQQ synthesis. Expression of the PQQ genes in Acinetobacter lwoffi and Escherichia coli K-12 led to the synthesis of the coenzyme in these organisms.

Pyrrolo-quinoline-quinone (PQQ) is used by a variety of organisms as cofactor in dehydrogenase reactions. In *Pseudomonas* species and *Acinetobacter calcoaceticus* PQQ is associated with glucose dehydrogenase (GDH) (1, 5, 22). In *Pseudomonas testosteroni* (7) and *Pseudomonas stutzeri* (M. van Kleef, personal communication) and PQQ-dependent alcohol dehydrogenase is present. *Thiobacillus versutus* (19) and *Paracoccus denitrificans* (2) synthesize methylamine dehydrogenase, to which PQQ is covalently linked.

Also in mammals the presence of PQQ as cofactor has been demonstrated. In bovine plasma (10, 15) and porcine kidney (20) PQQ-dependent amine oxidases have been identified, and it has been suggested (4, 15) that amine oxidases from other mammals, *Saccharomyces cerevisiae*, *Aspergillus*, and plants also use PQQ as a coenzyme.

In some bacterial species, viz., A. calcoaceticus, PQQ is synthesized constitutively in the absence of the enzyme's substrate (i.e., glucose), whereas in P. stutzeri PQQ can be detected only when ethanol is present in the culture medium as an inducing agent (M. van Kleef, personal communication). Escherichia coli K-12 and Acinetobacter lwoffi do not produce PQQ. These organisms synthesize the apo-GDH enzyme and are dependent on uptake of PQQ from the culture medium for the constitution of the holo-GDH (8, 21).

The biosynthetic pathway of PQQ has not yet been elucidated. Our approach to this problem was to clone the genes and to study the encoded gene products that are involved in PQQ synthesis. Recently we reported the isolation of a plasmid containing four cloned PQQ genes from A. calcoaceticus on a 5,000-base-pair (bp) fragment (6). In this paper we report the complete nucleotide sequence of this fragment and show that the genes from A. calcoaceticus can direct the synthesis of the cofactor in other microorganisms.

MATERIALS AND METHODS

Bacterial strains and culture conditions. The following bacterial strains have been previously described: *E. coli* JM101 (Δlac -pro thi F'traD36 proAB lacI^qZ Δ M15) (13), *E.*

coli PPA41 (thi ptsI) (8), and A. lwoffi (21). These strains were cultured in L broth, on L plates, or in defined minimal medium (14) as indicated. Bacterial matings were performed as described previously (6). Acid production by A. lwoffi was tested on L plates containing 0.4% glucose and a few drops of phenol red. Acid production resulted in yellow plates, whereas the plates of non-acid-producing strains remained red.

Chemicals and reagents. Restriction endonucleases were from Bethesda Research Laboratories, Inc. T4 DNA ligase and DNA polymerase (Klenow enzyme) were from Pharmacia Fine Chemicals. All recombinant DNA techniques were essentially as described previously (12). Purified PQQ was a gift from M. van Kleef. The universal primer for DNA sequencing (5'-GTAAAACGACGGCCAGT-3') was purchased from Pharmacia. The oligonucleotide primer corresponding to the Tn5 end sequences (5'-GGTTCCGTTCAG GACGCTAC-3') was kindly synthesized by J. H. van Boom. Radiochemicals and in vitro coupled transcriptiontranslation kits were from Amersham Corp.

DNA sequencing. Transformation of strain JM101 was performed as described previously (13). M13 phage particles were purified, and the single-stranded DNA was extracted by the method of Sanger et al. (16). For the sequencing reaction the primer extension method (17) was used. Sequences were compiled and analyzed by using the sequence analysis software package of the University of Wisconsin Genetics Computer Group (3).

Sequence strategy. A schematic representation of the sequence strategy is indicated in Fig. 1. The *Eco*RI-*Bam*HI fragment of pSS2, containing the four PQQ genes, was subcloned in M13mp19, resulting in pSS144. Deletion derivatives for DNA sequencing were isolated by an adaptation of the method of Hong (9). pSS114 was partially digested with *Sau*3A, *Rsa*I, or *Dra*I. Linear fragments were isolated, digested with *Bam*HI (for *Sau*3A) or *Hinc*II (for *Rsa*I and *Dra*I), recircularized, and transformed to JM101. Thus the different *Sau*3A, *Rsa*I, and *Dra*I sites were brought close to the primer for sequencing.

For sequencing of the opposing strand, different subclones

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FIG. 1. Schematic representation of the sequencing strategy. Plasmid pSS2, containing a 5.5-kb Sau3A insert in the Bg/II site of vector pRK290, has been described previously (6). Only restriction sites that occur with low frequency are indicated: a, AccI; b, BamHI; bgi, Bg/I; bgii, Bg/II; e, EcoRI; h, HindIII; hp, Hpa1; m, Mlu1; mi, Mst1; mii, Mst1I; n, NcoI; p, PvuII; s, SacI; sa, Sau3A; sp, SphI. pSS144 contains the EcoRI-BamHI fragment in M13mp19, pSS111 contains the HindIII fragment in M13mp19, pSS112 has the HindIII-BamHI fragment in M13mp18, pSS150 has the EcoRI(SalI)-SphI fragment in M13mp19, pSS116 contains the HindIII fragment in M13mp18, and pSS151 carries the SphI-BamHI fragment in M13mp18. The arrows show the location, direction, and length of nucleotide sequence obtained from each template.

were constructed. First the internal 2,600-bp *Hin*dIII fragment of pSS2 was cloned into M13mp19, the correct orientation was selected (pSS111), and deletion derivatives were isolated as described above. A *Sal*I linker fragment was inserted into the *Eco*RI site of pSS2, and then the 1,900-bp *SalI-SphI* fragment was subcloned in M13mp19 (pSS150). Also from pSS150 deletions were constructed by the method described above. The remaining right part of the *Eco*RI-*Bam*HI fragment was sequenced by subcloning the 210-bp *Hin*dIII fragment and the 320-bp *Hin*dIII-*Bam*HI fragment in M13mp18 (pSS116 and pSS112, respectively). Finally, the gap between *SphI* and *Hin*dIII was sequenced by insertion of the *SphI-Bam*HI fragment in M13mp18 (pSS151).

RESULTS

Nucleotide sequence of the PQQ genes. Plasmid pSS2 contains a 5.5-kilobase insert from the A. calcoaceticus chromosome which complements four different classes of chromosomal PQQ⁻ mutants and which is therefore expected to carry four different genes involved in PQQ synthesis (6). With Tn5 insertions these cloned genes (I, II, III, and IV) were approximately mapped within a 5-kilobase EcoRI-

BamHI fragment (6). We determined the complete nucleotide sequence of this fragment as described in Materials and Methods. It was comprised of 5,087 bp and showed a rather high A+T content (61%). Within the sequenced fragment different open reading frames (ORFs) were indicated. The complete nucleotide sequence and the deduced amino acid sequence of the ORFs are reported in Fig. 2, and a schematic representation of the ORFs is given in Fig. 3.

To determine whether these ORFs correspond to the different PQQ genes, we also determined the precise insertion points of the Tn5 insertions. Therefore the pSS2-Tn5 plasmids were restricted with *Eco*RI and *PstI*. Since *Eco*RI cuts at the left border of the 5-kilobase fragment (Fig. 1) and *PstI* cuts within Tn5, a fragment was generated containing one end of Tn5 and the PQQ sequences located to the left of the insertion point. This fragment was inserted into M13mp18, and the fusion point was sequenced by using a synthetic oligonucleotide (5'-GGTTCCGTTCAGGACGC TAC-3') that was complementary to the end of Tn5 as a primer. As a control also the *Bam*HI-*PstI* fragment containing the other end of Tn5 fused to PQQ sequences located to the right of the insertion point was cloned and sequenced. In

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this way the insertion points of nine different Tn5 insertions were determined (Fig. 2). The phenotypes of the pSS2 plasmids containing these Tn5 insertions (13) are listed in Table 1.

Transposon insertions Tn5-16, Tn5-20, and Tn5-7 were located within an ORF (indicated as gene V) starting with

ATG (position 1010) and ending with TAA (position 1921), which could code for a protein of M_r 33,600. It has been shown that chromosomal deletion mutants that lack the complete PQQ region (including gene V) can still be complemented by these Tn5 insertions (13). Apparently gene V is not involved in PQQ biosynthesis.

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Transposon insertion Tn5-17 inhibited the expression of both gene I and gene II (Table 1). We have suggested (6) that these two genes are located in the same operon and that, due to a polar effect on transcription, Tn5 affects expression of both genes. Indeed in the DNA sequence two ORFs were indicated that were closely linked. The first ORF (gene I) started at ATG (position 1930), ended at TGA (position 2688), and coded for a protein of M_r 29,700. Insertion Tn5-17 was located within this ORF. The stop codon (TGA) of gene I overlapped with the start ATG (position 2685) of a second ORF (gene II) that stopped at TGA (position 2969), coding for a protein of M_r 10,800. This overlap of start and stop

											36	00																365	0				
Gli CA GI	n G A G I C	lu (AG (IC (Gln CAA GIT	<i>Leu</i> CTG GAC	Thr ACA TGT	Ang OGA OCT	Ala GCI CGA	Glu GAA CIT	Arg CCC CCC	<i>Ile</i> ATT TAA	Thr ACC TGG	Asn AAT TTA	Glu GAA CIT	<i>Tyr</i> Tat Ata	Arg CCA CCT	Glu GAA CTT	<i>Lys</i> AAA TTT	<i>Leu</i> TTA AAT	<i>Lys</i> AAA TTT	Ala 603 030	Gln CAA GIT	ASN AAT TTA	His CAC GIG	Pro CCT GGA	Cys TGC ACG	<i>Lys</i> AAA TIT	Leu CIC GAG	Ile ATT TAA	Phe TTT AAA	Val GIT CAA	Val GIG CAC	Pro CCC GGG	Asp GAT CTA
											3																	3	750				
Ty. TA AI	r T T T A A	yr At TA	Glu GAG CIC	Glu GAA CIT	Arg CGA CCI	Pro CCA GGT	Lys AAA TIT	Ala GCC CGG	Cys TGI ACA	Met ATG TAC	Asn AAT TTA		Trp TGG ACC	<i>Gly</i> GGT CCA	<i>Lys</i> AAA TIT	Ile ATC TAG	Phe TTC AAG	Phe TIT AAA	Thr ACG TGC	Val GIT CAA	Ala GCT CGA	Pro CCA GGT	Asp GAT CTA	Gly GGT CCA	Met ATG TAC	A1a 600 000 000	Leu CIA GAT	Pro OCT GGA	Cys TGC ACG	His CAT GTA	Ala GCA CGT	Ala GCA CGT	Arg CGA CCT
												380																-	1850				
G1 CA GI	n L A C T G	eu TG AC	Pro CCC GGG	Ile ATT TAA	Ser TOG AGC	Phe TTT AAA	Pro 000 000 000	Asn AAT TTA	Val GIC CAG	Ang 030 030 030	Glu GAA CIT	His CAT GTA	Lys AAA TIT	Leu TIG AAC	Ser TCA AGT	Asp GAT CTA	<i>Ile</i> ATT TAA	Trp TGG ACC	Tyr TAC ATG	<i>Lys</i> AAA TTT	Ser TCA AGT	Thr ACT TGA	Gly GGA CCT	<i>Phe</i> TTT AAA	Asn AAT TTA	<i>His</i> CAT GTA	Phe TIC AAG	Arg CGT GCA	61y 600 000	Asp GAT CTA	<i>Ala</i> 600 000	Trp TGG ACC	Met ATG TAC
												39																	393				
Pr 80 80	ØG AG TC	lu AA TT	<i>Cly</i> 000 000	Cys TGC ACG	Ang OGI OCA	Ser AGC TOG	Cys TGI ACA	Pro CC CC CC CC CC CC CC CC CC CC CC CC CC	Asp GAT CTA	<i>Lys</i> AAA TTT	Asp GAT CIA	Arg CGT CCA	Asp GAC CIG	<i>Phe</i> TTT AAA	61y 600 000	Gly OGA CCT	Cys TGT ACA	Arg OGT OCA	Cys TGT ACA	Gln CAG GIC	Ala 600 006	<i>Tyr</i> TAT ATA	Met ATG TAC	Leu TIG AAC	Thr ACT TGA	Gly OGA CCI	Asp GAT CIA	Ala 600 000 000	Ala GCT CGA	Asn AAT TTA	<i>Ala</i> GCC CCG	Asp GAT CTA	Pro OCT GGA
												4	000																40	50			
Va GI CA		ys gi ca	61y 000 000	Lys AAA TTT	Ser TOG AGC	Pro 000 000	<i>Tyr</i> TAT ATA	<i>His</i> CAT GIA	Gln CAA GIT	Met ATG TAC	<i>Ile</i> ATT TAA	Glu GAA CTT	GIn CAA GIT	Ala GCA CGT	Arg 000 000	Ala GCA CGT	Glu GAA CTT	Ser AGT TCA	Gln CAG GIC	Leu TIG AAC	Val GIT CAA	Ala GCA OGT	Pro OCT GGA	<i>Leu</i> CTA GAT	Gln CAA GIT	Asn AAT TTA	Leu TTA AAT	Val GIC CAG	<i>Phe</i> TTC AAG	Arg OGT OCA	Asn AAT TTA	Ser AGT TCA	Arg AGA TCT
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												42	200																425	60			
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												4	300																43	350			
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															4900																49	950	
TT AC TC		isp AC TG	Pro OCA GGI	G1n CAG GIC	Leu CII GAA	Lys AAA TTT	Ala GCA CGI	Ile ATA TAT	Ang OGC GCG	Glu GAA CTT	Ser AGT TCA	Lys AAA TTT	<i>61y</i> 000 000	Met ATG TAC	Val GIG CAC	61y 600 000	Val GIA CAT	Asn AAT TTA	Phe TTC AAG	Asp GAT CIA	Val GIC CAG	Al CCI CCA	Phe TIT AAA	Leu TTA AAT	Arg 000	Ser TCA AGI	Asp GAI CIA	Gly GGA CCI	Gln CAA GIT	Arg CGA CCT	Asn AAT TTA	Ala OCA OCT	Asp GAT CTA
															50	00															!	5050	
TI AC T		Ser IOG VGC	<i>Ile</i> ATT TAA	Asp GAT CTA	Val GIA CAI	Ile ATT TAA	Leu TIG AAC	GAA GAA CTI	HIS CAT GTA	Leu TIA AAT	GAA GAA CIT	Tyr Tat Ata	Leu TIA AAI	Met ATG TAC	Asp GAT CTA	Ari 000	Val GII GCAA	Ala GCI CGA	Pro OCT GGA	Leu CTI GAA	Leu CTC GAG	His CAT GTA	Pro 000 000	Arg OGI CCA	Ser TCC AGG	Lys AAG TTC	E Let CTC GAC	Ang 000 000	Lys AAA TTT	61y 000	Thr ACC TGG	His CAT GTA	Lys AAG TTC

Arg Thr Pro Gly Arg Ala Gly Asp Ala Asp GT AGG CCT GT CGA GCA GCC GAC GCG GAT CC GCA TGC GGA CCA GCT CGT CGG CTG CGC CTA GG

FIG. 2. Sequence of the 5,085-nucleotide EcoRI-BamHI insert of pSS2. The predicted amino acid sequence of the different reading frames is indicated as follows (positions): gene L (613 through 1), gene V (1010 through 1921), gene I (1930 through 2688), gene II (2685 through 2969), gene III (2966 through 4118 or 3125 through 4118), and gene R (4139 through 5085). The putative 24-amino-acid polypeptide coded for by gene IV is indicated by one-letter symbols (positions 861 through 935). The ATG translation start sites and the putative ribosome-binding sites are underlined. The insertion sites of the different Tn5 insertions are indicated by a box, representing the 9 bp that are duplicated upon Tn5 insertion.

codons suggests that the polar effect that Tn5-17 exerted on the expression of gene II might also be due to a coupled translation of both genes.

The stop codon of gene II again overlapped with a putative start ATG (position 2966), followed by an ORF ending with

TAG (position 4118) which could code for a protein of M_r 43,600. This ORF might correspond to gene III, since Tn5-2 and Tn5-22, which abolished gene III expression, were located within this reading frame. However Tn5-9, which was mapped 20 bp downstream of this putative start of gene



FIG. 3. Schematic representation of the different ORFs (indicated by bars) present in the 5,085-bp EcoRI-BamHI fragment. The gene IV region is indicated with brackets. Relevant restriction sites: E, EcoRI; S, SphI; H, HindIII; B, BamHI. The inserts of the plasmids used for analysis of the proteins encoded by the PQQ genes are shown. pSS160 contains the EcoRI-BamHI fragment inserted in pUC12, pSQ100 contains the HindIII fragment inserted in pUC12. The arrows represent the P lac promoter from which the PQQ genes are expressed.

III (Fig. 2), did not affect PQQ expression. An alternative ATG start could be indicated at position 3125 from which a protein of M_r 37,400 could be synthesized. If this second ATG were used for gene III translation, there would be an intracistronic region of 150 bp between genes II and III. To test whether a promoter for gene III expression was located within this region we isolated two deletion derivatives of pSS2 containing Tn5-9. First, all the sequences to the left of Tn5-9 were deleted (Fig. 4a). The resulting plasmid (Tn5-9/ BgIII) still complemented gene III mutants, indicating that no sequences to the left of Tn5-9 are essential for gene III expression. Then 14 bp to the right of Tn5-9 were deleted (Fig. 4a). Complementation studies of the resulting plasmid (Tn5-9/HpaI) showed that as a result of this deletion gene III was no longer expressed. A possible explanation is that the promoter (or part of the promoter) for gene III was located within these 14 bp of the PQQ sequence. However, since in Tn5-9/HpaI also most of the Tn5 insertion had been deleted (Fig. 4a), it is more likely that a promoter was present in the inverted repeat of Tn5-9 which directed expression of gene

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TABLE 1. Complementation of different PQQ⁻ mutants by Tn5 insertion plasmids (6)

TnJ	Complementation of PQQ ⁻ mutant										
insertion	I	П	III	IV							
Tn5-2	+	+	-	+							
Tn5-7	+	+	+	+							
Tn5-9	+	+	+	+							
Tn5-14	+	+	+	+							
Tn5-16	+	+	+	+							
Tn5-17	_	_	+	+							
Tn5-18	+	+	+	-							
Tn5-20	+	+	+	+							
Tn5-22	+	+	_	+							

III and which was deleted in Tn5-9/HpaI. Evidence for a promoter in the inverted repeats of Tn5 from which transcription can proceed into sequences adjacent to the Tn5 insertion has already been obtained in *E. coli* (11). This promoter was mapped between the *BaII* and *HpaI* sites of the inverted repeat (Fig. 3). Recently, by subcloning the *gdh* gene of *A. calcoaceticus* we obtained evidence that this gene can be expressed in this organism from a promoter located within Tn5 (A. M. Cleton-Jansen et al., manuscript in preparation).

If indeed the Tn5 promoter is also active in A. calcoaceticus, the presence of a Tn5 insertion could be nonpolar for transcription, since all genes downstream from the Tn5 insertion could be expressed under the control of this promoter. In this case it is possible that genes I, II, and III are located in one operon. The presence of Tn5-17 in gene I might block expression of gene II by a polar effect on translation, whereas gene III could still be expressed under the control of the Tn5 promoter.

If the second ATG at position 3125 were the correct start site for gene III translation, Tn5-2 would be located between the ribosomal binding site and the translation start site (Fig. 2). The deficiency in gene III expression in this case would then probably be due to an inhibition of translation initiation.



FIG. 4. (a) Schematic representation of the translation start region of gene III. The possible translation start sites for gene III are ATG (position 2966) and ATG (position 3125). The position of Tn5-9 is shown. Tn5-9/Bg/II was constructed by deletion of the Bg/II fragment (Bg/II cuts to the left of the 5,085-bp insert and near the inside ends of the inverted repeats of Tn5). Tn5-9/HpaI was constructed by deletion of the HpaI fragment (HpaI cuts 14 bp to the right of Tn5-9 and 190 bp from the outside ends of the inverted repeats of Tn5). Relevant restriction sites: Bg, Bg/II; Hp, HpaI. (b) Nucleotide sequence of the junction between Tn5-9 and the gene III region of pSS2. Base 2987 is the first nucleotide of the PQQ sequence. Putative ribosomal binding sites and the translation start site within the Tn5 sequence are underlined. The amino acids of the proposed fusion protein are shown.

However, arguments could be given for the first ATG at position 2966 being the correct start codon. Examination of the nucleotide sequence of the Tn5 region that is transcribed by the putative Tn5 promoter (Fig. 4b) revealed the presence of an ATG codon that was preceded by a good Shine and Dalgarno sequence (5'-AGGAGGT-3') and followed by an ORF that continued until the end of the transposon. As far as we know, no evidence in the literature has been presented that this sequence can serve as a translation start site, but if it does so in A. calcoaceticus the presence of Tn5-9 might generate a fusion protein (Fig. 4b). This fusion protein should contain 22 amino acids from Tn5 and the amino acids of the gene III product starting with Pro (position 2987). If the ATG at position 2966 were the correct start site for gene III translation, the fusion protein would lack only the seven N-terminal amino acids of the gene III product and would therefore be very likely to retain activity. In conclusion, our results still leave two possible translation start sites for gene III, one generating a protein of M_r 37,400 and one generating a protein of M_r 43,600.

For the mapping of the gene corresponding to the fourth complementation group in PQQ synthesis (gene IV), the position of Tn5-18, which blocks the expression of this gene (Table 1), was determined. Surprisingly, only two very small ORFs were indicated in this region. One ORF started with ATG (position 861) and ended with TAA (position 933), which would code for a protein of 24 amino acids (Fig. 2). The second ORF was located in the opposing strand starting with ATG (position 898) ending with TGA (position 832) and coded for a protein of 22 amino acids. Even if we consider the unlikely possibility that start sites other than ATG, GTG, or TTG are used in A. calcoaceticus, the largest possible ORF is from ACC (position 846) to TAG (position 965), which would code for a protein of 39 amino acids. Tn5-18 could also block expression of gene IV if it is not located within the ORF but in the leader of the transcript of gene IV. If we consider the ORFs of more considerable length near Tn5-18, however, this possibility also seems very unlikely. The first ORF to the right of Tn5-18 was the ORF of gene V. which was not involved in POO expression (see above). The only considerable ORF located to the left of Tn5-18 started with ATG (position 613) and proceeded until the EcoRI site. Within this reading frame (indicated as gene L) Tn5-14 was mapped (Fig. 2). Since Tn5-14 did not affect the complementation of POO⁻ mutants (Table 1), gene L also is not involved in PQQ synthesis. Thus, the effect of Tn5-18 on PQQ synthesis cannot be due to an influence on expression of these larger ORFs. Since Tn5-18 did not affect the expression of genes I, II, and III (Table 1), the conclusion seems justified that the DNA region in which Tn5-18 is located has to code for a product that plays a role in PQQ synthesis. A closer examination of the gene IV DNA region revealed the presence of a G+C-rich hairpin structure (positions 956 through 984) followed by an A+T-rich stretch of DNA. This structure is very likely to be a terminator for transcription initiated within or to the left of the gene IV region. Two possibilities for the gene IV product can now be considered. First the RNA that terminates at the hairpin structure might code for the 24-amino-acid polypeptide starting at ATG (position 861). Second, the RNA itself might play a role in POO synthesis. In both cases an unusual pathway for PQQ biosynthesis can be expected.

The last ORF present in the sequence (indicated as gene R) started at position 4139 (ATG) and proceeded beyond the *Bam*HI site. Since no other classes of PQQ mutants like the



FIG. 5. Autoradiogram of $[^{35}S]$ methionine-labeled proteins produced by in vitro transcription-translation of different DNA templates. Lanes: 1, pSS160; 2, pSQ100; 3, pSQ105; 4, markers; 5, pUC18; 6, no DNA. The positions of the marker bands are indicated. The arrows represent the protein bands corresponding to translation products of genes I, III, and V.

four classes described above have been found (6), this reading frame is not likely to play a role in PQQ synthesis.

Analysis of the proteins encoded by the PQQ genes. To test whether proteins corresponding to the different ORFs could be detected, we used an in vitro coupled transcriptiontranslation system derived from E. coli. When pSS2 was used as template in this system, no specific proteins could be detected. This could be due to an improper recognition of A. calcoaceticus promoters by E. coli RNA polymerase. Therefore we placed the PQQ genes under control of the E. coli lac promoter by cloning the 5,085-bp EcoRI-BamHI fragment of pSS2 in pUC12, resulting in pSS160. The autoradiogram of the labeled proteins produced by this plasmid and run on a 12% polyacrylamide gel is shown in Fig. 5. Two specific protein bands that were not produced when the vector pUC12 was used as template could be detected. The first had a molecular weight of about 34,000, which might very well correspond to the product of gene V (M_r 33,600). The second protein band migrated at the position of approximately $M_{\rm r}$ 29,000 and is therefore likely to be the product of gene I (M_r) 29,700). To test whether these protein bands indeed correspond to the translation products of genes I and V, we constructed two other plasmids. pSQ105 contained the 3,175-bp SphI-BamHI fragment in pUC19 (Fig. 4) and was expected to express genes I, II, and III under control of the lac promoter. pSQ100 contained the 2,600-bp HindIII fragment in pUC12 (Fig. 4). Since HindIII cuts 15 bp downstream the postulated translation start of gene I, this plasmid was expected to express only genes II and III. Indeed, the M_r 34,000 protein band (gene V) was missing when both plasmids were translated (Fig. 5). The M_r 29,000 band was still present in pSQ105 but absent in pSQ100. So the M_r 29,000 protein was very likely to be the translation product of gene I, and the postulated translation start of this gene indeed was located between the SphI and HindIII sites.

Because the translation product of gene II was very small $(M_r \ 10,800)$, no band corresponding to this protein is visible in Fig. 5. The protein of gene III, however, should be large enough to be detectable. We have shown above that two possible starts for gene III translation can be considered, one resulting in a protein of $M_r \ 37,400$ and the other resulting in a protein of $M_r \ 37,400$ and the other resulting in a protein band of about $M_r \ 43,600$. With pSQ105 a weak protein band of about $M_r \ 44,000$ was visible. If this band corresponded to the gene III product, this would mean that translation of gene III

 TABLE 2. Acid production of A. lwoffi with or without pSS2 on different sugar substrates

S. h . turn to	Acid proc	luction
Substrate	Without pSS2	With pSS2
Glucose	_	+
Glucose + PQQ	+	+
Galactose	-	+
Galactose + PQQ	+	+
Arabinose	-	+
Arabinose + POO	+	+
Xylose	_	+
Xylose + POO	+	+
Lactose	-	_
Lactose + PQQ	-	-

starts with the first ATG (position 2966). However, the gene III translation product was not observed when pSS160 or pSQ100 were used as a template. Possibly the expression of gene III, which is already very low in pSQ105, is for an unknown reason even more reduced in the other two plasmids.

Expression of the PQQ genes in A. lwoffi and E. coli K-12. A. lwoffi and E. coli K-12 produce a PQQ-dependent GDH (8, 21). However, these bacterial species do not synthesize PQQ. Therefore the holo-GDH can be formed only when PQQ is supplied from the culture medium. To test whether our four cloned PQQ genes contain sufficient information for the biosynthesis of POO, we introduced these genes into A. lwoffi and E. coli and tested whether these bacteria produced an active GDH enzyme. First pSS2 was introduced in A. lwoffi by conjugation, and then the transconjugants were tested for acid production on different sugar substrates as described in Materials and Methods. The introduction of pSS2 in A. lwoffi resulted in acid production when GDHspecific sugars were used as substrates (Table 2). This indicates that in the presence of pSS2 a sufficient amount of PQQ is synthesized for the reconstitution of the holo-GDH enzyme. To test whether A. lwoffi is normally lacking all the PQQ enzymes and not just carrying a mutation in one of the PQQ genes, we also investigated whether the pSS2 plasmids with the different Tn5 insertions produced PQQ. A. lwoffi with pSS2 carrying the insertion Tn5-2, Tn5-17, or Tn5-18 did not produce acid on GDH-specific sugars, whereas upon introduction of pSS2 with Tn5-7, Tn5-9, Tn5-16, or Tn5-20 acid production due to GDH activity could be shown. Apparently all four genes are required for PQQ synthesis in A. lwoffi.

Next we tested whether also E. coli K-12 could synthesize POO upon introduction of the four genes. For this experiment an E. coli K-12 strain carrying a ptsI mutation (PPA41) was used. Due to the ptsI mutation, this strain no longer grows on glucose as the sole carbon source. In the presence of PQQ, however, the GDH enzyme can be used, and growth on glucose is restored (8). Previously we have shown (6) that PPA41 carrying pSS2 still does not grow on minimal medium plates with glucose. Since this might be due to an improper expression of the PQQ genes by the E. coli RNA polymerase, we also transformed pSS160 (carrying the PQQ genes under control of the lac promoter) to PPA41. The resulting transformants did form colonies on minimal medium plates with glucose after incubation at 37°C for 2 days. No growth was observed on control plates containing mannitol as the carbon source, indicating that the transformants were still mutated in *ptsI* and that growth on glucose had to be the consequence of PQQ synthesis. The PQQ production, however, was apparently low, since in the presence of additional PQQ in the culture medium colony formation on glucose plates was already observed after incubation for 1 day. We showed above that at least the in vitro synthesis of the gene III protein with E. coli extracts was very low, which could be the reason for the low level of PQQ production in vivo. To test whether in E. coli the expression of genes I, II, and III is sufficient for PQQ production, we also introduced pSQ105 (containing these three genes under control of the lac promoter) into PPA41. The resulting transformants did not form colonies on minimal medium plates with glucose even after prolonged incubation, meaning that also in E. coli the product of gene IV (which might be an RNA or a small polypeptide) is essential in the biosynthetic pathway of PQQ.

DISCUSSION

Biosynthesis of the coenzyme PQQ is thought to be a multistep process involving at least five or six different enzymes. In this paper we have shown that expression of four different PQQ genes from A. calcoaceticus in E. coli or A. lwoffi is sufficient for the synthesis of the coenzyme in these organisms. Sequence analysis of the PQQ genes showed that only three of them (genes I, II, and III) code for proteins of a size (M_r 29,700, 10,800, and 43,600, respectively) that can be expected for proteins with an enzymatic function. The fourth gene (gene IV), however, does not seem to code for an enzyme, since the most probable reading frame comprises only 24 amino acids. An explanation for the presence of so few PQQ-specific enzymes might be that a precursor resembling the mature coenzyme structure is already present, not only in A. calcoaceticus but also in A. lwoffi and E. coli.

The intriguing question is what the role of gene IV in PQQ synthesis might be. Complementation studies have shown that the gene IV region is coding for a *trans*-acting product. Since among 40 independently isolated PQQ⁻ mutants of A. *calcoaceticus* no gene IV point mutations were found (6; unpublished data), this product was already predicted to be relatively small. The 3' end of the gene IV region contains a G+C-rich hairpin followed by an A+T-rich stretch of DNA, which is characteristic of a transcription terminator. This suggests that a small transcript complementary to only gene IV DNA is formed. Two possible functions for this gene IV RNA can be considered.

First, the gene IV RNA itself might in some way play a role in PQQ synthesis. We consider it unlikely that this RNA would play a direct structural role, but a function as a positive regulator cannot be excluded. RNA has been shown to act in *trans* as a negative regulator in the replication of plasmid ColE1 (18). However until now it has not been reported that RNA can also act as a positive regulator.

As a second possibility the gene IV RNA might be translated in a 24-amino-acid polypeptide, which in turn might have a function in PQQ synthesis. Recently it has been shown that the amino acids tyrosine and glutamate are used as precursors for PQQ biosynthesis in *Hyphomicrobium* sp. strain X (20a) and *Methylobacterium* sp. strain AM1 (C. J. Unkefer, personal communication). Since both amino acids are present in the 24-amino-acid polypeptide, it is possible that this polypeptide is used as a precursor substrate. Through the tertiary structure of the polypeptide both amino acids could be brought together, the enzymes could make the bonds, and finally the complete (or almost complete) PQQ molecule could be cut out of the polypeptide. Still, when such a polypeptide is used as a precursor it remains unlikely that only three enzymes are sufficient for the complete synthesis of PQQ, since the chemical bonds that have to be made will require multiple enzymatic steps. However, enzymes could be used that also play a role in other biochemical processes.

Finally, the 24-amino-acid polypeptide might also play a role in the transport of POO across the cytoplasmic membrane. The active site of the PQQ-dependent GDH enzyme is located at the periplasmic side of the inner membrane (4). Therefore eventually also the PQQ has to be present in the periplasmic space. This could be achieved in two ways. First, the PQQ enzymes could be transported through the inner membrane, and the PQQ could be synthesized in the periplasm. The predicted amino acid sequences of the different PQQ enzymes, however, do not reveal the presence of N-terminal signal peptides (a stretch of hydrophobic amino acids flanked by hydrophilic residues). Alternatively, the PQQ could be synthesized in the cytoplasm and subsequently translocated to the periplasm. The 24-amino-acid polypeptide might be involved in this process, although it also is not highly hydrophobic.

Besides the putative transcription terminator of gene IV, no transcription terminator signals seem to be present at the end of the other PQQ genes. Moreover, the sequence data have shown that the translation start of gene II overlaps with the end of gene I, the start of gene III might overlap with the end of gene II, and the ORFs of genes V and I are separated by only 8 bp. Taken together, these results indicate that it is very likely that genes V, I, II, and III are transcribed from one promoter (although it is still possible that gene III has its own promoter). Gene V, however, which would be the first gene in this operon, is not involved in the synthesis of PQQ. Gene V also does not play a role in the transport of electrons from POO to the electron transport chain, since deletion mutants lacking the complete PQQ region (including gene V) show normal GDH activity upon addition of PQQ (13). A reason for the concerted expression of gene V and the PQQ genes might be that gene V codes for another PQQ-dependent enzyme.

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