OxlT is the oxalate/formate exchange protein that represents the vectorial component of a proton-motive metabolic cycle in Oxalobacter formigenes. Here we report the cloning and sequencing of OxlT and describe its expression in Escherichia coli. The OxlT amino acid sequence specifies a polytopic hydrophobic protein of 418 residues with a mass of 44,128 daltons. Analysis of hydrophathy and consideration of the distribution of charged residues suggests an OxlT secondary structure having 12 transmembrane segments, oriented so that the N and C termini face the cytoplasm. Expression of OxlT in E. coli coincides with appearance of a capacity to carry out the self-exchange of oxalate and the heterologous, electrogenic exchange of oxalate with formate. The unusually high velocity of OxlT-mediated transport is also preserved in E. coli. We conclude that the essential features of OxlT are retained on its expression in E. coli.

The Gram-negative anaerobe, Oxalobacter formigenes, derives metabolic energy from the decarboxylation of oxalate (1, 2) by using a “proton-motive metabolic cycle” (3, 4). In O. formigenes, which provided the first case study of such a proton-motive cycle (3, 4), entry of divalent oxalate is coupled to the exit of its decarboxylation product, monovalent formate, leading to formation of an internally negative membrane potential. Because intracellular oxalate decarboxylation consumes a cytosolic proton, entry of negative charge is accompanied in stoichiometric fashion by appearance of internal hydroxyl ion. As a result, the combined activities of the vectorial antipporter reaction and the scalar decarboxylation step comprise a thermodynamic proton pump (3, 4). In this way, O. formigenes establishes the proton-motive force required for both the synthesis of ATP by reversal of a dicyclohexylcarbodiimide-sensitive ATPase (29) and for the support of other membrane reactions requiring a proton-motive force.

Early experiments based on reconstitution of activity from crude detergent extracts suggested the oxalate/formate exchange reaction is mediated by a membrane carrier (3). This reasoning was strengthened by finding that oxalate transport is catalyzed by a single protein, OxlT, whose SDS-PAGE mobility (−38 kDa) resembles that of other bacterial carrier proteins (5). However, it was not possible to complete the argument by examination of the OxlT amino acid sequence. For this reason, the work described here was directed to the cloning and sequencing of OxlT. An additional objective was to determine whether OxlT function is retained after expression in Escherichia coli. If so, future studies of this unusual antipporter could exploit the advantages of a genetically tractable host. The work described here indicates that the amino acid sequence of OxlT conforms to the general pattern found for most membrane carriers, including the presence of twelve likely transmembrane segments. Functional studies further suggest that the main properties of OxlT, including its exceptionally high velocity (3, 5), are preserved on its expression in E. coli.

**EXPERIMENTAL PROCEDURES**

**Cells and Plasmids—**E. coli strain KW251 (Promega) was used for the screening of an O. formigenes lambda phage library; subcloning of positive restriction fragments was performed using pBluescript II KS− (Amp') carried in strain XL1 blue (Tet') (Strategene). Strain XL1 blue harboring pMS421 (spec', LacIq') was called strain XL3 and was used for expression of OxlT from pBK OxlTSK ; pBluescript II SK+ derivative in which the gene encoding OxlT is under control of the lac promoter. Cells were grown aerobically at 37 °C in Luria Broth with drugs as required (100 μg/ml carbenicillin, 12 μg/ml tetracycline, and 50 μg/ml spectinomycin).

**O. formigenes Genomic DNA—**Cells of O. formigenes from Dr. M. J. Allison (National Animal Disease Center, Ames IA) were the source of genomic DNA used in preliminary hybridization experiments. DNA was extracted using the Easy DNA extraction kit of Invitrogen.

**Determination of the OxlT N-Terminal Sequence and Preparation of a Peptide-directed Antibody—**OxlT was purified as described (5). After removing lipid (5) from the peak activity fraction appearing on CM-Sepharose chromatography, 100 μg of purified OxlT was subjected to SDS-PAGE and transferred at 4 °C to an Applied Biosystem ProBlott polyvinylidene difluoride membrane at 100 V for 1 h, using a transfer solution containing 25 mM Tris, 10 mM glycine, and 0.5 mM dithiothreitol. The membrane with adsorbed OxlT was washed four times with distilled water and provided to the Harvard Microchemistry Facility (Cambridge, MA), which reported NNPQGTGQSTLLGNRFYLYV (single-letter amino acid code) as the probable N-terminal sequence; there was indication of a ragged N terminus. A synthetic peptide of this same sequence was synthesized by the Peptide Core Facility (Department of Biological Chemistry, Johns Hopkins Medical School). After conjugation of the peptide to bovine serum albumin (6), rabbit polyclonal antibody was raised against the material by Hazleton Research Products (Denver, PA).

**Oligonucleotide Probes—**Based on the N-terminal amino acid sequence noted above, we prepared two degenerate oligonucleotide probes. Oligo1 had the nucleotide sequence AA(C/T)AA(C/T)TCCICA(A/G)GACIGGICA (where I indicates inosine), corresponding to amino acid residues 1–7 (NNPQTGQ); Oligo2 had the sequence AA(C/T)AA(C/T)GTTGTT(C/T)TA(C/T)CCT (and corresponded to residues 14–19 (NRW-)
IPTG-induced cells and uninduced control cells (each 5 mg of protein) at 4°C in an Eppendorf refrigerated microfuge (10). After incubation at 4°C for 20 min, the suspension was clarified by centrifugation and ether-purified ghosts were spun down and resuspended in 0.5 ml of ice-cold solubilization buffer, where expression of OxlT was regulated by the lac promoter. As a final step, pBKoxITSK+ was placed in E. coli XL3 for functional tests.

Sequence analysis—Double-stranded DNA was sequenced by the DNA Core Facility of the Johns Hopkins Medical School, using the dye-deoxy chain termination procedure of Sanger et al. (11). The nested deletion series was sequenced using universal primers for pBluescript II SK+ as primers for sequencing the oxIT opposite strand, we designed appropriate complementary synthetic oligonucleotides.

Expression of OxlT in E. coli—An overnight preculture of E. coli XL3 carrying pBKoxITSK+ was diluted 100-fold in fresh medium, and 1 ml IPTG was added 1 h later; IPTG-induced cell and uninduced control cells were harvested after an additional 15 min of growth.

SDS-PAGE and Immunoblots—SDS-PAGE with 12% acrylamide gel was performed as outlined by Laemmli (12). For routine immunoblotting, protein was transferred to nitrocellulose using standard techniques (13), and after exposure to immune serum diluted 1/2500, binding of the primary antibody was detected by chemiluminescence (Amersham Corp.) (14).

Solubilization and Reconstitution of OxlT and Assays of Transport— IPTG-induced cells and uninduced control cells (each 5 mg of protein) were harvested by centrifugation, resuspended in 5 ml of lysoycine (300 mM) and DNase (40 μg/ml), and incubated at 37°C for 10 min. Cells were repelleted and then resuspended in 5 ml of water. The resulting ghosts were spun down and resuspended in 0.5 ml of ice-cold solubilization buffer, and 1 ml of 100 mM potassium oxalate, 50 mM MOPS, 10% glycerol, and 0.1 mg oxalate. After incubation at 4°C for 20 min, the suspension was clarified by centrifugation at 4°C in an Eppendorf refrigerated microfuge (15,000 × g for 15 min) to give a crude detergent extract that was stored at −80°C until use.

OxlIT transport activity was monitored by reconstitution of protein into proteoliposomes (3, 15, 16). In a final volume of 250 μl, 50–100 μl of a detergent extract was mixed with 1.36 mg of bath-solubilized liposomes, additional detergent (to 1.25%), and either 50 μM MOPS/K or 50 μM MOPS/NMG (pH 7). After incubation at 4°C for 20 min, proteoliposomes were formed at 23°C by the addition of 5 ml of a detergent containing buffer (pH 7). For estimates of oxIT exchange (Table 1), the loading buffer contained 100 mM potassium oxalate, 50 mM MOPS/K, and 1 mM dithiothreitol. To assess oxIT exchange (see Fig. 5), the loading buffer was either 100 mM potassium formate or 100 mM NMG formate, along with 50 mM MOPS or 50 mM MOPS/ NMG dithiothreitol. Formate-loaded proteoliposomes were incubated within 20 min, at which point we used one of two protocols to assess oxIT activity. In a rapid filtration assay (17) to monitor oxIT exchange (Table 1), 0.2 ml of the proteoliposomal suspension was applied directly, under vacuum, to the center of a 0.22-μm GFST Millipore filter. The external medium was removed by two 5-ml rinses with assay buffer (100 mM K2SO4 and 50 mM MOPS/K, pH 7), and on release of the vacuum the assay began as proteoliposomes were covered with 0.25 ml of assay buffer containing 100 mM [35S]oxalate. The reaction was terminated 3 min later by filtration and three quick rinses with assay buffer. Alternatively (see Fig. 5), formate-loaded proteoliposomes were resuspended by centrifugation (16) and resuspended in a small volume of their K- or NMG-based loading buffers. Subsequently, they were diluted 120-fold into either NMG- or K-based assay buffers, as above, containing 100 μM [35S]oxalate, with or without 1 μM valinomycin. In this way, it was possible to generate a membrane potential whose polarity was either internal positive (potassium outside, NMG inside) or external negative (NMG outside, potassium inside). As an additional basis for comparison, proteoliposomes were loaded with NMG-formate and tested using the NMG-based assay buffer.

Protein Estimation—Protein content was estimated using a modification of the procedure of Schaffner and Weissman (18). Chemicals—[35S]Oxalate (4.8 mCi/mmol) was from DuPont NEN; octyl-β-D-glucoside was from Boehringer Mannheim; phospholipid was purified from crude E. coli lipid (Avanti Polar Lipids) as described earlier (16). Other reagents were of the highest purity available.

RESULTS

Cloning of the Gene Encoding OxlT—In the absence of a positive selection procedure, we cloned OxlT by obtaining N-terminal sequence information from the purified protein and designing appropriate oligonucleotide probes with which to screen an O. formigenes library (see "Experimental Procedures"). Initial screening of a λ-GE4 library gave positive inserts of 10–16 kb; subcloning eventually yielded a 3.2-kb fragment whose sequence included two overlapping open reading frames of a 1.4-kb interval. One of these open reading frames specified a hydrophobic protein whose N-terminal sequence matched that determined for purified OxlT (Fig. 1), and we tentatively identified this gene as our desired target, oxIT; later functional tests (below) verified the assignment. The oxIT sequence has been submitted to GenBank (accession number U40075).

The DNA sequence of the gene, oxIT, indicates that expression of its encoded protein (OxlT) follows patterns well established for bacterial systems. Thus, a likely promoter having 35 and −10 sequences of TTGAAA and TTCAAT, respectively, occupies a 29-base interval ending 70 nucleotides upstream of the initiating codon, AUG. Transcriptional termination is probably mediated by a 31-base stem-loop structure (AAAAAAGCCCGGCTTTCCGCCGGGCTTTTTT) that begins 72 nucleotides from the first of two in-frame stop (UAU) codons.

Characteristics of the Cloned Protein—Analysis of the deduced OxlT amino acid sequence (Fig. 2) reveals a novel hydrophobic protein of 418 amino acid residues having a predicted mass of 44,128 daltons. No proteins with significant homology to OxlT were found in an EMBL BLITZ search of the Swiss Protein Data Base using the Smith and Waterman (19) algorithm; similarly, we found no proteins related to the hypothetical hydrophilic protein specified on the oxIT noncoding strand. Analysis of OxlT hydropathy according to the method of Kyte and Doolittle (20) (Fig. 3) suggests the presence of 12 hydrophobic segments, each of sufficient length to constitute a transmembrane α-helix (TM1–12). A similar analysis according to Rost et al. (21) predicts 11 transmembrane α-helices, including TM1 and TM3–12 (Fig. 3), but excluding TM2, whose peak hydropathy value is the lowest of the 12 putative transmembrane segments (Fig. 3). Although membrane carriers with 11 transmembrane segments have been described in bacteria (22, 23), it is more typical to find examples with 10 or 12 transmembrane regions (4, 23, 24). For this reason, our initial model of OxlT topology (Fig. 3) assumes the 12 transmembrane segments suggested by analysis of hydropathy. This initial model

Protein: NNPETGQSSTGELGNRMWFLV
DNA: MNIPETGQSGTGLGNRMWFLV

Fig. 1. oxIT N-terminal sequences. The N-terminal sequence determined by microsequencing of purified OxlT (top) is compared with the N-terminal sequence specified by the cloned gene, oxIT (bottom).
Expression of oxalate self-exchange in E. coli

Table I

| Plasmid                  | Condition | Oxalate transport (μmol/mg protein) |
|--------------------------|-----------|-------------------------------------|
| pBluescript II SK +      | - IPTG    | 0.02                                |
| pBK0xITSK +              | - IPTG    | 0.14                                |
| pBluescript II SK +      | + IPTG    | 0.02                                |
| pBK0xITSK +              | + IPTG    | 2.30                                |

Fig. 3. Hydropathy profile and topological model of OxIT. Top, proposed topological model of OxIT derived from an analysis of hydropathy (bottom) and from consideration of the distribution of charged residues (see text). Individual amino acids are not indicated as such (see Fig. 2). Instead, negatively charged residues (Asp and Glu) are shown as gray squares, and except for Lys (25), positively charged residues (Arg and Lys) are given as solid circles. Enlarged circles show the expected locations of Cys (23), Cys (25), and Lys (35). Bottom, hydropathy profile of the OxIT amino acid sequence, performed according to Kyte and Doolittle (20) using a window of 13 residues. Transmembrane segments 1–12 are indicated.

Expression of oxalate self-exchange in E. coli

Also conforms to the common finding (4, 23, 24) of a central cytoplasmic loop that separates the regions containing TM1–6 and TM7–12.

To orient the proposed OxIT structure with respect to cytoplasmic and extracellular phases, we used the observation of von Heijne (25) that transmembrane segments often have an excess of positively charged residues at their cytoplasmic ends, whereas those facing the extracellular phase are negatively charged. Our analysis of OxIT (Fig. 3, top) confirms this expectation. Plotting the positions of charged residues of OxIT in both the cytoplasmic and extracellular phases of OxIT reveals that charged residues exhibit a clear separation of charge between the two phases (Fig. 3, bottom). Individual amino acids are not indicated as such (see Fig. 2). Instead, negatively charged residues (Asp and Glu) are shown as gray squares, and positively charged residues (Arg and Lys) are given as solid circles. Enlarged circles show the expected locations of Cys (23), Cys (25), and Lys (35). Bottom, hydropathy profile of the OxIT amino acid sequence, performed according to Kyte and Doolittle (20) using a window of 13 residues. Transmembrane segments 1–12 are indicated.

The experiments described in Figs. 4 and 5 document that the gene identified as oxIT specifies the OxIT transport protein and that the main features of OxIT function are retained in E. coli. Thus, antibody directed against the OxIT N terminus resembles that of authentic OxIT, from O. formigenes, including the presence of both monomeric (approximately 35 kDa) and dimeric (approximately 65 kDa) forms of the protein (Fig. 4, panels A and B). A more thorough examination of OxIT immunoactivity coincides with acquisition of induced cells of a capacity to catalyze both the oxalate self-exchange reaction and the electroneutral exchange of oxalate and formate. For such functional tests, we prepared detergent extracts from both induced and uninduced cells (Fig. 4). To examine oxalate self-exchange, oxalate-loaded proteoliposomes were washed free of external substrate by filtration on Millipore filters (0.22-μm pore size), and then, while still affixed to the filters, they were covered for 3 min with an assay medium containing 100 μM [14C]oxalate, followed by a final filtration and wash. This test (Table I) gave no indication of oxalate transport by cells bearing pBluescript II SK + (with or without IPTG) (Fig. 4). On the other hand, uninduced cells with pBK0xITSK + but not in uninduced cells or in cells carrying the parent pBluescript II SK + (with or without IPTG) (Fig. 4). It is also evident that SDS-PAGE profile of OxIT when expressed in E. coli resembles that of authentic OxIT, from O. formigenes, including the presence of both monomeric (approximately 35 kDa) and dimeric (approximately 65 kDa) forms of the protein (Fig. 4, panels A and B).

Equally important, in this same experiment we showed that appearance of OxIT immunoactivity coincides with acquisition of induced cells of a capacity to catalyze both the oxalate self-exchange reaction and the electroneutral exchange of oxalate and formate. For such functional tests, we prepared detergent extracts from both induced and uninduced cells (Fig. 4). To examine oxalate self-exchange, oxalate-loaded proteoliposomes were washed free of external substrate by filtration on Millipore filters (0.22-μm pore size), and then, while still affixed to the filters, they were covered for 3 min with an assay medium containing 100 μM [14C]oxalate, followed by a final filtration and wash. This test (Table I) gave no indication of oxalate transport by cells bearing pBluescript II SK + (with or without IPTG) (Fig. 4). On the other hand, uninduced cells with pBK0xITSK + but not in uninduced cells or in cells carrying the parent pBluescript II SK + (with or without IPTG) (Fig. 4). It is also evident that SDS-PAGE profile of OxIT when expressed in E. coli resembles that of authentic OxIT, from O. formigenes, including the presence of both monomeric (approximately 35 kDa) and dimeric (approximately 65 kDa) forms of the protein (Fig. 4, panels A and B).
Cloning, Sequencing, and Expression of OxlT in E. coli

The work summarized here had as its main goal the cloning and sequencing of OxlT, the oxalate/formate antiport protein of O. formigenes. Several criteria show this goal has been met. In particular, the cloned gene specifies the N-terminal sequence found in authentic OxlT (Fig. 1), and expression of this gene confers upon E. coli the capacity to mediate both the homologous self-exchange of oxalate and the heterologous, electrogenic exchange of oxalate with formate (Table I and Fig. 5). We therefore conclude that this antiport protein retains its most important functional properties when expressed in E. coli. It is likely the main physical characteristics of OxlT are also preserved in E. coli, because the OxlT SDS-PAGE profiles in E. coli and O. formigenes are equivalent (Fig. 4) and because the positive response to an N-terminal peptide-directed antibody suggests OxlT retains its natural N terminus (Fig. 4).

Analysis of the OxlT amino acid sequence reveals a polytopic hydrophilic protein (Fig. 3) whose general structure resembles that of known membrane carriers in the several respects (4, 22, 24): (i) the presence of 12 (or 11) presumed transmembrane segments; (ii) N- and C-terminal regions facing the cytoplasm (presuming an even number of transmembrane segments); (iii) the finding of a cytoplasmic loop midway along the sequence (resides 190-219), separating the region containing TM1-6 from that containing TM7-12; and (iv) an excess of positively charged residues at the presumed cytoplasmic surface. Although there is no apparent sequence homology between OxlT and known membrane carriers (or other transporters), these general features, along with the earlier biochemical characterization, are sufficient to classify OxlT as a conventional secondary transport protein.

The OxlT predicted structure has two additional features deserving of specific comment. First, we note the presence of a single charged residue (Lys355) within TM11 (Fig. 3, top). Because OxlT substrates are anionic (oxalate$^{2-}$ and formate$^{-}$), the presence of this apparently uncompensated positive charge in the hydrophilic sector prompts the hypothesis that Lys355 forms part of an anionic binding center within the substrate translocation pathway. Preliminary tests are compatible with this idea, because several uncharged substitutions at position 355 give variants that fail to transport, whereas the K355R derivative retains activity. As a second finding of interest is that OxlT has only two cysteine residues (Cys$^{36}$ and Cys$^{27}$). Because neither of these cysteines is required for function, OxlT presents an attractive target for cysteine scanning mutagenesis, an approach that has proven valuable to the study of several membrane transport systems (26-28).

Evaluation of oxalate transport (Table I and Fig. 5) supports the idea that the main features of OxlT selectivity are retained in E. coli. Moreover, calculations using these data suggest that the unusually high velocity of OxlT is also preserved in this expression system. Thus, detergent extracts from induced E. coli yielded a potential-stimulated oxalate/formate antiport rate of 24 μmol/min/mg protein (Fig. 5), whereas for the same conditions we found an exchange rate of 16 μmol/min/mg protein using O. formigenes (3). And in further work (not given), we found the kinetic parameters of oxalate self-exchange to be

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K. Abe and P. C. Maloney, unpublished results.
the same in E. coli and O. formigenes (3) (Michaelis constants of 0.2 ± 0.03 versus 0.24 mM, and maximal velocities of 102 ± 7 versus 99 μmol/min/mg protein, respectively). Because immunoblots gave about equal staining for nearly equivalent amounts of E. coli or O. formigenes membrane protein (see Fig. 4 legend), it appears that OxlT is expressed at comparable levels in the two cell types. Accordingly, the specific activity of OxlT is largely unaffected by expression in E. coli. We note that the transport rates observed in crude extracts from E. coli (20–100 μmol/min/mg protein) are unusually high but that this is anticipated for OxlT, which has the highest known maximal velocity among carriers of organic substrates (5). That this feature, too, is preserved in E. coli both confirms early work and suggests the value of further study in an environment, such as E. coli, conducive to both biochemical and genetic manipulations.

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Cloning, Sequencing, and Expression in *Escherichia coli* of OxlT, the Oxalate:Formate Exchange Protein of *Oxalobacter formigenes*

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