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Characterization of the Proton/Glutamate Symport Protein of Bacillus subtilis and Its Functional Expression in Escherichia coli

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Transport of acidic amino acids in *Bacillus subtilis* is an electrogenic process in which L-glutamate or L-aspartate is symported with at least two protons. This is shown by studies of transport in membrane vesicles in which a proton motive force is generated by oxidation of ascorbate-phenazine methosulfate or by artificial ion gradients. An inwards-directed sodium gradient had no (stimulatory) effect on proton motive force-driven L-glutamate uptake. The transporter is specific for L-glutamate and L-aspartate. L-Glutamate transport is inhibited by β -hydroxyaspartate and cysteic acid but not by α -methyl-glutamate. The gene encoding the L-glutamate transport protein of B. subtilis (gltP_{Bsu}) was cloned by complementation of Escherichia coli JC5412 for growth on glutamate as the sole source of carbon, energy, and nitrogen, and its nucleotide sequence was determined. Putative promoter, terminator, and ribosome binding site sequences were found in the flanking regions. UUG is most likely the start codon. $gltP_{Bsu}$ encodes a polypeptide of 414 amino acid residues and is homologous to several proteins that transport glutamate and/or structurally related compounds such as aspartate, fumarate, malate, and succinate. Both sodium- and proton-coupled transporters belong to this family of dicarboxylate transporters. Hydropathy profiling and multiple alignment of the family of carboxylate transporters suggest that each of the proteins spans the cytoplasmic membrane 12 times with both the amino and carboxy termini on the inside.

The amino acid transporters in the thermophile *Bacillus stearothermophilus* studied to date facilitate an electrogenic symport reaction in which Na⁺ is used as the coupling ion. The apparent affinity constants for Na⁺ are in the range of 0.5 to 1 mM (14). The transport of glutamate and aspartate is driven by the proton motive force (Δp) but also by an inwardly directed Na⁺ gradient (Δp Na). The transport of glutamate occurs most likely in symport with one H⁺ and one Na⁺ (7); the apparent affinity constant for Na⁺ is <10 μ M. So far, sodium/proton/glutamate transporters have been found in the thermophiles *Bacillus* sp. strain IS1 ($gltT_{\rm Bi}$) (42), *B. stearothermophilus* ($gltT_{\rm Bs}$), and *Bacillus caldotenax* ($gltT_{\rm Bc}$). The genes encoding GltT_{Bs} and GltT_{Bc} have been cloned and functionally expressed in *Escherichia coli* (43).

Studies on the transport of L-glutamate and L-aspartate in whole cells of B. subtilis W23, 60015, 6GM, and 8G5 suggested that Δp Na is not involved as a driving force in this mesophilic Bacillus species (41). The glutamate transporter of B. subtilis is likely to differ from those of thermophilic bacilli with respect to not only cation selectivity but also thermostability. In order to compare the sodium/proton/glutamate symport protein of the thermophile B. stearothermophilus with the glutamate transport protein of the closely related mesophile B. subtilis, the latter system was studied at the molecular level. This study confirms that glutamate uptake in B. subtilis is indeed coupled to the Δp . The primary sequence of the glutamate transporter of B. subtilis is highly similar to that of the glutamate transport proteins of B. stearothermophilus and B. caldotenax. In addition, the substrate specificity of these proteins is similar but the cation selectivity is different.

MATERIALS AND METHODS

Bacterial strains, plasmids, and growth conditions. The bacterial strains, plasmids, and phages used are listed in Table 1. B. subtilis 6GM was grown at 37°C with vigorous aeration in Luria-Bertani medium (LB) adjusted to pH 7.0 (33). E. coli strains were grown at 37°C with vigorous aeration in LB, M9, M9G (M9 in which ammonium chloride was replaced by L-glutamate at a final concentration of 10 mM), or M9CA medium (33, 43). The mineral media were supplemented with essential nutrients as indicated by the auxotrophic markers. When needed, carbenicillin and isopropyl-β-D-thiogalactopyranoside (IPTG) were added to a final concentration of 100 μg/ml and 100 μM, respectively.

DNA manipulations. Mini- and large-scale preparations of plasmid DNA were obtained by the alkaline lysis method (4, 15). Chromosomal DNA was isolated essentially as described previously (25), except that mutanolysine was omitted. The strains were transformed after rubidium chloride treatment of the cells (33) or by electrotransformation (8). Other DNA techniques were performed as described previously (33).

Cloning of the glutamate transport gene. The $gltP_{\rm Bsu}$ gene was cloned essentially as described previously (43). Partially EcoRI-, HindIII-, PstI-, or Sau3A-digested chromosomal DNA of B. subtilis was fractionated by agarose gel (1%, wt/voI) electrophoresis. Fragments of 2 to 10 kb were electroeluted from the gel and ligated into linearized and dephosphorylated pKK223-3. The resulting hybrid plasmids were used to transform E. coli JC5412 by electrotransformation. This strain does not grow on glutamate as the sole source of energy, nitrogen, and carbon. Transformants able to grow on M9G plates (supplemented with carbenicillin and IPTG) were analyzed with respect to their plasmid content. Purified plasmids were used to retransform E. coli JC5412 in order to distinguish between Glu⁺ revertants and true transformants.

Sequence determination. The nucleotide sequences of both strands of the *HindIII* fragment of pGTU100, or subclones derived thereof in pUC18/19 or M13mp18/19 (*AccI*, *AluI*, *HaeIII*, *HincII*, *HindIII*, *PstI*, *RsaI*, *Sau3*A, and *SphI* fragments), were determined by using the dideoxy-chain termination method (34). Single- or double-stranded DNA was sequenced with a T7 sequencing kit (Pharmacia). Micro Genie (release 5.0; Beckman, Palo Alto, Calif.) and PCGene (release 6.26; Genofit, Geneva, Switzerland) were used for computer-assisted sequence analysis. Amino acid sequences homologous to GltP_{Bsu} in the EMBL data bank were located with the TBLASTN program (1). **Transport assays with whole cells.** Cells (15 ml) of strain JC5412 harboring

Transport assays with whole cells. Cells (15 ml) of strain JC5412 harboring plasmid pKK223-3 or pGTU100, grown for 14 h in LB (supplemented with carbenicillin and IPTG), were harvested, washed three times in 50 mM potassium phosphate (pH 6.0) plus 5 mM MgSO₄, and resuspended to a final A_{660} of approximately 10 in the same buffer. Uptake of L-[\frac{14}{C}]glutamate by the *E. coli* cells was assayed at 37°C, upon 100-fold dilution of the cells into 200 μ l of 50 mM potassium phosphate (pH 6.0)–5 mM MgSO₄–10 mM glucose. This mixture was incubated for 1 min at 37°C under continuous aeration. To initiate the uptake

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Strain, plasmid, or phage	Relevant characteristics	Source or reference
Bacteria		
B. stearothermophilus		ATCC 7954
B. subtilis 6GM		Laboratory collection
E. coli		
JM101	$\Delta(lac-proAB) F' lacI^q \Delta M15$	50
JC5412	No growth on L-glutamate as the sole source of carbon, nitrogen, and energy	49
BK9MDG	GltP ⁻	47
Plasmids		
pUC18/19	Ap^{r}	
pKK223-3	Ap ^r , expression vector	Pharmacia
pGTU100	pKK223-3 carrying gltP of B. subtilis on a 2,122-bp HindIII-HindIII fragment	This study
pGTU2000	pUC18 carrying gltP of B. subtilis on a 2,122-bp HindIII-HindIII fragment	This study
Phage M13mp18/19		50

experiment, L-[14 C]glutamate was added to a final concentration of 1.9 μM . The uptake reactions were terminated by adding a 10-fold excess of ice-cold 0.1 M potassium chloride and immediately filtering over cellulose nitrate filters (pore size, 0.45 μm). The filters were washed once with 2 ml of ice-cold potassium chloride

Isolation of membrane vesicles. For studies of transport in membrane vesicles, cells of *B. subtilis* 6GM were grown in LB (33) to an A_{660} of 1.0. Cells were harvested and membrane vesicles were isolated as described previously by Konings et al. (23).

Cells of *E. coli* BK9MDG harboring plasmid pKK223-3 or pGTU100 were grown to an A_{660} of 1.0 in LB (supplemented with 100 μ g of carbenicillin per ml and 100 μ M IPTG) and membrane vesicles were isolated as described previously by Kaback (18). Cytoplasmic membranes of *B. subtilis* and *E. coli* were finally resuspended to 15 mg of protein per ml in 50 mM potassium phosphate, pH 6.0, and stored in liquid nitrogen.

Transport assays. (i) Sodium- and proton motive force-driven uptake. The electron donor system potassium-ascorbate (K-asc)–phenazine methosulfate (PMS) was used to generate a Δp . Membrane vesicles were diluted 100-fold into 50 mM potassium phosphate (pH 6.0)–5 mM MgSO $_4$ –10 mM K-asc–100 μ M PMS. The effect of the sodium motive force (Δs) was assessed by adding 10 mM NaCl to the assay buffer. When appropriate, valinomycin (2 nmol per mg of protein), nigericin (1 μ M), or cabonyl cyanide \emph{m} -chlorophenylhydrazone (10 μ M) (CCCP) was added to abolish the transmembrane electrical potential ($\Delta \Psi$), the transmembrane proton gradient (Δp H), or the Δp , respectively. After a 1-min incubation, uptake was initiated by adding L-[14 C]glutamate to a final concentration of 1.9 μ M. The uptake reaction was terminated as described above.

(ii) Artificial ion gradients. The buffers used to generate artificial gradients are listed in Table 2. Membrane vesicles were washed twice in buffer 1 and subsequently incubated for 2 h at 4°C in the same buffer. After centrifugation for 5 min

TABLE 2. Buffers used to generate artificial ion gradients and resulting forces

	Comp	oosition ^b			
Buffer ^a	MES (mM)	Other ingredient(s) ^d	Valinomycin ^c	Force(s)	
1 ^e	20	НАс, КОН	_	None	
2^e	120	Mglu	+	Δp	
3^e	20	HAc, Mglu	+	$\Delta\Psi$	
4^e	120	KOH	+	ΔpH	
5	20	HAc,	_	Δp Na	
		NaOH		-	
6	20	HAc,	+	$\Delta p \text{Na} + \Delta \Psi$	
		NaOH		_	
7	120	NaOH	_	$\Delta p \text{Na} + \Delta p \text{H}$	
8	120	NaOH	+	$\Delta p \text{Na} + \Delta p$	

^a Adjusted to pH 6.0 with methylglucamine or H₂SO₄; 5 mM MgSO₄ was present in all cases.

at $200,000 \times g$ the membranes were resuspended in buffer 1 to a concentration of approximately 40 mg of protein per ml. Uptake driven by specific ion gradients was initiated by diluting the membrane vesicles 100-fold into the appropriate buffer (Table 2) containing 1-[14 C]glutamate (1.9 μ M). The reaction was terminated as described above. Care was taken to avoid contamination of buffers with sodium ions; disposable plastic materials and ultrapure chemicals were used in all experiments. The uptake experiments were performed at 37° C unless stated otherwise. The kinetic parameters for transport, apparent K_m and $V_{\rm max}$ were estimated from the initial rates of uptake of the labeled amino acid determined after 10 s. Results were analyzed by fitting the data to the Michaelis equation.

Protein determination. Protein was measured by the method of Lowry et al. (26), using bovine serum albumin as the standard.

Nomenclature. In order to discriminate between Na $^+$ /glutamate, H $^+$ /glutamate and Na $^+$ /H $^+$ /glutamate transport proteins, the gene designations gltS, gltP, and gltT are used. Additionally, the subscripts Bs, Bc, Bsu, and Ec (B or K-12) are used to discriminate between the genes or proteins of B. stearothermophilus, B. caldotenax, B. subtilis, and E. coli (B or K-12), respectively.

Nucleotide sequence accession numbers. The nucleotide sequence accession numbers for the proteins discussed in this article are as follows: $GltP_{Bsu}$, U15147; $GltT_{Bs}$, M86508 (43); $GltT_{Bc}$, M86509 (43); $GltP_{Ec}$, M84805 (44); $DctA_{Rm}$, J03683 (48), M26399 (10), and M26531 (16); $DctA_{Rlp}$, S38912 (45); $DctA_{Rlp}$, Z11529 (31); $ASCT1_{Hs}$, L14595 (3); $SATT_{Hs}$, L19444 (36); $GluA_{Hs}$, U03504, D26443, and L19158 (2, 21, 37); $GluB_{Hs}$, U03505 (2); $GluC_{Hs}$, U03506 (2); GLAST (GLUT-1), X63744 (38) and S59158 (39); GLT-1, X67857 (29); EAAC1, L12411 (20).

RESULTS

Glutamate transport. (i) Effects of ionophores on glutamate transport. Membrane vesicles of B. subtilis accumulate L-glutamate at a high rate and at high steady-state levels in the presence of K-asc-PMS (Fig. 1). L-Glutamate in/out ratios of approximately 700 are reached when a specific internal volume of 3 µl/mg of protein is assumed (22, 24). Nigericin, which dissipates the transmembrane pH gradient (electroneutral K⁺/ H⁺ exchange), inhibited the uptake of L-glutamate partially. Valinomycin, which dissipates the membrane potential (K⁺ ionophore), decreased the uptake of L-glutamate even further (Fig. 1). Complete inhibition of glutamate uptake was observed in the presence of nigericin and valinomycin (Fig. 1). These findings, and the observation that NaCl (10 mM) did not affect transport (Fig. 1), suggest that L-glutamate is transported in B. subtilis by an electrogenic process in symport with protons. Similar results were obtained with membrane vesicles of E. coli BK9MDG/pGTU2000 in which the glutamate transport protein of B. subtilis was functionally expressed (data not shown).

(ii) Artificial gradients. Since L-glutamate is an anionic species at a physiological pH, the electrogenic nature of the transport process suggests that at least two cations are symported with the substrate. To specify the nature of the cotransported cations more precisely, experiments in which glutamate uptake

^b MES, morpholineethanesulfonic acid; Mglu, methylglucamine.

Final concentration, 2 nmol/mg of protein.

^d 100 mM each.

^e Sodium ion contamination, ≤10 μM.

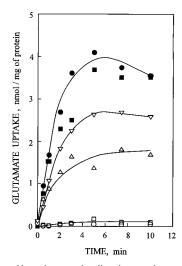


FIG. 1. Effects of ionophores and sodium ions on the uptake of L-glutamate in membrane vesicles of *B. subtilis*. Uptake of L-glutamate (1.9 μ M) was measured at 37°C in oxygen-saturated 50 mM potassium phosphate (pH 6.0) plus 5 mM MgSO₄. Uptake was performed in the absence (\bigcirc) or presence (\blacksquare) of the electron donor system K-asc–PMS either without ionophores or in the presence of nigericin (1 μ M) (\bigcirc), valinomycin (2 nmol/mg of protein) (\triangle), nigericin plus valinomycin (\square), or 10 mM NaCl (\blacksquare).

was driven by artificial ion gradients were carried out. The Δp as well as its components $\Delta\Psi$ and ΔpH were able to drive L-glutamate uptake (Fig. 2). A sodium gradient, whether or not in addition to an artificially generated $\Delta p, \, \Delta\Psi, \, \text{or} \, \Delta pH, \, \text{had no}$ effect on glutamate uptake (data not shown). The sodium gradients were generated by varying the external sodium concentration among 0, 0.2, 0.5, 1, 5, 10, 50, and 100 mM; the initial internal concentrations were less than 10 μM . These data strongly suggest that only protons are cotransported with glutamate.

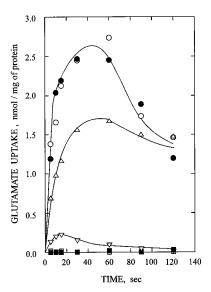


FIG. 2. Uptake of L-glutamate in membrane vesicles of *B. subtilis* driven by artificially imposed ion gradients. Glutamate uptake was performed in the presence of a $\Delta p(\bigcirc)$, Δp plus $\Delta p \text{Na}(\bullet)$, $\Delta p \text{H}(\triangle)$, $\Delta \Psi(\nabla)$, or sodium motive force (\square) as described in Materials and Methods. Control experiments were performed by diluting the membrane vesicles 100-fold into the buffer in which the membranes were resuspended (\blacksquare).

TABLE 3. Inhibition of the initial uptake rate of L-glutamate in membrane vesicles of *B. subtilis* and *E. coli* BK9MDG/pGTU2000

T 1724 a	% Inhibition			
Inhibitor ^a	B. subtilis	BK9MDG/pGTU2000		
L-Glutamate	91	64		
D-Glutamate	27	19		
L-Glutamine	12	8		
L-Aspartate	84	86		
L-Asparagine	5	18		
β-Hydroxyaspartate	84	83		
Cysteic acid	80	64		
α-methyl-Glutamate	1	0		

^a Added in a 50-fold excess. Final L-[¹⁴C]glutamate concentration, 1.9 μM.

(iii) Substrate specificity. The substrates used to examine the substrate specificity of the L-glutamate transporter are listed in Table 3. The effects of a 50-fold excess of unlabeled substrates on the initial rate of L-glutamate uptake indicate that the transport system is specific for L-glutamate, L-aspartate, β -hydroxyaspartate, and cysteic acid but not for D-glutamate, α -methyl-glutamate, L-glutamine, or L-asparagine (Table 3).

Cloning of the glutamate transport gene of B. subtilis. The $gltP_{\mathrm{Bsu}}$ gene was cloned as outlined in Materials and Methods. A Glu⁺ transformant, originating from the *HindIII* chromosomal digest, was grown in liquid M9G medium, and plasmid DNA was isolated. The isolated plasmid pGTU100 (pKK223-3 harboring a 2.1-kb HindIII insert) conferred upon retransformation a Glu⁺ phenotype on E. coli JC5412. Uptake of Lglutamate by whole cells (E. coli JC5412) harboring pGTU100 (GltP_{Bsu}) was severalfold higher than that in cells harboring pKK223-3 (data not shown). Membrane vesicles derived from strain BK9MDG/pGTU100 also showed significantly higher L-glutamate uptake than membrane vesicles derived from strain BK9MDG/pKK223-3 (data not shown). The kinetics of glutamate uptake in membrane vesicles of E. coli BK9MDG/ pGTU100 and BK9MDG/pKK223-3 as well as that of B. subtilis 6GM was determined. The apparent K_m and V_{max} for glutamate uptake in membrane vesicles of B. subtilis 6GM were 9 μM and 65 nmol·min⁻¹·mg of protein⁻¹, respectively (Fig. 3). The data for E. coli BK9MDG/pGTU100 were 9 μ M and $12.4 \text{ nmol} \cdot \text{min}^{-1} \cdot \text{mg of protein}^{-1}$, respectively (Fig. 3,

Nucleotide sequence and coding regions. From sequencing data of the 3' and 5' ends of the cloned DNA fragment, it became clear that the multiple cloning site of pKK223-3 had been partly duplicated, resulting in its presence at both ends of the cloned DNA fragment. Southern blot analysis revealed that the 1,820-bp *SphI-HindIII* fragment, together with a 275-bp fragment upstream of the *SphI* site of pGTU100, originates from *B. subtilis* 6GM. The sequencing strategy for this 2,095-bp fragment is presented in Fig. 4; the sequence is shown in Fig. 5 (the duplicated 27-bp vector sequence GCATGCAAGCTT GGCTGCAGGTCGACG upstream of the *B. subtilis* sequence is not included in this figure). Between positions 499 and 1741 an open reading frame of 1,242 bp was found. The deduced polypeptide contains 414 amino acid residues (molecular mass, 44,707 Da).

Amino acid composition and hydropathy. The amino acid composition of $GltP_{Bsu}$ is typical of an integral membrane protein; it contains 68.9% nonpolar and 31.1% polar residues (5). Of the 414 residues, 31 (7.5%) are basic (His residues not taken into account) and 27 (6.5%) are acidic. The hydropathy

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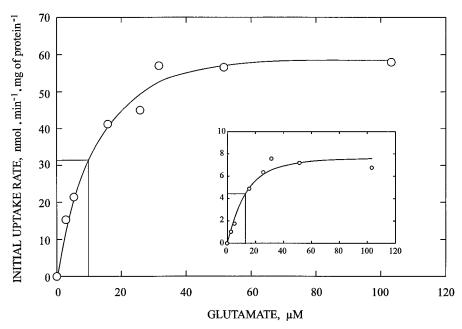


FIG. 3. Saturation kinetics of glutamate transport in membrane vesicles of *B. subtilis* 6GM and *E. coli* BK9MDG/pTU100 (inset). The kinetic parameters for transport, apparent K_m and V_{max} , were estimated from the Michaelis-Menten equation that was used to fit the experimental data. Uptakes were performed at 37°C by diluting membrane vesicles 100-fold into 50 mM potassium phosphate (pH 6.0)–5 mM MgSO₄–10 mM K-asc–100 μ M PMS. After a 1-min incubation, L-[1⁴C] glutamate (0 to 100 μ M) was added, and initial rates of uptake were determined after 10 s. Samples were further handled as described in Materials and Methods.

profile of $GltP_{Bsu}$, calculated by the method of Eisenberg et al. (9), predicts a minimum of 10 membrane-spanning regions (data not shown).

DISCUSSION

The studies of uptake in *B. subtilis* membrane vesicles demonstrate that L-glutamate is transported electrogenically in symport with at least two protons. This is shown by the effect of ionophores on K-asc-PMS-energized transport as well as L-glutamate transport in the presence of artificially imposed ion gradients. The $\Delta\Psi$ and Δ pH alone can drive transport but not an inwardly directed Na⁺ gradient. Also, Δp Na does not stimulate Δp -, Δp H-, or $\Delta\Psi$ -driven uptake. Our results are in accordance with previous observations of L-glutamate transport in whole cells of *B. subtilis* (41). Thus, it appears that L-glutamate transport in *B. subtilis* is coupled to protons whereas sodium ions and protons are used in the related thermophiles *B. stearothermophilus* and *B. caldotenax* (7, 14).

Studies in membrane vesicles of B. subtilis and E. coli

BK9MDG/pGTU2000, in which GltP_{Bsu} was functionally expressed, revealed that the L-glutamate transporter is specific for the substrates L-glutamate and L-aspartate. L-Glutamate transport is inhibited by the inhibitors β -hydroxyaspartate and cysteic acid, which also inhibit the H⁺/glutamate symport protein (GltP) of *E. coli* (35). The inhibitor of the Na⁺/glutamate symporter (GltS) of *E. coli*, α -methyl-glutamate (35), did not affect GltP_{Bsu}.

GltP_{Bsu} is homologous to various carboxylate transport proteins (see below). On the basis of the similarities between GltP_{EcK12}, GltT_{Bs}, and GltT_{Bc}, the putative start codon is located at positions 499 to 501, which correspond to the leucine codon UUG. UUG is not commonly used as a translation initiation codon, but its use has been described before (11). A putative ribosome binding site is located upstream of the UUG codon, which shows extensive similarity to the 3' end of *B. subtilis* 16S rRNA (13, 28). The stop codon (positions 1741 to 1743) is immediately followed by an inverted repeat (ΔG° , -23.4 kcal [ca. -97.9 kJ]/mol, calculated by the method of Tinoco et al. [40]) and has features typical of a putative

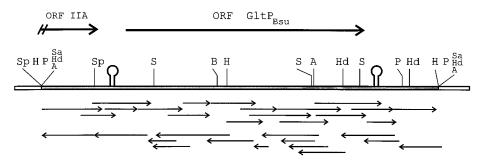


FIG. 4. Sequencing strategy. Part of the vector sequence (open box), the cloned fragment (shaded box), and the position and direction of transcription of the putative gene upstream of $gltP_{Bsu}$ and $gltP_{Bsu}$ are shown. ORF, open reading frame. The regions sequenced are indicated below (arrows). Sp, SphI; S, StuI; Sa, SalI, B, BalI; H, HindIII; A, AccI; Hd, HindIII; P, PstI.

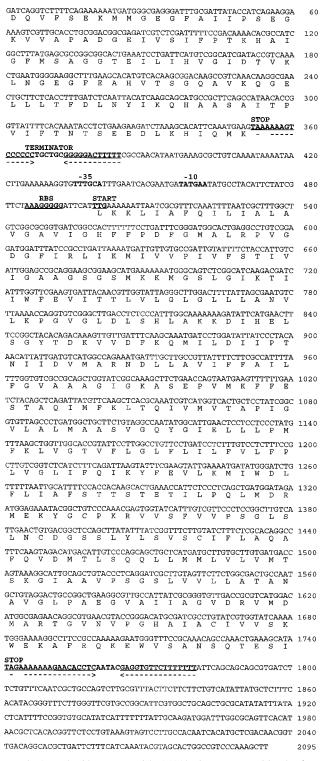


FIG. 5. Nucleotide sequence of the 2,095-bp fragment comprising the $gltP_{\rm Bsu}$ gene of B. subitlis and flanking regions. The start and stop codons, a putative promoter (-35/-10), a possible ribosome binding site (RBS), and possible terminator sequences (--><--) are indicated. The amino acid sequence deduced from the DNA sequence of the $gltP_{\rm Bsu}$ gene and the putative open reading frame upstream of $gltP_{\rm Bsu}$ are shown below the DNA sequence.

rho-independent transcription terminator sequence (32). A transcription termination sequence is also found at positions 352 to 384, i.e., immediately upstream of $gltP_{\rm Bsu}$. Several promoter elements can be identified between this terminator sequence and the start codon. For none of the sequences is the expected distance of 16 to 18 bp observed (13, 28). A putative promoter with a 15-bp spacing between the -35 and -10 regions is indicated in Fig. 5. Upstream of the $gltP_{\rm Bsu}$ gene the 3' end of a putative open reading frame was found (Fig. 5). This region encodes 117 amino acid residues of a polypeptide which is homologous to IIA proteins of several phosphoenol-pyruvate-sugar-phosphotransferase systems as well as the IIA domain of the lactose transport protein (LacS) of Streptococcus thermophilus (30).

Sequence comparison of the H⁺/glutamate symport protein of B. subtilis and sequences in the EMBL data bank revealed a number of homologous proteins. All these proteins transport one or more of the structurally related compounds glutamate, aspartate, fumarate, malate, and/or succinate. The systems comprise sodium as well as proton-coupled transporters. Extensive similarity was found between GltP_{Bsu} and the thermophilic Na⁺/H⁺/glutamate symport proteins of B. stearothermophilus and B. caldotenax (43) and between GltP_{BSU} and the mesophilic H⁺/glutamate symport protein of E. coli K-12 (44) (in each case the identity was approximately 44%). The similarity between GltP_{Bsu} and the C₄-dicarboxylate carriers of Rhizobium meliloti (10, 16, 48) and Rhizobium leguminosarum (31, 45) corresponds to approximately 34% identical residues. GltP_{Bsu} also is approximately 26% identical with a third group of proteins: the Homo sapiens Na⁺/alanine/serine/cysteine/ threonine transporter (ASCT1_{Hs} [adult motor brain]) (3), Na⁺/alanine/serine/cysteine transporter (SATT_{Hs} [hippocampus]) (36), excitatory glutamate transporters 1 to 3 (motor cortex) (2, 21, 37), and glutamate transporter (GLTRpa1 [brain and pancreas]) (27); the Rattus norvegicus Na⁺/glutamate/aspartate transporters GLAST (brain) (38) and GLUT-1 (brain) (39) and Na⁺/glutamate transporter GLT-1 (brain glial cells) (29); and the Oryctolagus cuniculus Na⁺/glutamate transporter (EAAC1 [rabbit small intestine]) (20). On the other hand, no significant similarity exists between GltP_{Bsu} and the Na⁺/glutamate symport proteins of E. coli B (6) and K-12 (19) (data not shown).

Alignment of the homologous proteins reveals that identical and similar residues are distributed along the entire amino acid sequence (Fig. 6). Also, when the proton- and sodium-dependent symporters are compared, it appears that differences are not confined to one or a few regions, making it difficult to predict whether a given residue or protein segment determines the cation selectivity. Moreover, changes such as substituting a single amino acid may already alter the cation selectivity, as has been observed for the melibiose transport protein of Klebsiella pneumoniae (12). The number of membrane-spanning helices of the proteins indicated in Fig. 6 as predicted according to the method of Eisenberg et al. (9) ranges from 9 to 12. In the case of the C₄-dicarboxylate carrier of R. meliloti, the secondarystructure predictions are substantiated by a limited number of PhoA and LacZ gene fusions, and the number of membranespanning helices was proposed to be 12 (17). In addition, indicative of similar secondary and tertiary structures are the gene fusions between $gltP_{\rm Ec}$ and $gltT_{\rm Bs}$ that result in fully functional glutamate transport proteins (41). On the basis of the similarity between the proteins, the hydropathy profiles of the individual sequences, and the topology rules proposed by Von Heijne (46), we propose that the transporters shown in Fig. 6 may have a similar secondary structure with 12 putative transmembrane-spanning α -helices. The locations of these putative

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GltPBsu	LKK	3	GltPBsu	KLTQIVMVTAPIGVLALMAASVGQYGIELLL - PMFKLVGTVFLGLFLIL	229
GltTBc	MKR	3	GltTBc	YVTNQIMKFAPFGVFALIGVTVSKFGVESLIPLSKLVIVVYATMLFFI	237
GltTBs	MKR	3	GltTBs	YVTNQIMKFAPFGVFALIGVTVSKFGVESLIPLSKLVIVVYATMVFFI	237
GltPEc DctARl	MKNIK MIAAPLDAVAGSKGKKPFY	5	GltPEc DctARl	KVTHMVMRYAPVGVFALÍAVTVANFGFSSLMPLAKLVLLVHFAILFFA KLVAILMKAAPIGAFGAMAFTIGKYGVGSIANLAMLIGTFYITSLLFV	245
DctARm	MLPDWACHVEDI-MIIEHSAEVRGKTPLY	19 28	DctARm	RLVAILMKAAPIGAFGAMAFTIGKYGIASIANLAMLIGTFYLTSLEV	247 256
DctARlp	MRGLRVCMHQVEEIILIVENLAEVRGKTPHY	31	DctARlp	RLVAILMKAAPIGAFGAMAFTIGKYGVASIANLAMLIGTFYLTSFLFV	258
SATTHS	MEKSNETNGYLDSAQAGPARRPGAPGPRRDARRCAASCG	39	SATTHS	VLVSWIMWYVPVGIMFLVGSKIVEMKDIIVLVTSLGKYIFASILGHVIHG	306
ASCT1Hs	MEKSNETNGYLDSAQAGPAAGPGAPGTAAGRARRCARFLRR	41	ASCT1Hs	VLVSWIMWYVPVGIMFLVGSKIVEMKDIIVLVTSLGKYIFASILGHVIHG	309
GLT-1 GluBHs	MASTEGANNMPKQVEVRMHDSHLSSEEPKHRNLGMRMCD-KLGK	43	GLT-1 GluBHs	EVSDHDHVVFPAGIACLICGKIIAIKDLEVVARQLGMYMITVIVGLIIHG	328
GLAST	MASTEGANNMPKQVEVRMPDSHLGSEEPKHRHLGLRLCD-KLGK MTKSNGEEPRMGSRMERFQQGVRKRTLLAKKKVQNITKEDVKSYL-FR	43 47	GLAST	KLVIMIMMYSPLGIACLICGKIIAIKDLEVVARQLGMYMVTVIIGLIIHG RLVAVIMMYAPLGILFLIAGKILEMEDMGVIGGQLAMYTVTVIVGLLIHA	328 329
GluAHs	MTKSNGEEPKMGGRMERFQQGVRKRTLLAKKKVQNITKEDVKSYL-FR	47	GluAHs	RLVAVIMWYAPVGILFLIAGKIVEMEDMGVIGGQLAMYTVTVIVGLLIHA	329
EAACl	MGKPARKGCDS-KRFLKN	17	EAAC1	KIVQIIMCYMPLGILFLIAGKIIEVEDWEIFR-KLGLYMVTVLSGLAIHS	297
GluCHs	MGKPARKGCPSWKRFLKN	18	GluCHs	KIVQIIMCYMPLGILFLIAGKIIEVEDWEIFR-KLGLYMATVLTGLAIHS	297
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GltPBsu	-LIAFQILIALAVGAVIGHFFPDFGMALR-PVGDGFIRLIKM	43	GltPBsu	FVLFPLVGL-IFQIKYFEVLKMIWDLFLIAFSTTSTETILPQLMDRME-K	277
GltTBc	IGLAWQIFIGLILGIIVGAIFYGNPKVAAYLQ-PIGDIFLRLIKM	47	GltTBc	FAVLGGVAK-LFGINIFHIIKILKDELILAYSTASSETVLPRIMDKME-K	285
GltTBs	IGLAWQIFIGLILGIIVGAIFYGNPKVATYLQ-PIGDIFLRLIKM	47	GltTBs	FVVLGGVAK-LFGINIFHIIKILKDELILAYSTASSETVLPKIMEKME-N	285
GltPEc	FSLAWQILFAMVLGILLGSYLHYHSDSRDWLVVNLLS-PAGDIFIHLIKM	54	GltPEc DctARl	LVVLGIVAR-LCGLSVWILIRILKDELILAYSTASSESVLPRIIEKME-A	293
DctAR1 DctARm	SHLYVQVLVAIAAGILLGHFYPELGTQLK-PLGDAFIKLVKM RHLYVQVLAATAAGILLGHFYPDIGTELK-PLGDAFIRLVKM	60 69	DctART	FIVLGAVAR-YNGFSIVALLRYIKEELLLVLGTSSSEAALPGLMNKME-K FIVLGAVAR-YNGFSILSLIRYIKEELLLVLGTSSSEAALPGLMNKME-K	295 304
DctARlp	RHLYVQVLAAIAVGILLGYFYPDVGSKMK-PLGDAFIMLVKM	72	DctARlp	FMVLGAVAR-YNGFSIVALIRYIKEELLLVLGTSSSEAALPGLMNKME-K	306
SATTHS	AKLVLLTVSGVLAGAGLGAALRGLSLSRTQVTYLAFP-GEMLLRIVRM	86	SATTHS	GIVLPLIYFVFTRKNPFRFLLGLLAPFATAFATCSSSATLPSMMKCIEEN	356
ASCT1Hs	QALVLLTVSGVLAGAGLGAALRGLSLSRTQVTYLAFP-GEMLLRMLRM	88	ASCT1Hs	GIVLPLIYFVFTRKNPFRFLLGLLAPFATAFATCSSSATLPSMMKCIEEN	359
GLT-1	NLLLSLTVFGVILGAVCGGLLR-LAAPIHPDVVMLIAFP-GDILMRMLKM	91	GLT-1	GIFLPLIYFVVTRKNPFSFFAGIFQAWÎTALGTASSAGTLPVTFRCLEDN	378
GluBHs GLAST	NLLLTLTVFGVILGAVCGGLLR-LASPIHPDVVMLTAFP-GDILMRMLKM NAFVLLTVSAVIVGTILGFALR-PYKMSYREVK-YFSFP-GELLMRMLOM	91 94	GluBHs GLAST	GIFLPLIYFVVTRKNPFSLFAGIFQAWITALGTASSAGTLPVTFRCLEEN VIVLPLLYFLVTRKNPWVFIGGLLQALITALGTSSSSATLPITFKCLEEN	378 379
GluAHs	NAFVLLTVTAVIVGTILGFTLR-PYRMSYREVK-YFSFP-GELLMRMLQM	94	GluAHs	VIVLPLLYFLVTRKNPWVFIGGLLQALITALGTSSSSATLPITFKCLEEN	379
EAAC1	NWLLLSTVVAVVLGIVIGVLVREYSNLSTLDKF-YFAFP-GEILMRMLKL	65	EAAC1	IVILPLIYFIVVRKNPFRFAMGMTQALLTALMISSSSATLPVTFRCAEEK	347
GluCHs	NWVLLSTVAAVVLGITTGVLVREHSNLSTLEKF-YFAFP-GEILMRMLKL	66	GluCHs	IVILPLIYFIVVRKNPFRFAMGMAQALLTALMISSSSATLPVTFRCAEEN	347
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GltPBsu	IVVPIVFSTIVIGAAGS-GSMKKMGSL-GI-KTIIWFEVITTLVLGLGLL	90	GltPBsu	YGCPKRVVSFVVPSGLSLNCDGSSLYLSVSCIFLAOAFOVDMTLSOOLLM	327
GltTBc	IVIPIVISSLVVGVASV-GDLKKLGKL-GG-KTIIYFEIITTIAIVVGLL	94	GltTBc	FGCPKAITSFVIPTGYSFNLDGSTLYQALAAIFIAQLYGIDMSVSQQISL	335
GltTBs	IVIPIVISSLVVGVASV-GDLKKLGKL-GG-KTIIYFEIITTIAIVVGLL	94	GltTBs	FGCPKAITSFVIPTGYSFNLDGSTLYQALAAIFIAQLYGIDMPISQQISL	335
GltPEc	IVVPIVISTLVVGIAGV-GDAKQLGRI-GA-KTIIYFEVITTVAIILGIT	101	GltPEc	YGAPVSITSFVVPTGYSFNLDGSTLYQSIAAIFIAQLYGIDLSIWQEIIL	343
DctARl	IIAĐVIFLTVATGIAGM-SDLQKVGRVAGKAMLYELTESTLALIIGLI	107	DctAR1	AGCKRSVVGLVIPTGYSFNLDGTNIYMTLAALFIAQATGTHLSWGDQILL	345
DctARm DctARlp	IIAPVIFLTVATGIAGM-TDLAKVGRVAGKAMIYFLAFSTLALVVGLV	116 119	DctARm DctARlp	AGCKRSVVGLVIPTGYSFNLDGTNIYMTLAALFIAQATDTPLSYGDQILL	354
SATTHS	IIAPVIFLTVATGIAGM-TDLAKVGRVAGKAMIYFLAFSTLALLVGLV IILPLVVCSLVSARLARCQLPRASGRHRVAYFGLTTLTASALAVA	131	SATTHS	AGCKRSVVGLVIPTGYSFNLDGTNIYMTLAALFIAQGTDTPISYGDQILL NGVDKRISRFILPIGATVNMDGAAIFQCVAAVFIAQLNNVELNAGQIFTI	356 406
ASCT1Hs	IILPLVVCSLVSGAASLDASCLGRL-GGIR-VAYFGLTTLSASALAVA	134	ASCT1Hs	NGVDKRISRFILPIGATVNMDGAAIFQCVAAVFIAQLNNIELNAGQIFTI	409
GLT-1	LILPLIISSLITGESGEDAKASGRE-GT-RAMVYYMSTTIIAAVEGVI	137	GLT-1	LGIDKRVTRFVLPVGATINMDGTALYEAVAAIFIAQMNGVILDGGQIVTV	428
GluBHs	LILPLIISSLITGLSGLDAKASGRL-GT-RAMVYYMSTTIIAAVLGVI	137	GluBHs	LGIDKRVTRFVLPVGATINMDGTALYEAVAAIFIAQMNGVVLDĞĞQIVTV	428
GLAST	LVLPLIISSLVTGMAALDSKASGKM-GM-RAVVYYMTTTIIAVVIGII LVLPLIISSLVTGMAALDSKASGKM-GM-RAVVYYMTTTIIAVVIGII	140	GLAST GluAHs	NGVDKRITRFVLPVGATINMDGTALYEALAAIFIAQVNNFDLNFGQIITI NGVDKRVTRFVLPVGATINMDGTALYEALAAIFIAQVNNFELNFGOIITI	429
GluAHs EAAC1	VILPLIVSSMITGVAALDSNVSGKI-GL-RAVLYYFCTTIIAVILGIV	140 111	EAAC1	NRVDKRITRFVLPVGATINMDGTALYEAVAAVFIAQLNDMDLSIGOIITI	429 397
GluCHs	IILPLIISSMITGVAALDSNVSGKI-GL-RAVVYYFCTTLIAVILGIV	112	GluCHs	NQVDKRITRFVLPVGATINMDGTALYEAVAAVFIAQLNDLDLGIGQIITI	397
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GltPBsu GltTBc	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVVDFKQMILDIIPTN	135	GltPBsu GltTBc	10> <iiiiiii><11><000000 MLVLYMTSKGIAAVPSGSLVVLLATANAV-GLPABGVÄIJAGVDRVMOMA</iiiiiii>	376
GltTBc	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVVDFKÖMÏLDÍTÞÍN AANIFQPGAGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN	143	GltTBc	10	384
	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVVDFKQMILDIIPTN			10> <iiiiiii><11><000000 MLVLYMTSKGIAAVPSGSLVVLLATANAV-GLPABGVÄIJAGVDRVMOMA</iiiiiii>	
GltTBc GltTBs GltPEc DctARl	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVVDFKÖMÏLDTIPŤN AANIFQPGAGVINKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN AANIFQPGTGVINKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN LANVFQPGAGVINSQLATVDISKYQSTTEAVQSSS-HGIMGTILSLVPTN VANVVQPGAGMNIDPASLDPAAVATFAAKAH-EQSIVĞFİTNIIPTT	143 143 150 153	GltTBc GltTBs GltPEc DctAR1	MLVLWMTSKGIAAVPSGSLVVLLATANAV-GLPÄRGVÄITAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPLEGLÄFIAGIDRILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPLEGLÄFIAGIDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGSV-GIPLEGLÄFIAGVDRILDMA LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALILGIDRTMSEG	384 384 392 395
GltTBe GltTBs GltPEc DctARl DctARm	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVVDFKÖMÍLDÍ TPŤN AANIFQPGAGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN AANIFQPGTGVNNKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN LANVFQPGAGVMSQLATVDISKYQSTTBAVQSSS-HGIMGTILSLVPTN VANVVQPGAGMNIDPASLDPAAVATFAAKAH-EQSIVĞPĽTNÍIPTT VANVVQPGAGMHIDPASLDAKAVATYAKKAH-EQSIVĞPĽTNÍIPTT	143 143 150 153 162	GltTBc GltTBs GltPEc DctAR1 DctARm	MLVLVMTSKGIAAVPSGSLVVLLATANAV-GLPAĞGVAIIAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGIDRILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGIDRILDMA VLTLMVTSKGIAGVPGYSFVVLLATLGTV-GIPLEGLAFIAGVDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGSV-GIPLEGLAFIAGVDRILDMA LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALLIGIDRRMSEC LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALLIGIDRRMSEC	384 384 392 395 404
GltTBc GltTBs GltPEc DctARl DctARm DctARlp	LANVLKPGVGLDLSHLAKKDIHELSGYT DKVV - D PKOMĬĹDŤIPŤN AANIFQPGAGVNNKSLEKTDLOSYVDTTNEVQH HSMVETFVNIVPKN AANIFQPGTGVNNKSLEKTDLOSYVDTTNEVQH HSMVETFVNIVPKN LANVFQPGAGVDMSQLATVDLSKYQSTTEAVQSSS-HGIMGTILSLVPTN VANVVQPGAGMNIDPASLDPAAVATFAAK AH - EQSIVŠFŽTŇITPTT VANVVQPGAGMHIDPASLDAKAATYAEK AH - EQSIVŠFŽMNITPŤT VANVVQPGAGMHIDPASLDAKAAIATYAEK AH - EQSIVŠFŽMNITPŤT VANVVQPGAGMHIDPASLDAKAAIATYAEK AH - EQSIVŠFŽMNITPŤT	143 143 150 153 162 165	GltTBc GltTBs GltPEc DctAR1 DctARm DctARlp	MLVLVMTSKGIAAVPSGSLVVLLATANAV-GLPASGVAITAGVDRVMDMA LLVLMVTSKGIAAVPSGSLVVLLATANAV-GLPASGVAITAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPPEGLAFIAGIDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGTV-GIPPEGLAFIAGVDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGSV-GIPPEGLAFIAGVDRILDMA LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALTLGIDRFMSEC LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALTLGIDRFMSEC LLIAMLSSKGAAGITGAGFITLAATLSAVPSVPVAGMALTLGIDRFMSEC	384 384 392 395 404 406
GltTBc GltTBs GltPEc DctARl DctARm DctARlp SATTHs	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVVDFKÖMÍLDÍ TPŤN AANIFQPGAGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN AANIFQPGTGVNNKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN LANVFQPGAGVMSQLATVDISKYQSTTBAVQSSS-HGIMGTILSLVPTN VANVVQPGAGMNIDPASLDPAAVATFAAKAH-EQSIVĞPĽTNÍIPTT VANVVQPGAGMHIDPASLDAKAVATYAKKAH-EQSIVĞPĽTNÍIPTT	143 143 150 153 162	GltTBc GltTBs GltPEc DctAR1 DctARm	MLVLVMTSKGIAAVPSGSLVVLLATANAV-GLPÄEGVÄIIAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGIDRILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGIDRILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPLEGLAFIAGVDRILDMA VLTLMVTSKGIAGVFGVSFVVLLATLGSV-GIPLEGLAFIAGVDRILDMA LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALLIGIDRFMSEC LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALLIGIDRFMSEC LLVAMLSSKGAAGITGAGFITLAATLSVPSVPVAGMALLIGIDRFMSEC LLVTATASSVGAAGVPAPGVLTIAIILEAI-GLPHHDLPLILAVDMYJVDRT	384 384 392 395 404 406 455
GltTBc GltTBs GltPEc DctARl DctARm DctARlp	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVVDFKÖMÍLDÍTPTN AANIFQPGAGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN AANIFQPGTGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN LANVFQPGAGVNDGOLATVDISKYQSTTEAVQSSS-HGIMGTLISLVPTN VANVVQPGAGMNIDPASLDPAAVATPAKAH-EQSIVÖFTÍNTÍPTT VANVVQPGAGMHIDPASLDAKAVATYAEKAH-EQSITÖFINNITPTT VANVVQPGAGMHIDPASLDAKAVATYAEKAH-EQSVTÖFINNITPTT LÄFTIKPGSGAQTLQSSDLGLEDSGPPFVPKETV-D-SFLDLARNLFPSN	143 143 150 153 162 165 179	GltTBc GltTBs GltPEc DctARl DctARm DctARlp SATTHs	MLVLVMTSKGIAAVPSGSLVVLLATANAV-GLPASGVAITAGVDRVMDMA LLVLMVTSKGIAAVPSGSLVVLLATANAV-GLPASGVAITAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPPEGLAFIAGIDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGTV-GIPPEGLAFIAGVDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGSV-GIPPEGLAFIAGVDRILDMA LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALTLGIDRFMSEC LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALTLGIDRFMSEC LLIAMLSSKGAAGITGAGFITLAATLSAVPSVPVAGMALTLGIDRFMSEC	384 384 392 395 404 406
GltTBc GltTBs GltPEc DctAR1 DctARM DctAR1p SATTHS ASCT1HS GLT-1 GluBHS	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVV-DFKÖMÍLDÍTPÍN AANIFQPGAGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN AANIFQPGTGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN LANVFQPGAGWIDDASLDFAVATFAKAH-EQSIVÖFÜNITPTT VANVVQPGAGMNIDPASLDFAVATFAKAH-EQSIVÖFÜNITPTT VÄNVVQPGAGMHIDPASLDAKAIATYAEKAH-EQSIVÖFÜNITPTT VÄNVVQPGAGMHIDPASLDAKAIATYAEKAH-EQSIVÖFÜNNITPTT VÄNVTQPGAGMIDPASLDAKAIATYAEKBH-EQSIVÖFÜNNITPTT LÄFTIKPGSGAQTLQSSDIGLEDSGPPVPETV-D-SFLDLARNLFPSN LAFIIKPGSGAQTLQSSDIGLEDSGPPVPETV-D-SFLDLARNLFPSN LAFIIKPGSGATTLGSDIGLEDSGPPVPETV-D-SFLDLARNLFPSN LÄVLÄHPGMPKLKKQLGPGKKNDEVSSLD-AFLDLIRNLFPEN LÜLAIHPGMPKLKKQLGPGKKNDEVSSLD-AFLDLIRNLFPEN	143 143 150 153 162 165 179 182 179	GltTBC GltTBS GltPEC DctARl DctARM DctARlp SATTHS ASCTIHS GLT-1 GluBHS	MLVLVMTSKGIAAVPSGSLVVLLATANAV-GLPABGVAIIAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVBGLAFIAGIDRILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVBGLAFIAGIDRILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVBGLAFIAGVDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGSV-GIPLEGLAFIAGVDRILDMA LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALILGIDRFMSEC LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALILGIDRFMSEC LLVATATASSVGAAGVPAGVLTIAATLEAT-GLPTHDLPLILAVDWIVDRT LVTATASSVGAAGVPAGGVLTTAIILEAT-GLPTHDLPLILAVDWIVDRT LVTATASSVGAAGVPAGGVLTTAIILEAT-GLPTHDLPLILAVDWIVDRT SLTATLASVGAASIPSAGLVTMLILITAV-GLPTEDISLLVAVDWILDRM SLTATLASVGAASIPSAGLVTMLILITAV-GLPTEDISLLVAVDWILDRM SLTATLASVGAASIPSAGLVTMLILITAV-GLPTEDISLLVAVDWILDRM	384 384 392 395 404 406 455 458 477 477
GltTBc GltTBs GltTBs GltPEc DctARl DctARRm DctARlp SATTHS ASCT1HS GLT-1 GluBHS GLAST	LANVLKPGVGLDLSHLAKKDLHELSGYT-DKVV-DFKÖMÍLÐÍ TPÍN AANIFQPGAGVNMKSLEKTDLQSYVDTTNEVQHHSMVETFVNIVPKN AANIFQPGTGVNMKSLEKTDLQSYVDTTNEVQHHSMVETFVNIVPKN LANVPQPGAGVDMSQLATVDLSKYQSTTEAVQSSS-HSIMGTLISLUPTN VANVVQPGAGMHIDPASLDPAAVATFAAKAH-EQSIVĞFÍTNÍIPTT VANVVQPGAGMHIDPASLDAKAVATYAEKAH-EQSIVĞFÍTNÍIPTT VANVVQPGAGMHIDPASLDAKAIATYAEKAH-EQSIVĞFÍTNIIPTT LÄFIIKPGSGAQTLQSSDLGLEDSGPPVPKETV-D-SFLDLARNLFPSN LÄTLIKPGSSAQTLQSSDLGLEDSGPPVPKETV-D-SFLDLARNLFPSN LÄTLAIHPGNFKLKKQLGPGKKNDEVSSLD-AFLDLIRNLFPEN LÜLAIHPGNPKLKKQLGPGKKNDEVSSLD-AFLDLIRNLFPEN LÜLAIHPGKTK-ENNYREGKLVQVTAAD-AFLDLIRNLFPEN	143 143 150 153 162 165 179 182 179 179	GltTBc GltTBs GltPEc DctARl DctARm DctARlp SATTHS ASCTIHS GLT-1 GluBHS GLAST	MLVLVMTSKGIAAVPSGSLVVLLATANAV-GLPÄGGVÄITAGVDRVMDMA LLVLMVTSKGIAAVPSGSLVVLLATANAV-GLPÄGGVÄITAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGIDR ILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGSV-GIPLEGLAFIAGVDR ILDMA VITLMVTSKGIAGVPGVSFVVLLATLGSV-GIPLEGLAFIAGVDR ILDMA LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALILGIDRFMSEC LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALILGIDRFMSEC LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALILGIDRFMSEC LLVATASSVGAAGVPAGGVLTTAIILEAI-GLPTHDLPLILAVDMIVDET LVTATASSVGAAGVPAGGVLTTAIILEAI-GLPTHDLPLILAVDMIVDET SLTATLASIGAASIPSAGLVTMLLILITAV-GLPTEDISLLVAVDWLLDRM SLTATLASVGAASIPSAGLVTMLILITAV-GLPTEDISLLVAVDWLLDRM SITATLASIGAASIPSAGLVTMLILITAV-GLPTEDISLLVAVDWLLDRM SITATAASIGAAGIPQAGLVTMVIVLTSV-GLPTEDITLILIAVDWFLDRL	384 384 392 395 404 406 455 458 477 477
GltTBc GltTBs GltPEc DctARl DctARm DctARlp SATTHS ASCT1HS GLT-1 GluBHS GLAST GluAHS	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVV-DFKGMŤLDÍŤPŤN AANIFQPGAGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN AANIFQPGTGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN LANVFQPGAGWINDFASLDPAAVATPAKBEIMETTLSLUPTN VANVVQPGAGMHIDPASLDAKAVATYAEKAH-EGSITGFTNITPTT VANVVQPGAGMHIDPASLDAKAVATYAEKAH-EQSITGFLMNITPŤT LÄPTIKPGSGAGTLQSSDLGLEDSGPPPVRETV-D-SFLDLARNLFPSN LAFTIKPGSGAGTLQSSDLGLEDSGPPPVRETV-D-SFLDLARNLFPSN LAFTIKPGNFLKKQLGPGKKNDEVSSLD-AFDLIRNLFPSN LVILAIHPGNFLKKQLGPGKKNDEVSSLD-AFDLIRNLFPEN LVILAIHPGNFLKKQLGPGKKNDEVSSLD-AFDLIRNLFPEN LVILAIHPGNFLKKQLGPGKKNDEVSSLD-AFDLIRNLFPEN LVILAIHPGNFLKKQLGPGKKNDEVSSLD-AFDLIRNLFPEN LVILAIHPGNFLKKQLGPGKKNDEVSALD-AFDLIRNLFPEN LVILAIHPGNFLKKQLGPGKKNDEVTAAD-AFLDLIRNMFPPN LVILIHPGKGTK-ENMYREGKIVQVTAAD-AFLDLIRNMFPPN LVILIHPGKGTK-ENMYREGKIVQVTAAD-AFLDLIRNMFPPN	143 143 150 153 162 165 179 182 179 179 181	GITTBC GILTBS GITPEC DCTAR1 DCTARN DCTARN DCTAR1 SATTHS ASCTIHS GLT-1 GLUBHS GLAST GLAST GLUAHS	MLVLVMTSKGIAAVPSGSLVVLLATANAV-ĞLPÄĞĞVAI IAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-ĞIPLÜĞLAFIAGIDR ILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-ĞIPLÜĞLAFIAĞIDR ILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-ĞIPLÜĞLAFIAĞVDR ILDMA VLTLMVTSKGIAGVPGVSFVVLLATLĞTV-ĞIPLÜĞLAFIAĞVDR ILDMA LLVAMLSSKGAAGITGAĞFITLAATLSVVPSVPVAĞMALLIĞIDRFMSEÇ LLVAMLSSKGAAĞITGAĞFITLAATLSVVPSVPVAĞMALLIĞIDRFMSEÇ LLVAMLSSKGAAĞITGAĞFITLAATLSVVPSVPVAĞMALLIĞIDRFMSEÇ LLVTATASSVGAAGVPAĞÇVLTLAIILEAI-ĞLPFHDLPLILAVDMIVDRT LVTATASSVGAAGVPAĞÇVLTTAIILEAI-ĞLPFHDLPLILAVDMIVDRT SLTATLASIĞAĞAĞIPSĞĞLVTMLİLITAV-ĞLPFEDISLLVAVDMLLDRM SLTATLASVGAAĞIPAĞĞLVTMLİLITAV-ĞLPFEDISLLVAVDMLLDRM SLTATLASVĞAAĞIPAĞĞLVTMLİLITAV-ĞLPFEDITLILAVDMELDRL SITATAASIĞAĞIPÇAĞĞLVTMLVLTSV-ĞLPFEDITLILAVDMELDRL SITATAASIĞAĞIPÇAĞĞLVTMLVLTSV-ĞLPFEDITLILAVDMELDRL SITATAASIĞAĞIPÇAĞĞLVTMLVLTSV-ĞLPFEDITLILAVDMELDRL	384 384 392 395 404 406 455 458 477 477 478
GltTBc GltTBs GltTBs GltPEc DctAR1 DctARm DctARnp SATTHS ASCTIHS GLT-1 GluBHS GLAST GluAHS EAAC1	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVV-DFKÖMÍLDÍTPÍN AANIFQPGAGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN AANIFQPGTGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN LANVFQPGAGWIDHSLAFVDISKYQSTTEAVOSSS-HGIMGTILSLVPTN VANVVQPGAGMNIDPASLDPAAVATPAKAH-EQSIVÖFÜNITPTT VANVVQPGAGMHIDPASLDAKAVATYAEKAH-EQSIVÖFÜNITPTT VANVVQPGAGMHIDPASLDAKAIATYAEKAH-EQSVTÖFIMNIIPTT VANVVQPGAGMHIDPASLDAKAIATYAEKAH-EQSVTÖFIMNIIPTT VANVVQPGAGMHIDPASLDAKAIATYAEKBH-EQSVTÖFIMNIIPTT VANVVQPGAGMHIDPASLDAKAIATYAEKBH-EQSVTÖFIMNIIPTT VANTVQPGAGMTIDPASLDAKAIATYAEKBH-EQSITGFIMNIIPTT VANTVQPGAGMTIDPASLDAKAIATYAEKBFLDLARNLFPSN LAFIIKPGSGAQTLQSSDLGLEDSGPPVPEKTV-D-SFLDLARNLFPSN LVIAIHPGNPKLKKQLGPCKKNDEVSSLD-AFLDLIRNLFPEN IVIIIHPGKGTK-ENMYREGKIVQVTAAD-AFLDLIRNMFPEN IVIIHPGKGTK-ENMYREGKIVQVTAAD-AFLDLIRNMFPEN LVYSIKPGVYQKYDEIDRTGSTPEVSTVD-AMLDLIRNMFPEN	143 143 150 153 162 165 179 182 179 179	GltTBC GltTBS GltPEC DctARl DctARM DctARlp SATTHS ASCTIHS GLT-1 GluBHS GLAST GLAST GLAST GLAHS EAAC1	MLVLVMTSKGIAAVPSGSLVVLLATANAV-GLPÄGVÄIIAGVDRVMDMA LLVLMVTSKGIAAVPSGSLVVLLATANAV-GLPÄGVÄIIAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGIDRILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGIDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGSV-GIPLEGLAFIAGVDRILDMA LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALILGIDRFMSEC LLVÄÄLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALILGIDRFMSEC LLVÄÄLSSKGAAGITGAGFITLAATLSVAVPSVPVAGMALILGIDRFMSEC LLVÄÄLSSVGAAGVPAGVLTTAIILEAI-GLPTHDLPLILAVDMIVDRT LVTATASSVGAAGVPAGGVLTTAIILEAI-GLPTHDLPLILAVDMIVDRT SLTATLASIGAASIPSAGLVTMILLITAV-GLPTEDISLLVAVDMILDRM SITATLASIGAAGIPQAGLVTMVIVLTSV-GLPTDDITLIIAVDMFLDRL SITATAASIGAAGIPQAGLVTMVIVLTSV-GLPTDDITLIIAVDMFLDRL SVTATAASIGAAGIPQAGLVTMVIVLTSV-GLPTDDITLIIAVDMFLDRL SVTATAASIGAAGIPQAGLVTMVIVLTSV-GLPTDDITLIIAVDMFLDRL	384 384 392 395 404 406 455 458 477 477 478 478 446
GltTBc GltTBs GltPEc DctARl DctARm DctARlp SATTHS ASCT1HS GLT-1 GluBHS GLAST GluAHS	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVV-DFKGMŤLDÍŤPŤN AANIFQPGAGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN AANIFQPGTGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN LANVFQPGAGWINDFASLDPAAVATPAKBEIMETTLSLUPTN VANVVQPGAGMHIDPASLDAKAVATYAEKAH-EGSITGFTNITPTT VANVVQPGAGMHIDPASLDAKAVATYAEKAH-EQSITGFLMNITPŤT LÄPTIKPGSGAGTLQSSDLGLEDSGPPPVRETV-D-SFLDLARNLFPSN LAFTIKPGSGAGTLQSSDLGLEDSGPPPVRETV-D-SFLDLARNLFPSN LAFTIKPGNFLKKQLGPGKKNDEVSSLD-AFDLIRNLFPSN LVILAIHPGNFLKKQLGPGKKNDEVSSLD-AFDLIRNLFPEN LVILAIHPGNFLKKQLGPGKKNDEVSSLD-AFDLIRNLFPEN LVILAIHPGNFLKKQLGPGKKNDEVSSLD-AFDLIRNLFPEN LVILAIHPGNFLKKQLGPGKKNDEVSSLD-AFDLIRNLFPEN LVILAIHPGNFLKKQLGPGKKNDEVSALD-AFDLIRNLFPEN LVILAIHPGNFLKKQLGPGKKNDEVTAAD-AFLDLIRNMFPPN LVILIHPGKGTK-ENMYREGKIVQVTAAD-AFLDLIRNMFPPN LVILIHPGKGTK-ENMYREGKIVQVTAAD-AFLDLIRNMFPPN	143 143 150 153 162 165 179 182 179 179 181 181	GITTBC GILTBS GITPEC DCTAR1 DCTARN DCTARN DCTAR1 SATTHS ASCTIHS GLT-1 GLUBHS GLAST GLAST GLUAHS	MLVLVMTSKGIAAVPSGSLVVLLATANAV-GLPÄÄGVÄIIAGVDRVMDMA LLVLMVTSKGIAAVPSGSLVVLLATANAV-GLPÄÄGVÄIIAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPUSGLAFIAGIDRILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPUSGLÄFIAGVDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGTV-GIPUSGLÄFIAGVDRILDMA VLTAMUSSKGAAGITGAGFITLAATLSVVPSVPVAGMALLGIDRFMSEC LLVÄMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALLGIDRFMSEC LLVÄMLSSKGAAGITGAGFITLAATLSVPSVPSVPAGMALLGIDRFMSEC LLVÄATASSVGAAGVPAGGVLTIAIILEAI-GLPHDLPLILAVDMIVDRT LVTATASSVGAAGVPAGGVLTTAIILEAI-GLPHDLPLILAVDMIVDRT SLTATLASIGAAGIPSGLVTMLILITAV-GLPFEDISLLVAVDWILDRM SLTATLASIGAAGIPGAGLVTMVIVLTSV-GLPTEDISLLVAVDWLLDRM SITATAASIGAAGIPQAGLVTMVIVLTSV-GLPTEDITLLIAVDMFLDRL SITATAASIGAAGIPQAGLVTMVIVLTSV-GLPTEDITLIIAVDMFLDRL SVTATAASIGAAGVPQAGLVTMVIVLSAV-GLPAEDVTLIIAVDMLLDRP SITATASIGAAGOVPQAGLVTMVIVLSAV-GLPAEDVTLIIAVDMLLDRP SITATASSIGAAGVPQAGLVTMVIVLSAV-GLPAEDVTLIIAVDMLLDRP	384 384 392 395 404 406 455 458 477 477 478
GltTBc GltTBs GltTBs GltPEc DctAR1 DctARm DctARnp SATTHS ASCTIHS GLT-1 GluBHS GLAST GluAHS EAAC1	LANVLKPGVGLDLSHLAKKDIHELSGYT DKVV-DPKGMĬLDĬŢPŤN ANNIFQPGAGVINMKSLEKTDIGGYVDTTIMEVOHHEMVETFUNIVPKN AANIFQPGTGVNMKSLEKTDIGGYVDTTIMEVOHHEMVETFUNIVPKN LANVFQPGAGWINDFASLDPAAVATTARK-LAH-EGGIVGFĪTNIIPTT VANVVQPGAGMHIDPASLDAKAVATTARKAH-EGSIVGFĪTNIIPTT VANVVQPGAGMHIDPASLDAKAVATTARKAH-EGSITGFĪMNIIPTT LÄFIIKPGSGAGTLQSSDLGLEDSGPPPVPKETV-D-SFLDLARNLFPSN LAFIIKPGSGAGTLQSSDLGLEDSGPPPVPKETV-D-SFLDLARNLFPSN LAFIIKPGSGAGTLQSSDLGLEDSGPPPVPKETV-D-SFLDLARNLFPSN LVĪLAIHPGNPKLKKQLGPGKKNDEVSSLD-AFLDLIRNLFPEN LVILAIHPGNPKLKKQLGPGKKNDEVSSLD-AFLDLIRNLFPEN LVILIHPGKGTK-ENMYREGKIVQVTAAD-AFLDLIRNLFPEN LVIJIHPGKGTK-ENMIREGKIVRVTAAD-AFLDLIRNMFPPN LVIJIHPGKGTK-ENMIREGKIVRVSTVD-AMLDLIRNMFPEN LVYSIKPGVTQKVGEIARTGSTPEVSTVD-AMLDLIRNMFPEN LVYSIKPGVTQKVGEIARTGSTPEVSTVD-AMLDLIRNMFPEN LVSIKPGVTQKVGEIARTGSTPEVSTVD-AMLDLIRNMFPEN	143 143 150 153 162 165 179 182 179 179 181 181	GltTBC GltTBS GltPEC DctARl DctARM DctARlp SATTHS ASCTIHS GLT-1 GluBHS GLAST GLAST GLAST GLAHS EAAC1	MLVLVMTSKGIAAVPSGSLVVLLATANAV-GLPÄEGVÄIIAGVDRVMDMA LLVLMVTSKGIAAVPSGSLVVLLATANAV-GLPÄEGVÄIIAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGIDR ILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPJEGLAFIAGVDR ILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGSV-GIPLEGLAFIAGVDR ILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGSV-GIPLEGLAFIAGVDR ILDMA LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALILGIDRFMSEC LLVAMLSSKGAAGITGAGFITLAATLSVVPSVPVAGMALILGIDRFMSEC LLVATASSVGAAGVPAGGVLTTAIILEAI-GLPTHDLPLILAVDMVIDRT LVTATASSVGAAGVPAGGVLTTAIILEAI-GLPTHDLPLILAVDMVIDRT SLTATLASIGAAGIFSAGLVTMLILILTAV-GLPTEDISLLVAVDWLLDRM SLTATLASVGAASIFSAGLVTMLILITAV-GLPTEDISLLVAVDWLLDRM SITATAASIGAAGIPOAGLVTMVIVLTSV-GLPTEDITLIIAVDWFLDRL SITATAASIGAAGIPOAGLVTMVIVLSV-GLPTEDITLIIAVDWFLDRL SVTATAASIGAAGQPOAGLVTMVIVLSAV-GLPAEDVTLIIAVDWLLDRF SITATSASIGAAGVPOAGLVTMVIVLSAV-GLPAEDVTLIIAVDWLLDRF SITATSASIGAAGVPOAGLVTMVIVLSAV-GLPAEDVTLIIAVDWLLDRF	384 384 392 395 404 406 455 458 477 477 478 478 446
GltTBc GltTBs GltPEc DctARn DctARn DctARlp SATTHS ASCTIHS GLT-1 GluBHS GLAST GluAHS EAAC1 GluCHS	LANVLKPGVGLDLSHLAKKDIHELSGYT-DKVV-DFKGMILDÍTPŤN AANIFQPGAGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN AANIFQPGTGVNMKSLEKTDIQSYVDTTNEVQHHSMVETFVNIVPKN LANVFQPGAGMNIDPASLDPAAVATPAKAH-EGSIVGFTÉNTIPTT VANVVQPGAGMNIDPASLDAKAVATYAEKAH-EGSIVGFTÉNTIPTŤT VANVVQPGAGMHIDPASLDAKAVATYAEKAH-EGSITGFLMNIIPŤT VANVVQPGAGMHIDPASLDAKAVATYAEKAH-EQSVTGFLMNIIPŤT LÄFTIKPGSGAQTLQSSDLGLEDSGPPPVPKETV-D-SFLDLARNLFPSN LAFTIKPGSGAQTLQSSDLGLEDSGPPPVPKETV-D-SFLDLARNLFPSN LAFTIKPGNFLKKQLGPCKKNDEVSSLD-AFLDLIRNLFPEN LVILAIHPGNFLKKQLGPCKKNDEVSSLD-AFLDLIRNLFPEN LVILIHPGKGTK-ENMYREGKIVQVTAAD-AFLDLIRNMFPEN IVIIHPGKGTK-ENMYREGKIVQVTAAD-AFLDLIRNMFPEN LVVSIKPGVTQKVDEIDRTGSTPEVSTVD-AMLDLIRNMFPEN LVVSIKPGVTQKVDEIDRTGSTPEVSTVD-AMLDLIRNMFPEN **	143 143 150 153 162 165 179 182 179 181 181 153	GltTBc GltTBs GltPEc DctAR1 DctARm DctARM DctARIp SATTHS ASCTIHS GLT-1 GluEHS GLAST GluEHS GLAST GluCHS	MLVLVMTSKGIAAVPSGSLVVLLATANAV-GLPÄEGVÄIIAGVDRVMDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGIDRILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGIDRILDMA LLVLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGVDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGTV-GIPVEGLAFIAGVDRILDMA VLTLMVTSKGIAGVPGVSFVVLLATLGSV-GIPLEGLAFIAGVDRILDMA LLVAMLSSKGAAGITGAGFITLAATLSVPSVPVAGMALILGIDRFMSEC LLVAMLSSKGAAGITGAGFITLAATLSVPSVPVAGMALILGIDRFMSEC LLVATATASSVGAAGVPAGGVLTIAAILEAI-GLPTHDLPLILAVDMIVDRT LVTATASSVGAAGVPAGGVLTIAIILEAI-GLPTHDLPLILAVDMIVDRT SLTATLASIGAAGIPSAGIVTMLILITAV-GLPTEDISLLVAVDWILDRM SLTATLASVGAASIPSAGLVTMLILITAV-GLPTEDISLLVAVDWILDRM SITATAASIGAAGIPQAGLVTMVIVLTSV-GLPTEDITLIIAVDMFLDRL SITATAASIGAAGIPQAGLVTMVIVLTSV-GLPTEDITLIIAVDMFLDRL SVTATAASIGAAGVPQAGLVTMVIVLSV-GLPTEDITLIIAVDWFLDRL SVTATAASIGAAGVPQAGLVTMVIVLSV-GLPTEDITLIIAVDWLLDRF SITATSASIGAAGVPQAGLVTMVIVLSV-GLPTEDITLIIAVDWLLDRF SITATSASIGAAGVPQAGLVTMVIVLSAV-GLPAEDVTLIIAVDWLLDRF SITATSASIGAAGVPQAGLVTMVIVLSAV-GLPAEDVTLIIAVDWLLDRF	384 384 395 404 406 455 477 477 477 478 446 446
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FIG. 6. Alignment of the deduced amino acid sequences of 15 members of the dicarboxylate transport protein family (see Discussion). The best fit was achieved by introducing gaps in order to maximize the identity score. The membrane-spanning fragments as predicted by the method of Eisenberg et al. (9) are shaded. <iii>and <000>, internal and external loops, respectively. The proposed transmembrane segments 1 to 12 are indicated. The positions of the transmembrane segments as predicted by the DctA-PhoA and DctA-LacZ gene fusions in the DctA protein of *R. meliloti* (17) are underlined. * and ①, identical and similar amino acid residues, respectively.

helices coincide with those predicted by the DctA-PhoA and DctA-LacZ gene fusions in the DctA protein of R. meliloti (17) (Fig. 6). The proposed transmembrane segment 4 is highly amphipathic in $GltP_{Bsu}$, $GltT_{Bc}$, $GltT_{Bs}$, $SATT_{Hs}$, $ASCT1_{Hs}$, GLT-1, $GluA_{Hs}$, EAAC1, and $GluC_{Hs}$.

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