Molecular Recognition by Ornithine and Aspartate Transcarbamylases

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The ability of molecules to recognize and interact selectively with other molecules underlies a wide variety of important research areas in both chemistry and biochemistry. Examples include chemical and biochemical catalysis, rational drug design, the development of sensors for environmental pollutants and clinical tests, taste and smell, and insect and weed control. Among biological molecules, proteins have evolved to have the greatest versatility and selectivity in molecular recognition (although RNA may prove a close second), and much of what we understand about the principles that underlie biological recognition has come from studying proteins. The ability of proteins to recognize and discriminate among molecules, both large and small, depends on their complex chemistry and surface properties and their ability to undergo changes in their three-dimensional structure as a result of changes in their environment or molecular interactions that alter both their chemistry and their surface properties. Since the underlying principles are

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FIGURE 1. Schematic drawings of reactions catalyzed by ATCase and OTCase.

similar for most proteins, these principles can be illustrated with almost any protein or protein family. Here we focus on the transcarbamylases, a family of enzymes that catalyze transfer of the carbamoyl group of carbamoyl phosphate (CP) to an amino group.

The most widely studied members of this family are the aspartate transcarbamylases (ATCases) and ornithine transcarbamylases (OTCases), enzymes that transfer the carbamoyl group of CP to the α -amino group of Laspartate (L-Asp) and the δ -amino group of L-ornithine (L-Orn), respectively (Figure 1). ATCases catalyze the first committed step in the biosynthesis of pyrimidines, one of the components of nucleic acids, while OTCases function in the urea cycle, which eliminates excess ammonia, and in the biosynthesis of the amino acid arginine. This laboratory was largely responsible for defining the thermodynamics of protein-protein and protein-ligand interactions in Escherichia coli ATCase by reaction and differential scanning microcalorimetry,1-4 electrostatic modeling,^{5,6} hydrogen exchange,^{7,8} solvent perturbation,^{9,10} and related methods¹¹⁻¹⁴ and has recently determined high-resolution crystal structures of both E. coli and human ornithine transcarbamylase,^{15,16} as well as examining the enzymology of the human enzyme.^{17,18} This work has provided important new insights into the molecular basis of ornithine transcarbamylase deficiency (OTCD), a relatively common clinical condition in which ammonia levels in the blood are elevated as a result of mutations in the OTCase gene.19

E. coli ATCase, the most thoroughly studied transcarbamylase, is a multisubunit protein containing two trimeric catalytic polypeptide chains and three dimeric regulatory chains which undergoes major changes in its threedimensional structure when substrates bind. It has been

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widely used for more than 30 years as a model system for understanding how protein-protein interactions mediate signal transduction.²⁰⁻²⁵ Although structural and mechanistic studies of OTCase have lagged behind ATCase, several OTCase crystal structures have recently been determined,^{26–28} including two high-resolution structures from this laboratory,^{15,16} generating increased interest and new research opportunities. The new crystal structures indicate that, while OTCases have considerable structural diversity, their fundamental building block is a trimer that is very similar to the catalytic trimers of ATCases, and that they share the conformational flexibility of ATCases. OTCases are important clinically, since OTCD is the most common cause of inherited hyperammonemia (elevated levels of blood ammonia), which in turn produces neurological symptoms, sometimes sufficiently severe to cause death. More than 130 mutations that give rise to OTCD in humans have been identified,¹⁹ many in this laboratory, and this laboratory is actively engaged in developing approaches to gene therapy.

The structural and functional similarities and differences within the transcarbamylase family provide an opportunity to ask a number of questions about molecular recognition. What differences in the L-Asp binding site of ATCase and the L-Orn binding site of OTCase result in ATCase binding L-Asp and OTCase binding L-Orn? Conversely, how similar are the binding sites for CP? Are there similarities between the catalytic mechanisms of the OTCases and ATCases? What are the similarities and differences between subunit interfaces, within the OTCase and ATCase families and between families? What determines whether the basic functional unit, a trimer, forms larger aggregates, or associates with other proteins? What is the relationship between the state of aggregation of the protein and its regulation? This review will focus on these questions.

Sequence Comparisons

More than 30 OTCase genes and more than 15 ATCase genes have been sequenced. These sequences are aligned in Figures 2 and 3, so that similarities and differences can be readily visualized. Similar sequences are likely to give rise to similar three-dimensional structure. Despite their similar folds, E. coli OTCase and the catalytic subunit of E. coli ATCase have only 32% identical sequence. Homology between OTCase and ATCase is greatest in the N-terminal half of the sequence, the region that binds their common substrate, CP, and much weaker in their C-terminal halves, which bind L-Orn in OTCase and L-Asp in ATCase. Although human OTCase has an even lower level of sequence homology with the catalytic subunit of E. coli ATCase (27%) than with that of E. coli OTCase, the homology model of human OTCase that we built using the catalytic subunit of E. coli ATCase as a model successfully predicted the effects on enzymatic function of many naturally occurring mutations found in patients with OTCD (Figure 5) and was in good agreement with the experimentally determined crystal structure.²⁹ Most mutations that produce neonatal OTCD are found at the active site, in the interior of the protein where they would interfere with folding, or between subunits where they would interfere with assembly of the trimer, whereas mutations that produce late onset symptoms are more likely to be found in loops on the exterior of the protein.

Tertiary Structure

As shown in Figure 4, the overall topology of the subunits of both OTCases and ATCases is α/β , with 14–16 α -helices and $9-10 \beta$ -sheets. Each chain consists of two domains, a carbamoyl phosphate binding domain and a second domain that binds either L-Orn or L-Asp. Each domain consists of a central core made up of a β -sheet surrounded by α-helices. Helices H5 and H11 in E. coli OTCase and analogous helices in other transcarbamylases connect the two domains, with a highly conserved hydrophilic cluster holding helices H1, H5, and H11 (H12 in ATCase) together. Active chimeras produced by recombinant DNA methods consisting of the CP domain of *E. coli* ATCase and the L-Orn domain of *E. coli* OTCase, or vice versa, with the substrate specificity of the second domain, were reported a number of years ago.³⁰ However, more recent efforts to reproduce this result and to exchange secondary structure elements between the two proteins yielded only insoluble proteins, highlighting the importance of specific sidechain packing, even in the context of a shared protein fold.31

The individual chains of both the catalytic subunit of E. coli ATCase and those of E. coli and human OTCases undergo domain closure when substrates and substrate analogues bind. A loop known as the 240s loop in E. coli ATCase swings in toward the active site, enabling a number of adjacent residues to interact with bound substrate. A second loop, known as the 80s loop, undergoes a smaller motion. These motions are illustrated in Figure 6, which superimposes the liganded and unliganded catalytic subunits of E. coli ATCase and liganded and unliganded subunits of E. coli OTCase. In E. coli ATCase, movement of these loops propagates to the subunit interfaces between catalytic subunits and between catalytic and regulatory subunits, resulting in a large change in quaternary structure, the T-to-R transition. This conformational change was one of the earliest models of ligand-induced signal transduction and has served as a paradigm for signal transduction in many other systems, including those involved in intercellular signaling in the nervous system and in regulating cellular proliferation of normal cells and neoplastic growth of cancerous cells.

Carbamoyl Phosphate Binding Site

The binding sites for CP in OTCase and ATCase are very similar (Figure 7). Both active sites contain a STRT motif (Ser55-Thr56-Arg57-Thr58 in *E. coli* OTCase), which binds the phosphonate oxygens of CP, and Arg and His residues (Arg 106 and His 133 in *E. coli* OTCase), which bind the carbonyl oxygen of CP. (Sequence numbers throughout are those of *E. coli* OTCase and ATCase, unless otherwise

Molecular Recognition by Transcarbamylases Allewell et al.

OTC_HUMAN	*NKVQ	LKGRDLLTLK	NFTGEEIKYM	LWLSADLKFR	IKQKGEYLPL	LQGKS	LGMIFEKRST	RTRLSTETGL	ALLGGHPCFL	TTQDIHLGVN
OTC_MOUSE	*SQVQ	LKGRDLLTLK	NFTGEEIQYM	LWLSADLKFR	IKQKGEYLPL	LQGKS	LGMIFEKRST	RTRLSTETGF	ALLGGHPSFL	TTQDIHLGVN
OTC_RAT	*SQVQ	LKGRDLLTLK	NFTGEEIQYM	LWLSADLKFR	IKQKGEYLPL	LQGKS	LGMIFEKRST	RTRLSTETGF	ALLGGHPSFL	TTQDIHLGVN
OTC_RANCA	*TYSQ	LKGRDLLTLK	NYSAEEIKYL	LWVAADLKYR	IKEKGEYLPL	LQGKS	LAMIFERRST	RTRLSTETGF	ALLGGHPSFL	TTQDIHLGVN
OTC_PACTA	*SSSAKMSSQ	AKPRHLVSML	ELSIKELESL	VNRAAYHKOO	IRSGLVN	. TTOPLSGKT	VSLIFNKRST	RTRVSSEGAA	AYLGGCPMFL	GKDDIQLGVN
OTC_SCHPO	~~~~MSFK	KFPRHLLSIR	DLSRGEIVKL	IDRSSEIKQA	YKQNFQNRRS	VQMSGLSSQN	VAMIFSKRST	RTRVSVESAV	SCLGGNAMFL	GKDDIQLGVN
OTC_YEAST	~~MSTTASTP	SSLRHLISIK	DLSDEEFRIL	VORAOHFKNV	FKANKTNDFO	SNHLKLLGRT	IALIFTKRST	RTRISTEGAA	TFFGAOPMFL	GKEDIQLGVN
		3	13	23	33	37	47	57	67	77
OTCL FCOLL	~~~~~SG	EAHRHEIRIT	DETPAELNSL	TOPPAKERAD	KKSG	KEEAKLIYSKN	TALTEEKDST	RTROSFEVAA	YDOGARWTYT.	GPSGSOTGHK
OTC HARIN	~~~~MAFN	MENRHUSIA	HHTERETKVL	LDLSEDLKEA	KVAG	TEOORIKGKN	TALTEEKTST	RURCAFEVAA	VDOGAOWTVI	DPNSSOIGHK
OTCP PSESH	~~~~MKTTS	LENENLLOWN	FENOSELSHI	TIRATECKRI.	KKUB	TENLOLNHIN	TOGIFLERSC	RUSTSHWAS	VDECAHEOFE	PADNIREGHK
OTC ASPTE	T KUCD	FADEHLICTA	DI TOTETT	TENATECIAE	TKSG STPT	NT COST ACKT	VAMMEGURGD	RIBISE VAS	VOLCCHEMET.	GKDDTOLGVN
OTCL DEFIE		. CODUEL CEM	DVCDEELTCL	TERCEPTED	IDMOCUTIVED	TVORT	T CMR TETER A CON	DUDICEDICA	TOLCCONTEN	CORDIQUOVIN
OTC2 PACET		I VOUDI LOI V	DISPEDIUSE	TICKOSEEK.D	VONUTOR		TAMTERVCCM	DUDICODIC	AOLOGGALEI	STIDIQUORG
OTC EVERI		LACEDULCIO	DUSEEDINAL	LALAGED	WONTGADADI	LECKT	LAMIFORDER	DTDUCEEUAM	ADDGGSALLT	NAODI OI PRO
OTCL MYCRO		- MIDUELDO	DIGDEONEV	LEINDER.I	MOVIOVENCE	DEGRI	UNITEDING	DEPERENT	ALLGGHALTL	
OTCA_MICBO		~MIRHFLRDD	DLSPAEQAEV	LELAAELK.K	DPVSRRPL	QGPRG	VAVIPUNIST	RIRPSPELGI	AQLGGHAVVV	DSGSTQLGRD
OTCC_PSEAE	~~~~~AFN	MHNRNLLSLM	HHSTRELRYL	LDLSRDLKRA	KY1G	TEQQHLKRKN	TALIFERTST	RTRCAFEVAA	YDQGANVTYL	DPNSSQIGHK
OTCC_NEIGO	~~~~~~MN	LKNRHFLKLL	DFTPEEITAY	LDLAAELKDA	KRAG	REIQRMKGKN	TALIFERTST	RTRCAFEVAA	RDQGADRTYL	EPSASQIGHK
OTCC_CLOPE	~~~~~MAVN	LKGRSFLTLK	DFTPAEIRIL	LDLSHDLKAK	KRAG	ILGDSLKGKN	VVLLFERTST	RTRCAFECGA	AEEGAHVIFL	TINSQPECKK
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OTC_HUMAN	ESLTDTARVL	SSMADAVLAR	VYKQSDLDTL	AKEASIPIIN	GLSDLYHPIQ	ILADYLTLQE	HYS	SLKGLTL	SWIGDG.NNI	LHSIMMSAAK
OTC_MOUSE	ESLTDTARVL	SSMTDAVLAR	VYKQSDLDTL	AKEASIPIVN	GLSDLYHPIQ	ILADYLTLQE	HYG	SLKGLTL	SWIGDG.NNI	LHSIMMSAAK
OTC_RAT	ESLTDTARVL	SSMTDAVLAR	VYKQSDLDIL	AKEATIPIVN	GLSDLYHPIQ	ILADYLTLQE	HYG	SLKGLTL	SWIGDG.NNI	LHSIMMSAAK
OTC_RANCA	ESLKDTARVL	SGMTDAVLAR	VYHQSDLEVL	AEEASIPIVN	GLSDDYHPIQ	ILADYLTIQE	HYG	HLKGLTI	SWIGDG.NNV	LHSIMMSAAK
OTC_PACTA	ESLHDTTKII	SSMTSSIFAR	VNKHSDIQEM	CKYSSVPIIN	ALCOTFHPLO	AITDILTIKE	SFGNT	TKGLKL	AWIGD.VNNV	INDLCIAALK
OTC_SCHPO	ESLYDTSKVI	SSMVSGIVAR	VNKYSDVATL	AKHASCPVIN	GLCDTFHPLQ	ALADLLTIKE	TF.KS	FDGLKV	AWVGD.ANNV	LHDLMIANAK
OTC_YEAST	ESFYDTTKVV	SSMVSCIFAR	VNKHEDILAF	CKDSSVPIIN	SLCDKFHPLO	AICDLLTIIE	NFNI SLDEVN	KGINSK.LKM	AWIGD.ANNV	INDMCIACLK
	87	97	107	117	127	137	147	153	159	169
OTCL FCOLT	FSTRDDARM.	CRMVDGTOVR	CVCORTVETT.	A EVA CUDUMNI	CI. TINEFHEIM	LLADLUTMOR	HLIDOKA	יתיאיזאיז	WACDARNNM	GNSMLEADAL
OTC HARIN	FOMULADA	CPMVICTEVD	CERCEIVORI	ADVACIONIN	CUTTOREUPTO	שבאת האמנו ש	W CDVD	TOPTOV	WINCOARCE	GNELLLGAK
OTC_INDIN	ESTIDEADIAL	CREEDCIARD	CEEUEV	AUTOOTICAN	ALIDEFIEIQ		FTC D	TECTOT	AVACEVEDNM	UTTEL A TOALK
OTCF_F3E3F	ESTRUCTION	GRUFDGIAFR	GEEREVALED	NULCERTRI	MODORNELO	VLADVMIVAE	DECOURT II	OCLOTECT KI	AIVGLGRINNI	LEDMATCANK
OTC_ASPIE	ESLIDIAVVV	CDM DOT MTD	OFALAEVADL	AKHSTVPVIN	ALCOSPHPLQ	AIADFQTIYE	IFTPKAH.HL	SEGLEGERI	AWVGD.AMMV	CHOWAISAAK
OTCA_PSEAE	EPIGDSARVM	SRMLDGVMIR	TFARATUTEF	AAHSKVPVIN	GLSDDLHPCQ	LLADMQTFRE	HRG	SIQGKTV	AWIGDG NNM	CNSTLEEPIK
UICZ_BACSU	ETVADIAKVL	SGIVDAIMIR	TFEREKVEEL	AKEADIPVIN	GLTDKYHPCQ	ADADDDTIKE	IKG	KLKGVKV	ATIGLG.NNV	AHSLMIGCAK
OIC_PYRFU	ETIADIARVL	SRYVDAIMAR	VYDHKDVEDL	AKYATVPVIN	GLSDFSHPCQ	ALADYMTIWE	KKG	TIKGVKV	VYVGDG.NNV	AHSLMIAGTK
OICA_MICBO	ETLQDTAKVL	SRYVDALVWR	TFOQERLDAM	ASVATVPVIN	ALSDEFHPCQ	VLADLQTIAL	RKG		SYFGLGANINM	AHSLLLUGGVT
OTCC_PSEAE	ESMKDTARVL	GRMYDAIEYR	GFKQEIVEEL	AKFAGVPVFN	GLTDEYHPTQ	MLADVLTMRE	H.SDKP	LHDISY	AYLGDARNNM	GNSLLLIGAK
OTCC_NEIGO	ESIKDTARVL	GRMYDAIEYR	GFAQETVEEL	AKYAGVPVFN	GLTNEFHPTQ	MLADALTMRE	H.SGKP	LNQTAF	AYVGDARYNM	GNSLLILGAK
OTCC_CLOPE	ESIEDTAKVL	GRMYDGIEFR	GFKQSTVEEL	AKHAGVPVWN	GLTDADHPTQ	ILADFLTIEE	H.AHKP	LSAIKL	VFTGHTRNNM	SYALMYGAAK
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OTC HEMAN	FOMMENT	KOVEDDACUT	YT ADOVATION	с т и			THE CMOODER	N NADI OVEO	CYCUMMEDAY	
OTC_HUMAN	FGMHLQAATP	KGYEPDASVT	KLAEQYAKEN	GT.K	LLLTNDPLEA	AHGGNVLITD	TWISMGQEEE	K.KKRLQAFQ	GYQVTMKTAK	V. AASDWTF
OTC_HUMAN OTC_MOUSE	FGMHLQAATP FGMHLQAATP	KGYEPDASVT KGYEPDPNIV	KLAEQYAKEN KLAEQYAKEN	GT.K GT.K	LLLTNDPLEA LSMTNDPLEA	AHGGNVLITD ARGGNVLITD	TWISMGQEEE TWISMGQEDE	K.KKRLQAFQ K.KKRLQAFQ	GYQVTMKTAK GYQVTMKTAK	V. AASDWTF V. AASDWTF
OTC_HUMAN OTC_MOUSE OTC_RAT	FGMHLQAATP FGMHLQAATP FGMHLQAATP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN	GT.K GT.K GT.R	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA	AHGGNVLITD ARGGNVLITD ARGGNVLITD	TWISMGQEEE TWISMGQEDE TWISMGQEDE	K . KKRLQAFQ K . KKRLQAFQ K . KKRLQAFQ	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK	V. AASDWTF V. AASDWTF V. AASDWTF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA	FGMHLQAATP FGMHLQAATP FGMHLQAATP FGMHLHIATP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV KGYEPNSSLT	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC	GT.K GT.K GT.R GT.K	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA LLMTNDPLEA	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWVSMGQEEE	K . KKRLQAFQ K . KKRLQAFQ K . KKRLQAFQ K . KKRLLDFK	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK	V AASDWTF V AASDWTF V AASDWTF L AAPNWIF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA	FGMHLQAATP FGMHLQAATP FGMHLQAATP FGMHLHIATP SGIDVSIAVP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV KGYEPNSSLT SGLKFEELIL	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN	GT.K GT.K GT.R GT.R GT.K	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA LLMTNDPLEA ITNDPLEA	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD INGANVIVTD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWVSMGQEEE TWISMGQEDE	K.KKRLQAFQ K.KKRLQAFQ K.KKRLQAFQ K.KKRLLDFK R.LQKLKQFE	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITKEMIS	V AASDWTF V AASDWTF V AASDWTF L AAPNWIF KGKAAENWKF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_SCHPO	FGMHLQAATP FGMHLQAATP FGMHLQAATP FGMHLHIATP SGIDVSIAVP VGIHTSVAKP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV KGYEPNSSLT SGLKFEELIL KDVNVRDDIL	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVNEAANEN	GT.K GT.K GT.R GT.K GTTLK GSTFE	LLLTNDPLEA LSMINDPLEA LSMINDPLEA LLMINDPLEA IINDPLEA IVNDPKVA	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD INGANVIVTD VKNADIVVTD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWVSMGQEEE TWISMGQEDE TWISMGQEAE	K.KKRLQAFQ K.KKRLQAFQ K.KKRLQAFQ K.KKRLLDFK R.LQKLKQFE K.EQRLKQFT	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITKEMIS GFQVTGEIMK	V AASDWTF V AASDWTF V AASDWTF L AAPNWIF KGKAAENWKF LAK PSCKF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_SCHPO OTC_YEAST	FGMHLQAATP FGMHLQAATP FGMHLQAATP FGMHLHIATP SGIDVSIAVP VGIHTSVAKP FGISVSISTP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV KGYEPNSSLT SGLKFEELIL KDVNVRDDIL PGIEMDSDIV	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVNEAANEN DEAKKVAERN	GT.K GT.K GT.R GT.K GTTLK GSTFE GATFE	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA LLMTNDPLEA ITNDPLEA IVNDPKVA LTHDSLKA	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD INGANVIVTD VKNADIVVTD STNANILVTD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWVSMGQEEE TWISMGQEDE TWISMGQEAE TFVSMGEEFA	K.KKRLQAFQ K.KKRLQAFQ K.KKRLQAFQ K.KKRLLDFK R.LQKLKQFE K.EQRLKQFT K.QAKLKQFK	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITKEMIS GFQVTGEIMK GFQINQELVS	V AASDWTF V AASDWTF V AASDWTF L AAPNWIF KGKAAENWKF LAK PSCKF V ADPNYKF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_SCHPO OTC_YEAST	FGMHLQAATP FGMHLQAATP FGMHLQAATP FGMHLHIATP SGIDVSIAVP VGIHTSVAKP FGISVSISTP 179	KGYEPDASVT KGYEPDPNIV KGYEPDSLT SGLKFEELIL KDVNVRDDIL PGIEMDSDIV 189	KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVNEAANEN DEAKKVAERN 194	GT.K GT.R GT.R GTTLK GSTFE GATFE 202	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA LLMTNDPLEA ITNDPLEA IVNDPKVA LTHDSLKA 212	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD INGANVIVTD VKNADIVVTD STNANILVTD 222	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWISMGQEEE TWISMGQEDE TWISMGQEAE TFVSMGEEFA 232	K.KKRLQAFQ K.KKRLQAFQ K.KKRLQAFQ K.KKRLLDFK R.LQKLKQFE K.EQRLKQFT K.QAKLKQFK 242	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GFQITMKTAK GFQITKEMIS GFQVTGEIMK GFQINQELVS 252	V. AASDWTF V. AASDWTF V. AASDWTF L. AAPNWIF KGKAAENWKF LAK. PSCKF V. ADPNYKF 262
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_SCHPO OTC_YEAST OTC1_ECOLI	FGMHLQAATP FGMHLQAATP FGMHLQAATP FGMHLHIATP SGIDVSIAVP VGIHTSVAKP FGISVSISTP 179 TGLDLRLVAP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV KGYEPNSSLT SGLKFEELIL KDVNVRDDIL PGIEMDSDIV 189 QACWP	KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVNEAANEN DEAKKVAERN 194 EAALVTEC	GT.K GT.R GT.R GT.K GTILK GSTFE GATFE 202 RALAQQNGGN	LLLTNDPLEA LSMTNDPLEA LLMTNDPLEA ITNDPLEA IVNDPKVA LTHDSLKA 212 ITLTEDVAKG	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD INGANVLVTD VKNADIVVTD STNANILVTD 222 VEGADFIYTD	TWISMQQEEE TWISMQQEDE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEAE TFVSMGEEFA 232 VWVSMGEAKE	K.KKRLQAFQ K.KKRLQAFQ K.KKRLQAFQ K.KKRLLDFK R.LQKLKQFE K.QAKLKQFT K.QAKLKQFK 242 KWAERIALLR	GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITMKTAK GFQITKEMIS GFQVTGEIMK GFQINQELVS 252 EYQVNSKMMQ	VAASDWTF VAASDWTF VAASDWTF LAAPNWIF KGKAAENWKF LAKPSCKF VADPNYKF 262 LTG.NPEVKF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RATCA OTC_PACTA OTC_SCHPO OTC_YEAST OTC1_ECOLI OTC_HAEIN	FGMHLQAATP FGMHLQAATP FGMHLQAATP FGMHLHIATP SGIDVSIAVP VGIHTSVAKP FGISVSISTP 179 TGLDLRLVAP LGMDVRICGP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV KGYEPNSSLT SGLKFEELIL KDVNVRDDIL PGIEMDSDIV 189 QACWP KALLP	KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVNEAANEN DEAKKVAERN 194 . EAALVTEC . EAALVTEC	GT.K GT.R GT.R GT.K GSTFE GATFE 202 RALAQQNGGN EKFAKESGAR	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA ITNDPLEA ITNDPLEA ITNDPLEA LTHDSLKA 212 ITLTEDVAKG ITLTEDVAKG	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD INGANVLVTD VKNADIVVTD 222 VEGADFIYTD VKGVDFIHTD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEAE TFVSMGEEFA 232 VWVSMGEAKE VWVSMGEAKE	K . KKRLQAFQ K . KKRLQAFQ K . KKRLQAFQ K . KKRLLDFK R . LQKLKQFE K . EQRLKQFT K . QAKLKQFK 242 KWAER IALLR TWGER IKLLL	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GFQITKEMIS GFQVTGEIMK GFQINQELVS 252 EYQVNSKMMQ PYQVTPELMK	VAASDWTF VAASDWTF VAASDWTF LAAPNWIF KGKAAENWKF LAKPSCKF VADPNYKF 262 LTG.NPEVKF RTG.NPEVKF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RATA OTC_PACTA OTC_PACTA OTC_YEAST OTC1_ECOLI OTC_HAEIN OTCP_PSESH	FGMHLQAATP FGMHLQAATP FGMHLAATP FGMHLHIATP SGIDVSIAVP VGIHTSVAKP FGISVSISTP 179 TGLDLRLVAP LGMDVRICGP FGYNLRIIAP	KGYEPDASVT KGYEPDPNIV KGYEPDPSIV SGLKFEELIL KDVNVRDDIL PGIEMDSDIV 189 QACWP KALLP NALHP	KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVNEAANEN DEAKKVAERN 194 . EAALVTEC . EANLVTEC . TDAVLAGI	GT.K GT.R GT.R GT.K GSTFE GSTFE 202 RALAQNCGN EKFAKESGAR YEQTPERNGS	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA LLMTNDPLEA ITNDPLEA IVNDPKVA LTHDSLKA 212 ITLTEDVAKG ITVTEDIDKA IEIFTEVAAG	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD INGANVIVTD VKNADIVVTD 222 VEGADFIYTD VKGVDFIHTD VHQADVIYTD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWISMGQEEE TWISMGQEAE TFVSMGEEFA 232 VWVSMGEAE VWVSMGEAE VWVSMGEPLE VWISMGESVS	K.KKRLQAFQ K.KKRLQAFQ K.KKRLDFK R.LQKLKQFE K.EQRLKQFT K.QAKLKQFK 242 KWAERIALLR TWGERIKLLL V.EERIALLK	GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GYQITMKTAK GFQITKEMIS GFQUTQELWS 252 EYQVNSKMMQ PYQVTPELMK PYKVTEKMMA	VAASDWTF VAASDWTF VAASDWTF LAAPNWIF KGKAAENWKF LAKPSCKF VADPNYKF 262 LTG.NPEVKF RTG.NPEVKF LTG.KADTIF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_SCHPO OTC_YEAST OTC1_ECOLI OTC1_ECOLI OTC1_ASETE	FGMHLQAATP FGMHLQAATP FGMHLQAATP FGMHLLHATP SGIDVSIAVP VGHTSVAKP FGISVSISTP 179 TGLDLRLVAP LGMDVRICGP GGVDLRIAP MGVDLAVATP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV KGYEPNSSLT SGLKFEELIL KGVEVRDDIL PGIEMDSDIV 189 QACWP KALLP KGYEIPASMR	KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVNEAANEN DEAKKVAERN 194 . EAALVTEC . EAALVTEC . TAAVLAGI ELLQEAGKGV	GT.K GT.K GT.K GTTLK GTTLK GSTFE 202 RALAQQNSGN EKFAKESGAR YEQTPERNGS ANFGK	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA LLMTNDPLEA ITNDPLEA LTNDPLEA LTNDSLKA 212 ITLTEDVAKG ITUTEDIJKA IEIFTEVAAG LIQTNVFEEA	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD INGANVLVTD VKNADLVVTD 222 VEGADFIYTD VKGADFIYTD VKGADVIYTD VKKADLIVTD	TWISMOQEEE TWISMOQEDE TWISMOQEDE TWISMOQEDE TWISMOQEDE TWISMOQEAE 232 VWVSMGEPAE VWVSMGEPLE VWISMGEPLE VWISMOQEEE	K. KKRLQAFQ K. KKRLQAFQ K. KKRLQAFQ K. KKRLDFK R. LQKLRQFE K. EQRLKQFT 242 KWAERIALLR TWEERIKLLL V. EERIALLK S. LKRMKAFE	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITKEMIS GFQVTGEIMK GFQUTGEIMK 252 EYQVNSKMMQ PYQVTPEIMK PYKVTEKMMA GFQITSELAK	V. AASDWTF V. AASDWTF U. AASDWTF L. AAPNWIF KGKAAENWKF LAK. PSCKF V. ADPNYKF 262 LTG. NPEVKF RTG. NPEVKF LTG. KADTIF LTG. KADTIF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RAT OTC_PACTA OTC_SCHPO OTC_YEAST OTC1_ECOLI OTC_HAEIN OTC_ASPTE OTC4_PSEAE	FGMHLQAATP FGMHLQAATP FGMHLLQAATP FGMHLHIATP SGIDVSIAVP VGIHTSVAKP FGISVSISTP 179 TGLDLRLVAP LGMDVRICGP FGYNLRIIAP MGVDLAVATP FDFQLRVACP	KGYEPDASVT KGYEPDPNIV KGYEPDSIV SGLKFEELIL KDVNVRDDIL PGIEMDSDIV 189 QACWP KALLP NALLP KGYEIPASMR EGYEPIASMR EGYEPAEFV	KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVNEAANEN DEAKKVAERN 194 EAALVTEC EAALVTEC TDAVLAGI ELIQEAGKGV	GT.K GT.R GT.R GT.K GTILK GATFE 202 RALAQONGGN EKFAKESGAR YEQTPERNGS ANPGK	LLLTNDPLEA LSMTNDPLEA LLMTNDPLEA LLMTNDPLEA I VNDPKVA L. THDSLKA 212 ITLTEDVAKG ITUTEDUAKG ITUTEDIDKA IEIFTEVAAG LIQTNVPEEA LIQTNVPERA	AHGGNVLITD ARGGNVLITD ARGGNVLITD INGANVLIVTD VKNADIVVTD 222 VKGVDFINTD VKGVDFINTD VKGADLIVTD VKADILIVTD VAGAHLVSTD	TWISMQQEEE TWISMQQEDE TWISMQQEDE TWISMQQEDE TWISMQQEAE TPVSMGEFA 232 VWVSMGEFA VWVSMGEPLE VWVSMGEPLE VWISMGESVS TWVSMQEEDE	K. KKRLQAFQ K. KKRLQAFQ K. KKRLDAFQ K. KKRLDFK R. LCKLKQFE K. QAKLKQFK 242 XWAERIALLR TWGERIKLLL V. EERIALLK S. LKRMKAFE A. AARIAMFR	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITKEMIS GFQITKEMIS GFQITKEMIS SZ EYQVTSEIMK GYQVTPELMK PYKVTEXMAA GFQITSELAK	V. AASDWTF V. AASDWTF L. AASDWTF L. AAPNWTF LAK. PSCKF V. ADPNYKF 262 LTG. NPEVKF RTG. NPEVKF RTG. NPEVKF RTG. NPEVKF GGANENWKF G. AADDUF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_YEAST OTC1_ECOLI OTC_HAEIN OTC_PSESH OTC_ASPTE OTC_SEASE OTC2_BACSU	FGMHLQAATP FGMHLQAATP FGMHLHAATP FGMHLHAATP SGIDVSIAVP VGIHTSVAKP FGISVSISTP 179 TGLDLRLVAP LGMDVRICGP FGVNLRIIAP FGVDLAVATP FDFQLRVACP	KGYEPDASVT KGYEPDPNIV KGYEPDSLT SGLKFEELIL KDVNVRDIL PGIEMDSDIV 189 QACMP KALLP KGLEIPASMR EGYEPKAEFV EGYEPLAEA	KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVNEAANEN DEAKKVAERN 194 EAALVTEC EANLVEMC TDAVLAGI ELIQEACKGY ALAGDR	GT.K GT.K GT.K GTIK GTIK GSTFE Z02 RALAQQNGGN EKFAKESGAR YEQTPERNGS ANFGK S.S	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA ITNDPLEA ITNDPLEA ITNDPLEA ITNDPLEA LITHDSLKA 212 ITLTEDVAKG IITTTEDLKA IEIFTEVAAG LIQTNVPEEA LRVVRDPREA	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGGNVLITD INGANVLVTD INGANVLVTD 222 VEGADFIYTD VKGVDFIHTD VKGVDFIHTD VKGADLIVTD VKGADLVTD VKGADLVSTD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWISMGQEAE TWISMGQEAE TWISMGEAE WWSMGEPLE WWSMGEPLE WWSMGEPLE WWSMGEPLE WWSMGQEEE WWSMGQEAE	K.KKRLQAFQ K.KKRLQAFQ K.KKRLQAFQ K.KKRLDFK R.LQKLKQFE 242 KWAERIALLR TWGERIKLLL V.EERIALLK S.LKRMKAFE A.AARIAMFR E.GERLAVFA	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITKEMIS GFQITELIMK GFQINQELVS 252 EYQVNSKMMQ PYQVTPELMK PYQVTPELMK PYQVTALKMA GPQITSELAK PYQVNAALUS	V. AASDWTF V. AASDWTF U. AASDWTF L. AARMUF KGKAAENWKF LAK. PSCKF V. ADPNYKF 262 LTG. NEVKF LTG. KADTIF RGGANENWKF G. AADDVLF H. AKEDYTF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_SCHPO OTC_YEAST OTC_YEAST OTC_HAST OTC_PSESH OTC_ASPTE OTCA_PSEAE OTCA_PSEAE OTCA_PSEASU OTC_PYRFU	FGMHLQAATP FGMHLQAATP FGMHLHAATP FGMHLHATP SGIDVSIAVP VGHHTSVAKP FGISVSISTP TGLDLRLVAP LGMDVRICGP FGVNLRIAP FDFQLRVACP MGCDISIASP MGCDISIASP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV SGLKFEELIL KDVNVRDDIL PGIEMDSDIV QACWP KALLP KGYEIPASMR BGYEPKAEFV KGYEVLDEAA EGYEPDEKVI	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC EAAKQFSKEC SIVNEAANEN DEAKKVAERN 194 . EAALVTEC . EAALVTEC . TDAVLAGI ELIQEAGKGV ALAGDR EAAKTYALQS EWAEQNAAES	GT.K GT.R GT.R GT.K GTILK GSTFE GATFE 202 RALAQQNGGN EKFAKESGAR YEQTPERNGS ANFGK GS.S GS.S	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA L.MTNDPLEA INNDPKA INNDPKA INDPKA ITNDPLEA II.TTEDVAKG IITTEDIAKA LITTEDIAKA LITTEDIAKA LITTNPFEA LRVVRDPREA VTLTDDPIEA	AHGGNVLITD ARGGNVLITD ARGGNVLITD INGANVLVTD VKNADIVVTD STNANILVTD VKADIVVTD VKGADFIYTD VKGADFIYTD VKGADLVTD VKKADILVTD VKGAHLVTD VKDADVIYSD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEAE TWISMGQEAE TWVSMGEEAE VWVSMGEPLE VWISMGEPLE VWISMGEDE VFTSMGQEDE VFTSMGQEAE	K. KKRLQAFQ K. KKRLQAFQ K. KKRLQAFQ K. KKRLDFK K. QORLKQFT K. QAKLKQFT X. QAKLKQFT X. QAKLKQFK 242 KWAERIALLR TWERIALLR V. EERIALLK S. LIKRMKAFE A. AARIAMTR E. QERLAVFA A. EERRKIFR	GYQUTMKTAK GYQUTMKTAK GYQUTMKTAK GYQITMKTAK GFQITKEMIS GFQUTGEIMK GFQITNQELVS 252 EYQUNSKMMQ PYQUTPEIMK PYKVTEKMMA GFQITSELAK PYQUNAALLVS PYQUNAALVS	V. AASDWTF V. AASDWTF L. AAPNWTF L. AAPNWTF LAK., PSCKF V. ADPNYKF 262 LIG.NPEVKF RTG.NPEVKF LTG.KADTIF RGGANENWKF G. AADDVLF H. AKPDYTF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_SCHPO OTC_YEAST OTC_HAEIN OTC_HAEIN OTC_ASPTE OTCA_PSEAE OTC2_BACSU OTC2_PKFU OTCA_MYCEO	FGMHLQAATP FGMHLQAATP FGMHLLQAATP FGMHLHIATP SGIDVSIAVP VGIHTSVAKP PGISVSISTP 179 TGLDLRLVAP LGMDVRICGP FGVNLRIIAP MGVDLAVATP FDFQLRVACP MGCDLSIASP LGADVVVATP	KGYEPDASVT KGYEPDPNIV KGYEPDSIV SGLKFEELIL KDVNVRDDIL PGIEMDSDIV 189 QACWP KALLP NALHP NALHP KGYEIPASMR BGYEPKAEFV KGYEVLDEAA EGYEPDEKVI EGFLPDESVR	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SIVNEAANEN DEAKVAERN ISIVNEAANEN DEAKVAERN . EAALVTEC . EAALVTEC . TDAVLAGI ELIQEAGKGV ALAGDR EAAKTYALQS KWAEQNAAES KAAERAQDT	GT.K GT.R GT.R GT.K GTILK GSTFE GATFE 202 RALAQONGEN EKFAKESGAR YEQTPERNGS ANEGK S.S GS.S GS.S	LLLTNDPLEA LSMTNDPLEA LLMTNDPLEA LLMTNDPLEA I VNDPKVA L THDSLKA 212 ITLTEDVAKG ITUTEDIDKA IEIFTEVAAG LIQTNVPEEA LIQTNVPEEA LIQTNVPEEA FELLHDPVKA YUTTADAHAA	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD STNANILVTD 222 VKGADFIYTD VKGVDFIHTD VKGADFIYTD VKGADUIYTD VAGAHLVSTD VKGADVIYTD VKGADVIYTD VAGAALVVTD	TWISMOQEEE TWISMOQEDE TWISMOQEDE TWISMOQEDE TWISMOQEDE TWISMOQEDE TWISMOQEDE VWVSMGEPLE VWVSMGEPLE VWISMOGENE VWASMOQEDE VFTSMOQENE VWASMOQENE TWISMOQENE	K. KKRLQAFQ K. KKRLQAFQ K. KKRLDFK K. LQKLKQFE K. DQRLKQFE K. DQRLKQFE K. QAKLKQFK Z42 WAERIALLR TWGERIKLLL V. EERIALLK S. LKRMKAFE A. AARIAMFR E. QERLAVFA A. EERKIFR G. LDRVKPFR	GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GYQITMKTAK GFQITKEMIS GFQTKEMIS GFQTKEMIS EYQVTGEIMK GYQTSELAK GFQITSELAK GFQITSELAK GPQTSELAALD PYQVNAALUS PPQUNKDLVK	V. AASDWTF V. AASDWTF U. AASDWTF L. AAPNWIF LAK. PSCKF V. ADPNYKF 262 LTG. NPEVKF RTG.NPKVKF LTG.NPKVKF LTG.NPKVKF LTG.KADTIF RGGANENWKF H. AKPDYTF H. AKPDYTF H. AKPDYTF L. ADSDATV
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_PACTA OTC_YEAST OTC_YEAST OTC_HAEIN OTC_HAEIN OTC_ASPTE OTC_APSEAE OTC_PSEAE OTC_PSEAE OTC_PSEAE	FGMHLQAATP FGMHLQAATP FGMHLHATP SGIDVSIAVP VGIHTSVAKP FGISVSISTP 179 TGLDLRLVAP LGMDVRICGP FGVNLRIAP MGVDLAVATP MGCDISIASP LGADVVVATP AGIHVTVAAP	KGYEPDASVT KGYEPDPNIV KGYEPDSLT SGLKFEELIL KDVNVRDDIL PGIEMDSDIV 189 QACMP KALLP KGYEIPASMR BGYEPKAEFV KGYEVLDEAA EGYEPDEKVI EGFLPDESVI	KLAEQYAKEN KLAEQYAKEN EAAKQYSKEO SIVNEAANEN DEAKKVAERN 194 .EAALVTEC .EANLVTEC .TDAVLAGI ELIQEAGKGV ALAGDR EAAKTYALQS KWAEQNAAES AAAERRAQDT .HDEFYAQC	GT.K GT.K GT.K GT.K GTILK GSTFE GATFE 202 RALAQQNGGN EKFAKESGAR YEQTPERNGS ANPGK GS.S GS.S GA.S	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA LLMTNDPLEA LLMTNDPLEA ITNDPLEA ITNDPLEA ITNDPLEA ITHDSLKA 212 ITLTEDVAKG ITLTEDVAKG LIQTNVPEEA VTLTDDPLEA FELLHDPVKA VTVTADAHAA LTLTEDPKEA	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGGNVLITD INGANVIVTD INGANVIVTD STNANILVTD 222 VEGADFIYTD VKGVDFIHTD VKGVDFIHTD VKADAULYTD AAAADVLVTD AAAADVLVTD	TWISMQQEEE TWISMQQEDE TWISMQQEDE TWISMQQEDE TWISMQQEAE TWISMQQEAE TWISMQEAE VWISMGEAEE VWISMGEAEE VWISMQEDE VFTSMQQEDE VFTSMQQEDE TWTSMQQEDE TWTSMQQEDE	K. KKRLQAFQ K. KKRLQAFQ K. KKRLDFK R. LQKLKQFE K. SQRLKQFT K. QAKLKQFK 242 KWAERIALLR TWGERIKLLL V. EERIALLK S. LKRMKAFE G. ZERLAVFA A. EERRKIFR G. LDRVKPFR	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITKEMIS GFQITELIMK GFQINQELVS 252 EYQVNSKMMQ PYQVTPELMK PYQVTPELMK PYQVTAALLD PYQVNAALLS PFQUNKDLVK PPQUNKLIVK	VAASDWTF VAASDWTF UAASDWTF LAANNUF KGKAAENWKF 262 LTG. NPRVKF RTG.NPRVKF RTG.NPRVKF RTG.NPRVKF HAKPDYF HAKPDYF HAKPDYF LADSDAIV ATG.NPRAF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_PACTA OTC_PACTA OTC_PACTA OTC_PACTA OTC_PSESH OTC_PSESH OTC_PSEASU OTC_PYRFU OTCA_PYRFU OTCA_PYRFU OTCA_NYCBO OTCC_NEIGO	FGMHLQAATP FGMHLQAATP FGMHLHATP FGMHLHATP SGIDVSIAVP VGHHTSVAKP FGISVSISTP TGLDLRLVAP LGMDVRICGP FGYNLRIAP FDFQLRVACP MGCDISIASP LGADVVVATP AGHNTVAAP LGMDVRIGAP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV SGLKFEELIL KDVNVRDDIL PGIEMDSDIV QACWP KALLP KALLP KGYEIPASMR BGYEPZKAEFV KGYEVLDEAA EGYEPDEKVI EGYELPDESVR KALWP QSLWP	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN SAAKOFSKEC SAAKOFSKEC SGAKEISAEN JUPA SIVIFEANEN DEAKKVAERN 194 . EAALVTEC . EAALVTEC . TDAVLAGI ELIQEAGKGV ALAGDR KWAEQNAAES AAAERRAQDT BEGIIAAA	GT.K GT.R GT.R GT.K GT.K GTILK GATFE 202 RALAQQNGGN EKFAKESGAR YEQTPERNGS ANFGK S.S GS.S GS.S GA.S KKFAEESGAK	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA L.MTNDPLEA INNDPKA INNDPKA INNDPKA INDPKA IIITTEDJKAG IITTEDJKAG LIQTNVPEEA LRVVRDPREA VTLTDDPIEA VTLTDDPIEA LTUTEDYKA VTTTADAHAA	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD VKNADIVVTD STNANILVTD VKNADIVVTD VKGADFIYTD VKGADFIYTD VKKADILVTD VKKADILVTD VKDADVIYSD VKDADVIYTD AAAADVLVTD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEDE VWVSMGEPLE VWVSMGEPLE VWISMGEDE VFTSMGQEDE VFTSMGQEDE VFTSMGQEDE TWTSMGQEDE TWTSMGQEDE VWVSMGEPLE	K. KKRLQAFQ K. KKRLQAFQ K. KKRLQAFQ K. KKRLDFK K. QORLKQFT K. QORLKQFT K. QAKLKQFT X. QARLKQFK 242 KWAERIALLR TWGERIKLLL V. EERIALLA S. LKRMKAFE A. AERRKIFR G. LDRVKPFR AWGERIKELL AWGERIKELL	GYQUTMKTAK GYQUTMKTAK GYQUTMKTAK GYQITMKTAK GFQITKEMIS GFQUTGEIMK GFQITNQELVS 252 EYQUNSKMMQ PYQUTPEIMK PYQUNSKIMA PYQUNAALLO PYQUNAALLO PFQUNKCLVK PFQUNKCLVK PFQUNKCLVK	V. AASDWTF V. AASDWTF U. AASDWTF L. AAPNWTF LAK. PSCKF V. ADPNYKF 262 LIG. NPEVKF RTG. NPKVKF G. AADDVLF H. AKPDYTF H. AKPDYTF L. ADSDAIV ATG. NPRAKF ASG. NPOVKF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_PACTA OTC_PACTA OTC_LECOLI OTC_HAEIN OTC_ASPTE OTCA_PSEAE OTCA_SEASU OTC_PYRFU OTCA_PYRFU OTCA_PYRFU OTCA_PSEAE OTCC_PSEAE OTCC_PSEAE OTCC_PSEAE OTCC_PSEAE	FGMHLQAATP FGMHLQAATP FGMHLMAATP FGMHLHIATP SGIDVSIAVP VGHTSVAKP FGSVSISTP 179 TGLDLRLVAP LGMDVRIGP FGYNLRIAP FDFQLRVACP MGCDLSIASP AGHHVVAAP LGMDVRIAAP LGMDVRIAAP	KGYEPDASVT KGYEPDPNIV KGYEPDSIV SGLKFEELIL KDVWNRDDIL PGIEMDSDIV 189 QACWP KALLP NALHP KGYEIPASMR EGYEPDKAEFV KGYEVLDEAA EGYEPDEKVI EGFLPDPSVR KALWP QSLWP DSLKP	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SIVNEAANEN DEAKKVAERN 194 . RAALVTEC . EANLVEMC . TDAVLAGI ELIQEAGKGV ALAGDR EAAKTVALQS AAAERRAQDT . HDEFVAQC . SEGIIAAA . DEDLIKEM	GT.K GT.K GT.K GT.K GTIK GSTFE GATFE 202 RALAQQNCGN EKFAKESGAR YEQTPENGS GS.S GS.S GS GS KKFAEESGAK HAAAKETGAK	LLLTNDPLEA LSMTNDPLEA LLSMTNDPLEA LLMTNDPLEA L. TNDPLEA I VNDPKVA L THDSLKA 212 ITLTEDVAKG ITUTEDIDKA IELFTEVAAG VTUTDDPLEA LRVVRDPREA LRVVRDPREA LTUTEDPKA VTUTADAHAA LTUTEDPKEA ITLTEDAHAA	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD STNANILVTD 222 VEGADFIYTD VKGVDFIHTD VKGADVIYTD VAGAHLVSTD VKDADVIYTD VKDADVIYTD VKGADVIYTD VKGADVIYTD	TWISMQQEEE TWISMQQEE TWISMQQEE TWISMQQEE TWISMQQEE TWISMQEET 232 VWVSMGEAKE VWVSMGEAKE VWSMGEAKE VWSMGEQEE VWSMGQEEE VWSMGQEAE VWSMGEPVE VWVSMGEPVE VWVSMGEPVE	K. KKRLQAFQ K. KKRLQAFQ K. KKRLQAFQ K. KKRLQFK R. LQKLKQFE K. QORLKQFT K. QAKLKQFK 242 KWARTIALLR TWGERIKLLL V. EERIALLK S. LKRMKAFE A. AARIAMFR E. QERLAVFA A. EERRKIFR G. LDRVKPFR AWGERIKLLL WWGERIKLLL VWGERIKLL	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITKENIS GFQTKENIS SFQVTGEIMK GFQINQELVS 252 EYQVNSKMMQ PYQVTPELMK PYQVNALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLA PYQVMEIMK DYRVTPELMA	V. AASDWTF V. AASDWTF U. AASDWTF L. AAPNWIF LAK. PSCKF V. ADDNYKF 262 LITG. NPEVKF RTG. NPEVKF RTG. NPEVKF G. AADDVLF H. AKEDYTF H. AKEDYTF H. AKEDYTF H. AKEDYTF ASG. NPQVKF XTG. NPRAFF ASG. NPQVKF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_SCHPO OTC_YEAST OTC1_HAEIN OTC_HAEIN OTC_ASPTE OTC2_BACSU OTC2_PARFU OTC2_PSEAE OTC2_PSEAE OTC2_PSEAE OTC2_PSEAE OTCC_NEIGO OTCC_CLOPE	FGMHLQAATP FGMHLQAATP FGMHLHATP SGIDVSIAVP VGIHTSVAKP FGISVSISTP 179 TGLDLRLVAP FGYNLRIAP FGYNLRIAP FDFQLRVACP FDFQLRVACP FDFQLRVACP AGHVTVAAP AGHVTVAAP LGMDVRIAAP LGMDVRIAAP	KGYEPDASVT KGYEPDPNIV KGYEPDSIV KGYEPNSLV SGLKFEELIL KDVNVRDDIL PGIEMDSDIV 189 QACWP KALLP KALLP KGYEIPASMR EGYEPDEAVI EGYEPDEAVI EGYEPDEAVI EGYEPDEVDEAA EGYEPDESVR KALWP QSLWP DSLKP	KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVNEAANEN DEAKKVAERN ISALVTEC EAALVTEC TDAVLAGI ELIQEAGKGV ELIQEAGKGV ALAGDR EAAKTYALQS KWAEQNAAES AAAERRAQDT HDEFVAQC SEGIIAAA DEDILKEM	GT.K GT.R GT.R GT.K GTILK GSTFE GATFE 202 RALAQQNGGN EKFAKESGAR YEQTPERNGS ANPGK GS.S GS.S GS.S KKFAEESGAK HAAAKETGAK QEYSKETGAT	LLLTNDPLEA LSMTNDPLEA LLMTNDPLEA LLMTNDPLEA I VNDPKVA I TNDPLEA I VNDPKVA L THDSLKA 212 ITLTEDVAKG ITUTEDJAKA IEIFTEVAAG LIQTNVPEEA VTUTDDPLEA FELLHOPVKA ITLTEDPKEA ITLTEDAHAA LITTEDPKEA ITLTENAHEA IEFSSNVDEA	AHGGNVLITD ARGGNVLITD ARGGNVLITD INGANVLVTD VKNADIVVTD 222 VEGADFIVTD VKGVDFIHTD VKGVDFIHTD VKADILVTD VKADLIVTD VKADVIYTD VKADVIYTD VKGADVLVTD VKGQGFIHTD VKGADVIYTD	TWISMQQEEE TWISMQQEDE TWISMQQEDE TWISMQQEDE TWISMQQEAE TFVSMGQEAE TFVSMGEFA 232 UWUSMGEAKE UWUSMGEAKE UWUSMGEDE UWASMQQEDE UWASMQQEDE UWASMQQEDE UWASMQEDE UWUSMGEPVE UWUSMGEPVE UWUSMGEPVE	K. KKRLQAFQ K. KKRLQAFQ K. KKRLDFK R. LQKLKQFE K. DQRLKQFT Z42 K. QAKLKQFK 242 X. MAERIALLR TWGERIKLLL V. EERIALLK S. LKRMKAFE G. JERVKPR A. AARIAMFR E. QERLAVFA A. BERRKIFR G. LDRVKPFR AWGERIKELL WWQERIDLLK LYPERVKLLT	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITKEMIS GFQITKEMIS GFQITKEIK EYQVISKMMQ PYQVTPELMK PYKVTEKMMA GFQITSELAK GFQITSELAK PYQVNAALUS PFQUNKLUK PYQVNAALUS PFQUNKLIX PYQVNAALUS PFQUNKLIX PYQVNAELMK DYRVTPELMA PYKVTREMMI	VAASDWTF VAASDWTF LAASDWTF LAASDWTF LAK PSCKF VADPNYKF 262 LTG. NPEVKF RTG. NPEVKF RTG. NPEVKF RGGANENWKF LTG. KADTLF RGGANENWKF LAKPDYTF HAKPDYTF HAKPDYTF HAKPDYTF A.GNPAXF ASG. NPQVKF KTG. NKNTLF
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OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_PACTA OTC_PACTA OTC_PACTA OTC_PACTA OTC_PAST OTC_PSESH OTC_ASPTE OTCA_PSEAE OTCA_PSEAE OTCA_PSEAE OTCA_PSEAE OTCA_PYRFU OTCA_PYRFU OTCC_PSEAE OTCC_NEIGO OTCC_CLOPE	FGMHLQAATP FGMHLQAATP FGMHLMAATP FGMHLMIATP SGIDVSIAVP VGHHTSVAKP FGISVSISTP TGLDLRLVAP LGMDVRIGP FGYNLRIAP FDPQLRVACP MGCDISIASP AGHVTVAAP LGMDVRIAAP LGMDVRIAAP LGMDVRIAAP	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV SGLKFELIL KDVNVRDDIL PGIEMDSDIV 189 QACWP KALLP NALHP KGYEIPASMR BGYEPGKAEFV KGYEVLDEAA EGYEPDEKVI EGFLPDPSVR KALWP QSLWP DSLKP	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKOPSKEC SGAKEISAEN SIVNEAANEN DEAKKVAERN 194 .BAALVTEC .CDAVLAGI ELIQEAGKGV ALAGDR EAAKTVALQS AAAERRAQDT .HDEFVAQC .SEGIIAAA .DEDILKEM	GT.K GT.K GT.K GT.K GTIK GSTFE GATFE 202 RALAQQNCGN EKFAKESGAR YEQTPERNGS GS.S GS.S GA.S KKFAEESGAK HAAAKETGAK QEYSKETGAT	LLLINDPLEA LSMINDPLEA LSMINDPLEA LLMINDPLEA L. TNDPLEA I VNDPKVA L THDSLKA 212 ITLTEDVAKG ITUTPEDIDKA IEIFEVAAG LIUTPEEA LRVVRDPEEA LRVVRDPEEA LRVVRDPEEA LRVVRDPEA LIUTPEDPKEA ITLTEDPKEA ITLTEDAHEA LEFSSNVDEA	AHGGNVLITD ARGGNVLITD ARGGNVLITD INGANVLITD VKNADIVVTD STNANILVTD 222 VEGADFIYTD VKGVDFIHTD VKGADVIYTD VKGADVIYTD AAADVLVTD VKGADVIYTD VKGADVIYTD VKGADVIYTD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEDE VWISMGEAKE VWISMGEDE VWISMGEDE VWISMGEDE VWISMGENE TWISMGEDES TWISMGEDES ••	K. KKRLQAFQ K. KKRLQAFQ K. KKRLQAFQ K. KKRLQFK R. LQKLKQFE K. QQRLKQFT K. QAKLKQFK 242 KWAERIALLR TWGERIKLLL V. EERIALLK S. LKRMKAFE A. AARIAMFR E. QERLAVFA A. EERRIFR G. LDRVKPFR AWGERIKELL VWQERIDLLK LYPEVKLLT	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GFQITKENIS GFQTKENIS SFQVTGEIMK GFQITVELVS PYQVTPELMK PYQVTPELMK PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLA PYQVNMEIMK DYRVTPELMA PYKVTREMMN	V. AASDWTF V. AASDWTF U. AASDWTF L. AAPNWIF LAK. PSCKF V. ADPNYKF 262 LTG. NPEVKF RTG. NPEVKF G. AADDVLF H. AKPDYTF H. AKPDYTF H. AKPDYTF L. ADSDAIV ATG. NPRAKF ASG.NPQVKF KTG. NKNTLF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_SCHPO OTC_YEAST OTC_HAEIN OTC_HAEIN OTC_PSEAE OTC2_BACSU OTC2_PSEAE OTC2_PSEAE OTC2_PSEAE OTC2_PSEAE OTC2_PSEAE OTC2_PSEAE OTC2_PSEAE OTC2_PSEAE	FGMHLQAATP FGMHLQAATP FGMHLHATP SGIDVSIAVP VGIHTSVAKP FGSVSISTP 179 TGLDLRLVAP LGMDVRICGP FGVNLRIAP FGVNLRIAP FDFQLRVACP FDFQLRVACP AGHVTVAAP AGHVTVAAP LGMDVRIAAP LGMDVRIAAP LGMDVRIAAP LGMDVRIAAP LGMDVRIAAP	KGYEPDASVT KGYEPDPNIV KGYEPDSIV SGLKFELIL KDVNVRDDIL PGIEMOSDIV 189 QACWP KALLP NALHP KGYEIPASMR BGYEPKAEFV KGYEVLDEAA EGYEPDEKVI EGYEPDESVR KALWP QSLMP DSLKP	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SIVNEAANEN DEAKKVAERN IP4 .RAAUTEC .EANLVEMC .TDAVLAGI ELIQEAGKGV ALAGDR EAAKTYALQS AAAERRAQDT HDEFVAQC SEGIIAAA .DEDILKEM	GT.K GT.R GT.R GT.K GTILK GATFE 202 RALAQONGEN EKFAKESGAR YEQTPERNGS ANEGK GS.S GS.S GS.S GS.S KKFAEESGAK HAAAKETGAK QEYSKETGAT	LLLTNDPLEA LSMTNDPLEA LLSMTNDPLEA LLMTNDPLEA LNNDPKVA LTHDSLKA 212 ITLTEDVAKG ITUTEDIDKA IELFTEVAAG LIQTNVPEA LIQTNVPEA LIQTNVPEA FELLHDPVKA ITLTEDAHAA LTLTEDPKEA ITLTEDAHAA SLVPPEAENR SLVPPEAENR	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD STNANILVTD 222 VKQADFIYTD VKGVDFIHTD VKGADFIYTD VKGADVIYTD VKGADVIYTD VKGADVIYSD VKGADVIYTD VKGADVIYTD VKGADVIYTD VKGADVIYTD	TWISMQQEEE TWISMQQEDE TWISMQQEDE TWISMQQEDE TWISMQQEDE TWISMQQEAE TPVSMGEEFA 232 VWVSMGEPE VWVSMGEPLE VWVSMGEPLE VWSMGEDE VFTSMQQEAE VWASMQQEAE VWASMQQEAE VWASMQEDE VWSMGEPVE VWVSMGEPVE VWVSMGEPVE VWVSMGEPVE VWVSMGEPZE ••	K. KKRLQAFQ K. KKRLQAFQ K. KKRLDFK R. LQKLKQFE K. EQRLKQFT K. QAKLKQFK 242 XWAERIALLR TWGERIKLLL V. EERIALLK S. LKRMKAFE G. LDRVKPFR AWGERIKELL WQERIDLLK LYPERVKLLT KPKF KDKF	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GPQITMKTAK GPQTIQELWS 252 EYQVISKIMMQ PYQVTPELMK PYKVTEKIMA GPQITSELAK GPQITSELAK PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLS PPQUNKDLVK DYKVTPELMA PYQVNMEIMK DYKVTPELMA	VAASDWTF VAASDWTF UAASDWTF LAASDWTF LAKPSCKF VADPNYKF 262 LTG.NPEVKF RTG.NPEVKF RTG.NPEVKF RTG.NPEVKF HAKPDYTF HAKPDYTF HAKPDYTF HAKPDYTF HAKPDYTF KTG.NPRAKF ASG.NPQVKF KTG.NKNTLF
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OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_PACTA OTC_PACTA OTC_PACTA OTC_HAST OTC_HAST OTC_PSESH OTC_PSESH OTC_PSEAE OTC2_PACASU OTC_PYRFU OTCA_MYCBO OTCC_PSEAE OTCC_NEIGO OTCC_CLOPE	FGMHLQAATP FGMHLQAATP FGMHLHATP FGMHLHIATP SGIDVSIAVP VGHHTSVAKP FGISVSISTP TGLDLRLVAP LGMDVRIGP FGVNLRIIAP MGVDLAVATP FDPQLRVACP MGCDISIASP MGCDISIASP LGMDVRIGAP MGMHFVALGP LHCLPRKPE LHCLPRKPE LHCLPRKPE	KGYEPDASVT KGYEPDPNIV KGYEPDPNIV SGKFEELIL KDVNVRDDIL PGIEMDSDIV QACWP KALLP NALHP KGYEIPASMR BGYEPDEKAI EGYEPDEKAI EGYEPDEKVI EGFLPDPSVR KALMP QSLMP DSLKP	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN SIVNEAANEN JEAKKVAERN 194 .EAALVTEC .EAALVTEC .TAAVLAGI .ELQEAGKGV ALAGDR EAAKTYALQS KWAEQNAAES AAAERRAQDT .BEGIIAAA .DEDILKEM .E 	GT.K GT.R GT.R GT.K GT.K GT.K GSTFE 202 RALAQQNGGN EKFAKESGAR YEQTPERNGS ANFGK ANFGK GS.S GA.S KKFAEESGAK HAAAKETGAK VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA L.MTNDPLEA INNDPLEA INNDPLEA INNDPKVA ITNDPLEA II.TTEDVAKG ITTTEDJAKA IEIFTEVAAG ITTTEDJAKA LRTVTDDPLEA LRTVTDDPLEA LRTVTDADAHAA LTTTEDPKEA ITTTEDAHEA IEFSSNVDEA SLVPPEAENR SLVPPEAENR SLVPPEAENR	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD STNANILVTD 222 VKGADFIYTD VKGADFIYTD VKGADFIYTD VKGADVIYTD VKGADVIYTD XKADILVTT VKGADVIYTD XKGADVIYTD XKGADVIYTD XKGADVIYTD XKGADVIYTD XKGADVIYTD XKGADVIYTD XKGADVIYTD XKGADVIYTD	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEAE TWISMGQEAE TWISMGQEAE TWISMGQEDE VWISMGEPLE VWISMGEPLE VWISMGEPLE VWISMGEPLE TWISMGQEAE TWISMGQEAE TWISMGEPLE TWISMGEPLE TWISMGEPLE TWISMGEPLE TWISMGEPLE TWISMGEPLE TWISMGEPLE TWISMGEPLE TWISMGEPLE TWISMGEPLE	K. KKRLQAFQ K. KKRLQAFQ K. KKRLQAFQ K. KKRLQFK 242 K. QRLKQFE K. QQRLKQFT K. QAKLKQFK 242 KWABRIKLLL V. EERIALLK V. GERIALFA A. ARRIAMFR E. QERLAVFA A. EERRIF G. LDRVKPFR AWGERINELL VWQERIDLLK LYPERVKLLT KEKF KEKF KEKF EPETF	GYQUTMKTAK GYQUTMKTAK GYQUTMKTAK GYQITMKTAK GFQITKEMIS GFQUTGEIMK GFQITNQELVS 252 EYQUNSKMMQ PYQUTPEIMK PYQUTPEIMK PYQUNSALLD PYQUNAALLD PYQUNAALLD PYQUNAALLD PYQUNAALLD PYQUNAALLD PYQUNAALLA PYQUNAALLA PYQUNAALLA PYQUNAALLA PYQUNAALLA PYQUNAALMA PYQUNMEIMK DYRVTPELMA PYKVTREMMN	V. AASDWTF V. AASDWTF J. AASDWTF L. AAPNWIF LAK. PSCKF V. ADPNYKF 262 LTG. NPEVKF RTG. NPEVKF RTG. NPEVKF G. AADDVLF H. AKEDYTF H. AKEDYTF L. AADDVLF H. AKEDYTF L. ADSDAIV ATG. NPRAKF ASG. NPQVKF KTG. NKNTLF
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OTC_HUMAN OTC_MOUSE OTC_RANCA OTC_PACTA OTC_PACTA OTC_SCHPO OTC_YEAST OTC_HAEIN OTC_PSESH OTC_ASPTE OTC_ASPTE OTC_PSEAE OTC_PSEAE OTC_PSEAE OTCC_PSEAE OTCC_PSEAE OTCC_PSEAE OTCC_REIGO OTCC_PSEAE OTCC_RANCA OTC_PACTA OTC_SCHPO OTC_YEAST	FGMHLQAATP FGMHLQAATP FGMHLUQAATP FGMHLHIATP SGIDVSIAVP VGIHTSVAKP FGISVSISTP 179 TGLDLRUVAP LGMDVRICGP FGYDLRIIAP MGDDISIASP LGMDVRIGAP MGCDISIASP LGADVUVATP AGHUVVATP AGHUVVADP LCMDVRIGAP MGMHFVALGP LHCLPRKPE LHCLPRKPE LHCLPRKPE LHCLPRKPE LHCLPRKPE HCLPRHPE MHCLPRHPE 271	KGYEPDASVT KGYEPDDNIV KGYEPDSLT SGLKFEELIL KDVNVRDDIL PGIEMDSDIV RALLP NALLP NALLP NALLP KGYEIPASMR EGYEPDEKVI ESFLPDESVR KALWP DSLKP DSLKP 281	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC SGAKEISAEN SIVIFEANEN DEAKKVAERN 194 . EAALVTEC . EAALVTEC . EAALVTEC . TDAVLAGI ELIQEAGKGV ALAGDR EAAKTYALQS KWAEQNAAES AAAERAQDT . HDEFVAQC 	GT.K GT.R GT.R GT.R GTTLK GSTFE GATFE 202 RALAQQNGGN EKPARESGAR PACAGON RALAQQNGGN EKPARESGAR ANPGK GS GS GS GS GS GS GS GS GS GS GS GS C.	LLLTNDPLEA LSMTNDPLEA LSMTNDPLEA ITNDPLEA ITNDPLEA ITNDPLEA ITNDEKXA ITHDSLKA 212 ITLTEDVAKG ITVTEDIDKA LIUTNPEEA LRVVRDREA LRVVRDREA FELLHDPVKA VTT.TDDPLEA FELLHDPVKA VTT.TDDPLEA FELLHDPVKA VTT.TDDPLEA FELLHDPVKA VTT.TDDPLEA SLVFPEAENR	AHGGNVLITD ARGGNVLITD ARGGNVLITD ANGANVLVTD VKNADIVVTD STNANILVTD VKNADIVVTD VKADIVTD VKGQFHTD VKGDFHTD VKADILVTD VKADLIVTD VKADLIVTD VKADLIVTD VKADLIVTD VKADLIVTD VKADLIVTD VKADLIVTD VKGVFHTD VKGVFHTD VKGVFHTD VKGVFHTD VKGVFHTD VKGVFHTD VKGVFHTD VKGVFHTD VKGVFHTD VKGVFHTD VKGVFHTD VKGVFHTD VKGVFHTD VKGADVIYTD VKGVFHTD VKGVFHTD VKGVFHTD VKGADVIYTD VKGVFHTD VKGADVIYTD VKGVFHTD VKGADVIYTD	TWISMQQEEE TWISMQQEE TWISMQQEE TWISMQQEE TWISMQQEE TWISMQEAE TWISMQEAE TWISMQEAE TWISMGEEX TWISMGEEX TWISMGEEX TWISMGEEX TWISMGEEX TWISMGEEN UWASMQEAE TWISMGEN UWSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE TUTTYSPULQ LLTDYSPULQ LLTDYSPULQ SFVUNKGKLL LLTVNRGELLP FVUNKGNFKD 330	K. KKRLQAFQ K. KKRLQAFQ K. KKRLQAFQ K. KKRLDFK K. 20RLKQFE K. 20RLKQFE K. 20RLKQFT X. 242 KWAERIALLR TWGERIKLL V. EERIALLR S. LKRMKAFE A. AARIAMTR E. 20RLAVFA A. EERRKIFR G. LDRVKPER AWGERIKELL LYPERVKLLT KPKF KPKF KPKF KPKF KPKF KPKF RPTF PASA LK	GYQUTMKTAK GYQUTMKTAK GYQUTMKTAK GYQITMKTAK GFQITKEMIS GFQUTKEMIS GFQUTKEMIS GPQINSKIMO PYQVTREIMK GPQITSELAK PYQVNAALLO PYQVNAALVS PFQUNKALVS PPQUNAALVS PPQUNAALVS PPQUNAALVS PYQVNAALVS PYQVNAALVS PYQVNAALVS PYQVNAALVS PYQVNAEIMK PYQVNAEIMK	V. AASDWTF V. AASDWTF L. AAPNWTF L. AAPNWTF L. AAPNWTF LAK. PSCKF V. ADPNYKF 262 LTG. NPEVKF RTG. NPEVKF RTG. NPEVKF RTG. NPEVKF G. AADDULF H. AKPDYTF L. AADDULF H. AKPDYTF L. AADDULF KTG. NFAKF ASG. NPQVKF KTG. NKNTLF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_PACTA OTC_PACTA OTC_LECCL OTC1_ECCL OTC1_ECCL OTC_PSESH OTC_ASPTE OTC_ASPTE OTC2_PACASU OTC_PYRFU OTC2_PACASU OTC_PYRFU OTC2_NEIGO OTCC_NEIGO OTCC_NEIGO OTCC_NEIGO OTCC_NEIGO OTC_CAPEA OTC_RANCA OTC_PACTA OTC_RANCA	FGMHLQAATP FGMHLQAATP FGMHLHATP FGMHLHATP SGIDVSIAVP VGHHTSVAKP FGISVSISTP TGLDLRLVAP LGMDVRICGP FGYNLRIIAP MGVDLAVATP FDFQLRVACP MGCDISIASP LGADVVATP AGHHVTVAAP LGMDVRIGAP MGMHFVALGP LHCLPRKPE LHCLPRKPE LHCLPRKPE LHCLPRKPE MHCLPRHPE MHCLPRHPE MHCLPRHPE MHCLPRHPE MHCLPRHPE	KGYEPDASVT KGYEPDPNIV KGYEPDSIT SGLKFEELIL KDVNVRDDIL PGIEMDSDIV QACWP KALLP NALHP KALLP KGYEIPASMR BGYEPDEKVI EGYEPDEKVI EGYEPDEKVI EGYEPDEKVI EGYEPDEKVI DSLKP DSLKP 281 QTTLGKKMAE	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKQFSKEC EAAKQFSKEC SIVUFEANEN DEAKKVAERN 194 . EAALVTEC . EAALVTEC . EAALVTEC . TDAVLAGI . DEDILKEN . DEDILKEN . E . E . E . E . E . E . E . E . E . E	GT.K GT.K GT.K GT.K GT.K GTILK GSTFE GATFE 202 RALAQQNGGN EKFAKESGAR YEQTPERNGS ANFGK ANFGK ANFGK GS.S GA.S GA.S KKFAEESGAK HAAAKETGAT VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYGEN VSDDVFYGEH 300	LILITNDPLEA LSMTNDPLEA LSMTNDPLEA L.SMTNDPLEA INNDPLEA INNDPLEA INNDPKVA ITNDPLEA IINNDPKVA ITHDSLKA 212 ITTTEDUAKG ITTTEDUAKG ITTTEDUAKA VTUTDDPLEA LRVVRDPREA LRVVRDPREA LRVVRDPREA FELLHDPVKA VTUTDDPLEA IEFSSNVDEA SLVFPEAENR	AHGGNVLITD ARGGNVLITD ARGGNVLITD ARGGNVLITD INGANVLVTD STNANILVTD 222 VKQDFIHTD VKQADFIHTD VKQADFIYTD VKGADLIVTD VKADAUIYTD AAADVLVTD VKGADVIYTD XKADFIHTD VKGAFIHTD VKGAFIHTD VKGAFIHTD VKGAFIHTD VKGAFIHTD VKGAVIYTD XKWTIMAVMVS KWTIMAVMVS KWTIMAVMVS KWTIMAVMVS ZNTAAIAVLE XWTTVAVLEA LYAAMSATDI 320	TWISMGQEEE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGQEAE TWISMGQEAE TWISMGQEAE TWISMGQEDE VWISMGEDE VWISMGEDE VWISMGEDE TWISMGQEDE TWISMGQEDE TWISMGQEDE TWISMGENE TWISMGENE LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ SFVNIKGKLL LLINYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ LLIDYSPULQ	K. KKRLQAFQ K. KKRLQAFQ K. KKRLQAFQ K. KKRLQAFQ K. CARLAGFE K. DQRLKQFT K. QARLAQFK 242 KWAERIALLR TWGERIKLL V. EERIALLK S. LKRMKAFE A. AARIAMFR E. QERLAVFA A. EERRKIFR G. LDRVKPFR A. EERRKIFR G. LDRVKPFR AWGERINELL LYPERVKLLT KPKF KPKF KPKF KPKF KPKF RPTF PASA LK	GYQUTMKTAK GYQUTMKTAK GYQUTMKTAK GYQITMKTAK GFQITKEMIS GFQUTGEIMK GFQITNOELVS 252 EYQUNSKMMQ PYQUTPEIMK PYQVINSKLIX PYQVINALLUS PYQVINALLUS PYQVINALLUS PYQVINALLUS PYQVINALLUS PYQVINALLUS PYQVINALLUS PYQVINALLUS PYQVINALLUS PYQVINALLUS PYQVINALUS PYQVINALUS PYQVINALUS PYQVINALUS PYQVINALUS PYQVINALUS PYQVINALUS	V. AASDWTF V. AASDWTF V. AASDWTF L. AAPNWTF LAK. PSCKF V. ADDNYKF 262 LTG. NPEVKF RTG. NPEVKF RTG. NPEVKF H. AKDPYTF H. AKDPYTF L. AADDVLF H. AKDPYTF L. ADDALF KTG. NRNTLF
OTC_HUMAN OTC_MOUSE OTC_RAT OTC_RANCA OTC_PACTA OTC_PACTA OTC_YEAST OTC_YEAST OTC_HAEIN OTC_HAEIN OTC_PSEAE OTC2_PACA OTC2_PARFU OTC3_PSEAE OTC2_PACA OTC2_PARFU OTC2_PARFU OTC2_PARFU OTC2_PARFU OTC2_PACA OTC2_PACA OTC2_PACA OTC2_RANCA OTC_PACTA OTC_SCHPO OTC1_ECOLI OTC1_ECOLI	FGMHLQAATP FGMHLQAATP FGMHLHATP SGIDVSIAVP VGIHTSVAKP FGMTLHIATT FGSVSISTP 179 TGLDLRLVAP LGMDVRICGP FGYNLRIAP GDDLAVATP FDFQLRVACP FDFQLRVACP FDFQLRVACP LGMDVRIGAP MGCDISIASP LGADVVATP AGHVTVAAP LGMDVRIGAP MGCHFVALGP LHCLPRKPE LHCLPRKPE LHCLPRKPE LHCLPRKPE HHCLPRHPE MHCLPRHPE MHCLPRHPE 271 LHCLPAFHDD MHCLPAFHDS	KGYEPDASVT KGYEPDPNIV KGYEPDSIV KGYEPNSIV SGLKFEELIL KDVNVRDDIL PGIEMDSDIV 189 QACWP KALLP NALHP KALLP KGYEIPASMR BGYEPKAEFV KGYEPDEKVI EGFLPDPSVR KALWP QSLWP DSLKP 281 QTTLGKKMAE ETKVGRQIAE	KLAEQYAKEN KLAEQYAKEN KLAEQYAKEN EAAKOPSKEC SIVNEAANEN DEAKKVAERN 194 .BAALVTEC .EANLVEMC .TDAVLAGI ELIQEAGKGV ALAGDR EAAKTVALQS .AAERRAQDT .HDEFVAQC .SEGIIAAA .DEDILKEM .E E E E E E E 	GT.K GT.K GT.K GT.K GT.K GTIK GSTFE 202 RALAQQNGGN EKFAKESGAR YEQTPENGS ANPGK AS.S GS.S GS.S GS.S GS.S GS.S GS.S GS.S KKFAEESGAK HAAAKETGAK QEYSKETGAT VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYSPR VDDEVFYDEE VSDEVFYGEN VSDEVFYGEN S300 VTDEVFSSAA VTDEVFSSAA	LLLTNDPLEA LSMTNDPLEA LLSMTNDPLEA LLMTNDPLEA LL.TNDPLEA LTNDPLEA LTNDPLEA LTNDPLEA LTNDPLEA LLMTNDPLEA LTTTEDVAKG ITTTEDVAKG ITTTEDVAKG VTVTDDPLEA LRVVRDPEA LRVVRDPEA LRVVRDPEA LLTTEDPKA VTVTADAHAA LTTTEDPKEA LTTTEDPKEA LTTTEDPKEA SLVFPEAENR	AHGGNVLITD ARGGNVLITD ARGGNVLITD ARGANVLITD VKADIVVTD STNANILVTD 222 VKGADFIYTD VKGADFIYTD VKGADFIYTD VKGADVIYTD VKGADVIYTD VKGADVIYTD VKGADVIYTD VKGADVIYTD VKGADVIYTD VKGVGFIHTD VKGVGFIHTD VKGVGFUH	TWISMQQEEE TWISMQQEEE TWISMQQEE TWISMQQEE TWISMQQEAE TWISMQEAE TWISMQEAE TWISMQEAE VWSMGEAKE VWSMGEAKE VWSMGEAE VWSMGEQEE VWSMGEQEE VWSMGEQEE VWSMGEDE WWSMGEDE UFTSMQQEAE VWSMGEPKE IWVSMGEPKE IWVSMGEPKE IWVSMGEPKE LLTDYSPQLQ LLTDYSPQLQ LLTDYSPQLQ LLTDYSPQLQ LLTDYSPVLQ LLTDYSPVLQ LLTDYSPVLQ LLTDYSPVLQ LLTDYSPVLQ LLTDYSPVLQ LLTDYSPVLQ LLTDYSPVLQ TLSK-SLA-~	K. KKRLQAFQ K. KKRLQAFQ K. KKRLQAFQ K. KKRLQFK K. QRLKQFE K. QRLKQFE K. QRLKQFE X. QAKLKQFK 242 XWAERIALLR TWGERIKLLL V. EERIALLK V. GERIALLR TWGERIKLLL V. EERIALLK S. LKRWKAF A. AARIAMFR E. QERLAVFA A. GERLAVFA A. GERLAVFA A. GERLAVFA MGERIKELL VWQERIDLLK LYPERVKLLT KPKF KPKF KPKF KPKF KPKF KPKF KPKF KPK	GYQVTMKTAK GYQVTMKTAK GYQVTMKTAK GYQITMKTAK GPQITMKTAK GPQITMKTAK 252 EYQVISKIMMQ PYQVTPELMK PYQVTPELMK PYQVTSELMA PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNAALLD PYQVNMEIMK DYRVTPELMA PYKVTREMMN	V. AASDWTF V. AASDWTF V. AASDWTF L. AAPNWIF LAK. PSCKF V. ADDNYKF 262 LITG. NPEVKF RTG. NPEVKF G. AADDVLF H. AKPDYTF H. AKPDYTF H. AKPDYTF H. AKPDYTF H. AKPDYTF ASG.NPQVKF KTG. NKNTLF
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FIGURE 2. Sequence alignment of selected OTCase sequences (four ureotelic OTCases, three yeast OTCases, eight anabolic bacterial OTCases, and three catabolic bacterial OTCases, separated by solid lines). For a more complete list, see ref 19. PALO binding residues are indicated by

•, and residues proposed to be catalytically important are indicated by
•. Sequence numbering is based on the sequence of *E. coli* OTCase. The organisms used in the alignment were *Homo sapiens* (human), *Mus musculus* (mouse), *Rattus norvegicus* (rat), *Rana catesbeiana* (bull frog), *Pachysolen tannophilus, Schizosaccharomyces pombe, Saccharomyces cerevisiae, Escherichia coli, Haemophilus influenzae, Pseudomonas syringae, Aspergillus terrus, Bacillus subtilis, Pyrococcus furiosus, Mycobacterium bovis, Pseudomonas aeruginosa, Neisseria gonorrheae, and Clostridium perfringens. * indicates sequences not shown for clarity.*

		2	13	23	31	27	12	52	62	73
	7NT	DI VORHITET	TT COLODI NU		JI	3/	45	22	03	/3
DVDD CALEY	AN	PLIQKHIISI	NDLSRDDLNL	VLATAAKL	KANPQP	ELLKHK	VIASCEFEAS	TRTRESFETS	MHRLGASVVG	FSDSANTSLG
PYRB_SALTY	~~~~~AN	PLYQKHIISI	NDLSRDDLNL	VLATAAKL	KANPQP	ELLKHK	VIASCFFEAS	TRTRLSFETS	MHRLGASVVG	FSDSANTSLG
PYRB_SERMA	~~~~AN	PLYHKHIISI	NDLSRDDLEL	VLATAAGL	KANPQP	ELLKHK	VIASCFFEAS	TRTRLSFETS	MHRLGASVVG	FADGSNTSLG
PYRB_PYRAB	~~~~M	DWKGRDVISI	RDFSKEDIET	VLATAERLER	ELKEKGQL	EYAKGK	ILATLFFEPS	TRTRLSFESA	MHRLGGAVIG	FAEA.STSSV
PYRB_SULSO	~~~~~~~~~	~~~MKHIISA	YNFSRDELED	IFALTDKYSK	NLNDTRKI	LSGK	TISIAFFEPS	TRTYLSFOKA	IINLGGDVIG	FSGE.ESTSV
PYRB_ARATH	*MOAGTRELK	KFELSDVIEG	KOFDREMLSA	IFDVAREMEK	IE. KSSSOS	ETLKGY	LMATLEYERS	TRTRISFESA	MKRLCCEVUT	TENAREESSA
PYRB BACCL	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~MTHLEAL	SELPLOFTHR	LLOFAFRERS	CRIWR	DAA DM	VUANT FFFDC	TOTVOCEDMA	PRUCCUUTD	
PYRE BACSI	~~~~~~~~~~~~	~~~MKHT.TTM	CEL CUERTED	LIONACEIKS	OVTION	OLD CK	TVANLETERS	TRICOPENA	ERREGENVEP	ID. CECESI
DVDD IACTE		TT DT DVENOU	TOLONDATI	TTODIOUTION	GRIDN	QLIGK	FAANLFFEPS	TRIKESPEVA	EKKLGMINVLIN	LD. GISISV
FIRD_LACEE	A E I EDKÖDIA	LLRLPIFVSV	EQUSADDVLH	LLQRAQYFKN	GGEVP	ALSRPI	FCINMFFENS	TRIHISFEVA	ERREGETVIP	FD. PSHSSV
PIRE_LACPL	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	MKTSQNLVSV	EQFSNQDVMA	YLKLAQAFKN	GKTV	QLSQPT	FAMNLFFENS	TRTHTSFEMA	ERRLGLQVIP	FDPKTSSV
PYRB_PSEAE	*AKRPLQLND	QGQLRHFISL	DGLPRELLTE	ILDTADSFLE	.VGARAVKKV	PLLRGK	TVCNVFFENS	TRTRTTFELA	AQRLSADVIS	LNVSTSST
PYRB_PSEPU	*AKRPLQLND	QGQLRHFLSL	DGLPRELLTE	ILDTADSFLE	.VGARAVKKV	PLLRGK	TVCNVFFENS	TRTRTTFELA	AQRLSADVIS	LN. VSTSST
PYRB_MYCTU	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~MTPRHLLTA	ADLSRDDATA	ILDDADRFAQ	ALVGRDIKKL	PTLRGR	TVVTMFYENS	TRTRVSFEVA	GKWMSADVIN	VSAAGSSV
PYRB_SYNY3	~~~~MTMVA	SWTRNHILDL	TDWRGEELDI	VLOTATTFOO	VLSGO.TKKV	PALOGO	VVTNLFFEPS	TRTRSSFELA	AKRLSADVMN	FS. PGTSSL
PYRB_TREDE	~~~~~MEN	KFMGRSLTVI	DDLSIDERKY	LFDKTKRLKK	AIOEDDOKVM	DEFRINDKDF	GIYEVFLEPS	TRTKESFRNA	AKE HOVKL	SDLAAESSSE
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	83	03	102	110	110	100	100	140	150	100
DVDD FOOTT	VVORUT NOUT	CUT ONLY NON	102	112	110	122	132	142	152	100
PIRE_ECOLI	KKGETLADTI	SVISTY.VDA	IVMRHPQEGA	ARLATE	FSGN	VPVLNAGDGS	NOHLIQUETT	LFTTQETQGR	LDN	LHVAMVGDLK
PYRB_SALTY	KKGETLADTI	SVISTY.VDA	IVMRHPQEGA	ARLATE	FSGQ	VPVLNAGDGS	NQHPTQTLLD	LFTIQETQGR	LDN	LHIAMVGDLK
PYRB_SERMA	KKGETLADTI	SVISTY.VDA	IVMRHPQEG.	ARMASE	FSGN	VPVLNAGDG.	NQHPTQTLLD	LFTIQETQGR	LSN	LSIAMVGDLK
PYRB_PYRAB	KKGESLRDTI	KTVEQY.CDV	IVIRHPKEGA	ARLAAE	VA.E	VPVINAGDGS	NQHPTQTLLD	LYTIKKEFGR	IDG	LKIGLLGDLK
PYRB_SULSO	AKGENLADTI	RMLNNY.SDG	IVMRHKYDGA	SRFASE	IS.D	IPVINAGDGK	HEHPTOAVID	IYTINKHFNT	IDG	LVFALLGDLK
PYRB_ARATH	AKGETLEDTI	RTVEGY.SDI	IVMRHFESGA	ARKAAA	T	IPVINAGDGP	GEHPTOALLD	VYTIOSEIGK	LDG	ISVALVGDLA
PYRB_BACCL	QKGETLYDTV	RTLEAIGVDA	VVIRHHEDAY	FEALR	H AVG	IPIINAGDOC	GHHPTOSLUD	LUTTROFFG	AFT/2	LTVATIONIE
PYRB BACSU	OKGETT VDTT	RTLESTONDY	CVIRHSEDEV	YEELV	S OUNT	TPILNACICC	COHPROCLID			LUNGTOOTY
PYRB LACLE	NKGENI VITTE	LTMASICIE	SVIBHDENNV	VNETTODEC	~····v	MCLININCICC	CORDGOUNU D	MMUTVIN,		TALADIA
DVDB LACDI	TROPELIDIE	KULLEN LOUDE	AVADUDDDDV	V ODLID		MGLINNAGLGS	GONPOQUED	MATTINEFG.		LKIMIVGDLT
DVDD DCENE	CKOERT RDBT	RITERIGAND	AVVKHPKDKI	IQPLLD	AGFD	MSLINAGDGS	GQHPSQSLLD	MLTIYEEFG.	HFDG	LKIAIVGDLA
PIRD_PSEAE	SKGETLTDTL	RINLEAMAADM	FVVRHSDSGA	AHFIAEHV		VAVINGGDGR	HAHPTQGMLD	MLTIRRHKGN	FEQ	LSVAIVGDIL
PYRB_PSEPU	SKGETLFDTL	RNLEAMAADM	FVVRHSDSGA	AHFIAEHV	CPD	VAVINGGDGR	HAHPTQGMLD	MLTIRRHKGS	FEN	LSVAIVGDIL
PYRB_MYCTU	GKGESLRDTA	LTLRAAGADA	LIIRHPASGA	AHLLAQWIGA	HNDG	PAVINAGDGT	HEHPTQALLD	ALTIRQRLGG	IEG	RRIVIVGDIL
PYRB_SYNY3	TKGETILDTA	KTYLAMGSDI	FVIRHQQAGV	PHFIASQMDR	LQTG	VKVLNAGDGQ	HEHPSQGLLD	LFTICSQFAP	DNPAIQCLQG	KKIAVVGDIL
PYRB_TREDE	NKGESYADTF	NTLAGYQNSI	FIVRSEVEGV	CRWLEDEAQA	FYQRNNLKRK	PAFINAGDGK	HEHPTQELLD	EFTFIED	NNWSFDK	IHIALVGDLY
	•		•			$\nabla \nabla$	• V V			
	165	174	184	194	204	214	224	234	242	246
DVDB FOOT.T	165 VORTATI SLA	174 OALAKEIYANR	184 Evetaddala	194 MPOVILIDMED	204 EKGIAWSI HS	214 SIFE MARID	224	234 PL DESEVA	242	246 OFUL RASDI H
PYRB_ECOLI	165 YGRTVH.SLT	174 QALAKFDGNR	184 FYFIAPDALA	194 MPQYILDMLD	204 EKGIAWSLHS	214 SIEEVMAEVD	224 ILYMTRVQKE	234 RL. DPSEYA	242 NVKA	246 QFVLRASDLH
PYRB_ECOLI PYRB_SALTY	165 YGRTVH.SLT YGRTVHFAKP	174 QALAKFDGNR RTLAKFSGNR	184 FYFIAPDALA FYFIAPDALA	194 MPQYILDMLD MPQYILDMLD	204 EKGIAWSLHS EKGMAWSLHG	214 SIEEVMAEVD SIEEVMADVD	224 ILYMTRVQKE ILYMTRVQKE	234 RLDPSEYA RLDPSEYA	242 NVKA NVKA	246 QFVLRASDLH QFVLR.PDLN
PYRB_ECOLI PYRB_SALTY PYRB_SERMA	165 YGRTVH.SLT YGRTVHFAKP YGRTVH.SLT	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA	194 MPQYILDMLD MPQYILDMLD MPQYILKMLE	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD	224 ILYMTRVQKE ILYMTRVQKE ILYMTRVQKE	234 RLDPSEYA RLDPSEYA RLDPSEYA	242 NVKA NVKA	246 QFVLRASDLH QFVLR.PDLN QFVL.AADLA
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB	165 YGRTVH.SLT YGRTVHFAKP YGRTVH.SLT YGRTVH.SLA	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD	224 ILYMTRVQKE ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE	234 RLDPSEYA RLDPSEYA RLDPSEYA RFPDEQE.YL	242 NVKA NVKA NVKA ŔVKG	246 QFVLRASDLH QFVLR.PDLN QFVL.AADLA SYQVNLKVLE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SULSO	165 YGRTVH.SLT YGRTVHFAKP YGRTVH.SLT YGRTVH.SLA YARTVN.SLL	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR VYLISPQLLR	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL.	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT NYPVKEVE	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD	224 ILYMTRVQKE ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE	234 RLDPSEYA RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE	242 NVKA NVKA NVKA KVKG KIKG	246 QFVLRASDLH QFVLR.PDLN QFVL.AADLA SYQVNLKVLE SYIVSLDLAN
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SULSO PYRB_ARATH	165 YGRTVH.SLT YGRTVHFAKP YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK	184 FYFIAPDALA FYFIAPDALA YLISPELLR VYLISPQLLR IYFVSPEIVK	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT NYPVKEVE SSGVEWEESS	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD	224 ILYMTRVQKE ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE	234 RLDPSEYA RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE	242 NVKA NVKA NVKA KVKG KIKG AARG	246 QFVLRASDLH QFVLR.PDLN QFVL.AADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRB PYRB_SULSO PYRB_ARATH PYRB_BACCL	165 YGRTVH.SLT YGRTVHAKP YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N	184 FYFIAPDALA FYFIAPDALA .YLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWK	194 MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT DETNPYGT	204 EKGIAWSLHS EKGMAWSLHG EKGMKVVETT NYPVKEVE SSGVEWEESS YVE	214 SIEEVMAEVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD	224 ILYMTRVQKE ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE	234 RLDPSEYA RLDPSEYA RFDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK	242 NVKA NVKA KVKG KIKG AARG EEYHA	246 QFVLRASDLH QFVLR.PDLN QFVL.AADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SULSO PYRB_BACATH PYRB_BACCL PYRB_BACSU	165 YGRTVH.SLT YGRTVHASLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R	184 FYFIAPDALA FYFIAPDALA YLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWK VLFSGPEEWK	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL D. ETNPYGT D. ETNPYGT D. ETNPTGT	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT NYPVKEVE SSGVEWEESS YVE YVS	214 SIEEVMAEVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD	224 ILYMTRVQKE ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VVMLLRIONE	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHOSAVSO	242 NVKA NVKA KVKG KIKG AARG EEYHA EGYLN	246 QFVLRASDLH QFVL.ADLN QFVL.AADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SULSO PYRB_BACCL PYRB_BACCL PYRB_BACSU PYRB_LACLE	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA NSR.VARSNM	174 QALAKFDGNR RTLAKFSGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.R EVLTRLGA.R EILNTLGA.E	184 FYFIAPDALA FYFIAPDALA YLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWK VLFSGPEEWQ VYFSGPEYWY	194 MPQYILDMLD MPAYILMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT DETNPYGT DEENTFGT NAEEFSKYGT	204 EKGIAWSLHS EKGMAWSLHG EKGIEVSSHG EKGMKVVETT NYPVKEVE SSGVEWEESS YVE YVS	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VLMLLRQNE	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE	242 NVKA NVKA KVKG KIKG AARG EEYHA EGYLN OLFDAKDYNA	246 QFVLRASDLH QFVL.ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNORRYD
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_STRA PYRB_SULSO PYRB_ARATH PYRB_BACCL PYRB_BACCL PYRB_LACLE PYRB_LACLE	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLL YGRTVH.SLA NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E	184 FYFIAPDALA FYFIAPDALA YYIISPELLR VYLISPELLR VYLISPELVK VLFSGPEEWK VLFSGPEEWK VYFSGPEEWY VYFSGPEEWY	194 MPQYILDMLD MPAYILMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EENTFGT NAEEFSKYGT GEDFEAVGE	204 EKGIAWSLHS EKGMAWSLHG EKGMKVVETT .NYPVKEVE SSGVEWEESS YVE YVS YVK	214 SIEEVMAEVD SIEEVVPELD TLEDVIGKLD NFFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TWDOLVATMD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VLMLLRIQHE VLMLLRVQHE	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RFVDEME.YE RHAETMGLTK RHQSAVSQ RHNGAEAKTE E LSOVNN	242 NVKA NVKA KVKG KIKG AARG EEYHA EGYLN QLFDAKDYNA QUFDASAYHO	246 QFVLRASDLH QFVLR.PDLN QFVL.AADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNQRRYD OVGLTAERAA
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SULSO PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_LACLE PYRB_LACPL PYRB_CFAP	165 YGRTVH.SLT YGRTVHFAKP YGRTVH.SLT YGRTVH.SLA YARTVN.SLL MGRTVR.SLA HSR.VARSNA MSR.VARSNM HSR.VARSNM HSR.VARSNM	174 QALAKFDGNR RTLAKFSGNR QALAKFESNR EALTFYDVEL RILTRFRFKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q	184 FYFIAPDALA FYFIAPDALA YLISPELLR VYLISPQLLR VLFSGPEEWK VLFSGPEEWK VLFSGPSEWQ VYFSGPEYWY VYFGGPKEWY VYFGGPKEWY	194 MPQYILDMLD MPAYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EINPYGT D. EENTFGT NAEEFSKYGT .GRDFEAYGE UIGLEF	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT .NYPVKEVE SSGVEWEESS YVE YVS YVS YVK	214 SIEEVMAEVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VVYVTRIQKE VVYQTRIQRE VVMLLRIQHE VLMLLRIQHE VMMLLRVQHE VMMLLRVQHE	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHQSAVSQ RHNGAEAKTE RLSQVIN	242 NVKA NVKA KVKG KIKG AARG EEYHA EGYLN QLFDAKDYNA QTFDASAYHQ ULDSPETET	246 QFVLRASDLH QFVL.ADLN QFVL.ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNQRRYD QYGLTAERAA
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SULSO PYRB_BACCL PYRB_BACCL PYRB_BACSJ PYRB_LACLE PYRB_LACPL PYRB_PSEAE PYRB_DEEPU	165 YGRTVH.SLT YGRTVHFAKP YGRTVH.SLT YGRTVH.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q LALKTLGCPD	184 FYFIAPDALA FYFIAPDALA YLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWK VJFSGPEEWK VYFSGPEWY VYFGGPKEWY IRVIAPATLL IRVIAPATLL	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDVLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE DIGL E	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT NYPVKEVE SSGVEWEESS YVE YVS YVS YVG YVQ	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD ULMEVASKCD NDDEIPELD MDEAVESSD NIDDEIPELD TMDQLVATMD NADEGLKDVD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQNE VVMLLRIQNE VMMLLRVQHE VVMLLRVQHE VVMLLRQRE	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RHAETMGLTK RHQSAVSQ RHNGAEAKTE RLSQVNN RMQGGL	242 NVKA NVKA KVKG KIKG AARG EEYHA EGYLN QLFDAKDYNA QLFDASAYHQ .LPSEGEFFK	246 QFVLRASDLH QFVL. ADLN QFVL. ADLA SYQVNLKVLE SYTVSLDLAN KFTVDKDLLG RYGLTVERAE AYGLTVERAE AYGLNQRRYD QYGLTAERAA LYGLTEKRLK
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SULSO PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_LACLE PYRB_LACPL PYRB_PSEAE PYRB_PSEAE	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLA NGRTVR.SLA HSR.VARSNA NSR.VARSNA NSR.VARSNM HSR.VARSNM HSR.VARSNM	174 QALAKFDGNR RTLAKFSGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.R EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q LALKTLGCPD LALKALGCPD	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA VYLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWQ VYFSGPEEWQ VYFSGPEWQ VYFGGPKEWY IRVIAPATLL IRVIGPKTLI	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. ETNPYGT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PIGLEE	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT NYPVKEVE SSGVEWEESS YVE YVS YVS YVK .QYGVRVFT QYGVKVYT	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD LMEVASKCD .VDEAIARAD MDEAVESSD NIDDEIPELD TMDQLVATMD NADEGLKDVD DLAEGLKDVD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VLMLLRVQHE VVMLLRVQHE VVIMLRLQRE VVIMLRLQRE	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL RMQGGL	242 NVKA NVKA KVKG AARG EGYLN QLFDAKDYNA QLFDAKDYNA QLFDAKDYNA DLPSEGEFFK LPSEGEFFK	246 QFVLRASDLH QFVLR.PDLN QFVL.ADDLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR AYGLTVERAE AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_LACLE PYRB_LACLE PYRB_PSEAE PYRB_PSEAE PYRB_PSEPU PYRB_MYCTU	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q LALKTQCPD LALKALGCPD MLLDTLGA.E	184 FYFIAPDALA FYFIAPDALA .YLISPELLR VYLISPELLR VLFSGPEWK VLFSGPEWK VVFSGPEYWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL	194 MPQYILDMLD MPAYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EINPYGT D. EENTFGT NAEEFSKYGT IGDFEAYGE PIGLEE PVGVT	204 EKGIAWSLHS EKGIEYSSHG EKGIEYSSHG EKGMKVVETT .NYPVKEVE SSGVEWEESS YVE YVS YVS YVS QYGVRVFT .QYGVRVFT .GWPATVSH	214 SIEEVMAEVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD NADEGLKDVD DFDAELPAAD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VVYQTRIQKE VVYQTRIQRE VVMLLRIQHE VMMLLRIQHE VMMLRVQHE VVIMLRQRE VVIMLRLQRE AVLMLRVQAE	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHQSAVSQ RHNGAEAKTE RLSQVNN RMQGGL RMAGGL	242 NVKA NVKA KVKG KIKG AARG EEYHA EGYLN QLFDAKDYNA QTFDASAYHQ .LPSEGEFFK .LPSEGEFFK .FPSVREYSV	246 QFVLRASDLH QFVL.ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA RYGLTERRAA
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_VRAB PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_LACLE PYRB_LACLE PYRB_PSEAE PYRB_PSEAE PYRB_PSEPU PYRB_SYNY3	165 YGRTVH. SLT YGRTVHFAKP YGRTVH. SLT YGRTVH. SLA YARTVN. SLL NGRTVR. SLA HSR. VARSNA HSR. VARSNA HSR. VARSNM HSR. VARSNM HSR. VARSNM HSR. VARSNM	174 QALAKFDGNR RTLAKFSGNR QALAKFESNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q LALKTLGCPD MLLDTLGA.E WSLTTAGA.D	184 FYFIAPDALA FYFIAPDALA YLISPELLR VXLISPQLLR VXLISPQLLR VLFSGPEEWK VLFSGPEEWK VYFSGPEWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VHLAGPPTLL	194 MPQYILDMLD MPAYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PIGLEE PKEFQQLTLA	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT .NYPVKEVE SSGVEWEESS YVE YVS YVS YVS QYGVRVFT .QYGVRVFT .GWPATVSH PGSGKLHCHW	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD NADEGLKDVD DLAEGLKDVD DFDAELPAAD QLQPALEGAD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VVYVTRIQKE VVMLLRIQKE VVMLLRIQNE VVMLLRQNE VVMLLRVQHE VVMLLRQRE AVLMLRVQAE IVMTLRLQKE	234 RLDPSEYA RL.DPSEYA RFPDEQE.YL RFVDEME.YE RHGERLDLYE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL RMNGGF RMNGGF	242 NVKA NVKA KVKG KIKG AARG EGYLN QLFDAKDYNA QTFDASAYHQ .LPSEGEFYR .LPSEGEFYR .FPSVREYSV .LPSLREYHH	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTVERAE AYGLTVERAE AYGLTVERAE LYGLTEKRLA LFGLTTARLA RYGLTERRQA YFGITHDRLK
PYRB_ECOLI PYRB_SALTY PYRB_SEMA PYRB_VRAB PYRB_SULSO PYRB_BACCL PYRB_BACCL PYRB_BACCL PYRB_LACLE PYRB_LACLE PYRB_PSEAE PYRB_PSEAE PYRB_PSEPU PYRB_MYCTU PYRB_SYNY3 PYRB_TREDE	165 YGRTVH.SLT YGRTVHFAKP YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNV HSR.VARSNL HGRTVH.SKA	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.C ALLTQLGA.Q LALKTLACPD MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK	184 FYFIAPDALA FYFIAPDALA YLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWK VLFSGPSEWQ VYFSGPEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VHLAGPPTLL VDLIAPAELA	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDVLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PIGI.E PVGVT PKEFQQLTLA MPEYYKVRMQ	204 EKGIAWSLHS EKGMAWSLHG EKGIKVVETT NYPVKEVE SSGVEWEESS YVE YVS YVS QYGVRVFT QYGVKVYT GWPATVSH PGSGKLHCHW ENGFTVREFS	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD ULVDEAIARAD MDEAVESSD NIDDEIPELD TMDQLVATMD NADEGLKDVD DFAEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VVMLLRIQNE VVMLLRVQHE VVIMLRQRE AVLMLRVQAE IVMTLRLQRE VXIMLRQAE VXLRVQAE	234 RLDPSEYA RL.DPSEYA RFPDEQE.YL RFVDEME.YE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL RMNGGF RMNGGF RMTAHL QL.ERMGEQ	242 NVKA NVKA KVKG KIKG EEYHA EGYLN QLFDAKDYNA QTFDASAYHQ .LPSEGEFFK .LPSEGEFFYR .FPSVREYSV .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTVERAE AYGLTVERAE AYGLTVERAE LYGLTVERAE LYGLTERRQA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SULSO PYRB_BACCL PYRB_BACCL PYRB_BACCL PYRB_LACLE PYRB_LACLE PYRB_PSEAE PYRB_PSEAE PYRB_PSEPU PYRB_MYCTU PYRB_SYNY3 PYRB_TREDE	165 YGRTVH.SLT YGRTVHFAKP YGRTVH.SLT YGRTVH.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNV HSR.VARSNV HSR.VARSNL HGRTVH.SKA	174 QALAKFSGNR RTLAKFSGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA. R EVLTRLGA. R EILNTLGA. C LALKTLGCPD LALKALGCPD LALKALGCPD LALKALGCPD DGLKIFKSVK	184 FYFIAPDALA FYFIAPDALA YLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWK VJFSGPEEWK VYFSGPEWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLL VVLVAPPTLL VHLAGPPTLL VDLIAPAELA	194 MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDVLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PIGI.E PVGVT PKEFQQLTLA MPEYYKVRMQ	204 EKGIAWSLHS EKGMAWSLHG EKGIKVVETT NYPVKEVE SSGVEWEESS YVE YVS YVS .QYGVRVFT QYGVKVFT GWPATVSH FGSGKLHCHW ENGFTVREFS	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD ULVEAIARAD NDDEIPELD TMDQLVATMD NADEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VVMLLRIQNE VVMLLRVQHE VVIMLLRQRE VVIMLRQRE VVIMLRQRE IVMTLRQRE VVIMLRQAE IVMTLRQKE VALIWYFTRP	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL RMAGGL RMAGGF RMTAHL QLERMGEQ	242 NVKA NVKA KVKG KIKG AARG EGYLN QLFDAKDYNA QLFDAKDYNA QTFDASAYHQ LPSEGEFFK LPSEGEFFK .LPSEGEFFYR .FPSVREYSV .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SULSO PYRB_BACCL PYRB_BACCL PYRB_BACCL PYRB_LACLE PYRB_LACLE PYRB_PSEAE PYRB_PSEAE PYRB_SYNY3 PYRB_TREDE	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNL HSR.VARSNL HSR.VARSNL HSR.VARSNL	174 QALAKFDGNR RTLAKFSGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q LALKTLGCPD LALKALGCPD MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA VLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWK VYFSGPEWV VYFGGPKEWY IRVIAPATLL IRVIAPATLL IRVIGPKTLL VVLVAPPTLL VDLIAPAELA	194 MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. ETNPYGT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PVGVT PKEFQQLTLA MPEYYKVRMQ	204 EKGIAWSLHS EKGMAWSLHG EKGIKVVETT NYPVKEVE SSGVEWEESS YVE YVS YVS YVG QYGVRVFT QYGVKVYT GWPATVSH PGSGKLHCHW ENGFTVREFS	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD NADEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VVMLLRVQHE VVMLLRVQHE VVIMLRQRE AVLMLRVQAE IVMTLRLQRE VVIMLRQRE VVIMLRQRE VVIMLRQRE VVIMLRQRE VVIMLRQRE VVIMLRQRE VVIMLRQRE	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFPDEQE.YL RFGERLDLYE RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL RMAGGL RMAGGL RMMGGF QLERMGEQ	242 NVKA NVKA KVKG KIKG AARG EEYHA EGYLN QLFDAKDYNA QLFDAKDYNA QTFDASAYHQ .LPSEGEFYK .LPSEGEFYK .FPSVREYSV LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL.ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA RYGLTERRQA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_LACLE PYRB_LACLE PYRB_PSEAE PYRB_PSEAE PYRB_PSEPU PYRB_MYCTU PYRB_SYNY3 PYRB_TREDE	165 YGRTVH. SLT YGRTVH. SLT YGRTVH. SLA YARTVN. SLL NGRTVR. SLA HSR. VARSNA HSR. VARSNA HSR. VARSNM HSR. VARSNM HSR. VARSNM HSR. VARSNM HSR. VARSNM HSR. VARSNM HSR. VARSNM HSR. VARSNM HSR. VARSNM SR. VARSNM HSR. VARSNM HSR. VARSNM HSR. VARSNM SR. VARSNM HSR. VARSNM HSR. VARSNM SR. VARSNM	174 QALAKFDGNR RTLAKFSGNR QALAKFEONR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q LALKTLGCPD LALKTLGCPD LALKTLGCPD MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK 266	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR VYLISPQLLR VLFSGPEEWK VLFSGPEEWK VLFSGPEEWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VHLAGPPTLL VDLIAPAELA 274	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EINPYGT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PVGVT PKEFQQLTLA MPEYYKVRMQ 283	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT .NYPVKEVE SSGVEWEESS YVE YVS YVK .QYGVRVFT .QYGVRVFT .QYGVKVT GWPATVSH FGSGKLHCHW ENGFTVREFS	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD NADEGLKDVD DLAEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VVYQTRIQKE VVYQTRIQRE VVMLLRIQHE VMMLLRIQHE VMMLLRVQHE VVMLLRIQRE VVIMLRLQRE AVLMLRVQAE IVMTLRLQRE VALIWYFTRP	234 RLDPSEYA RLDPSEYA RFFDEQE.YL RFFDEQE.YL RFGERLDLYE RHAETMGLTK RHQSAVSQ RHNGAEAKTE RLSQVNN RMQGGL RMAGGL RMAGGL RMAGGF QLERMGEQ	242 NVKA NVKA KVKG KIKG AARG EGYLN QLFDAKDYNA QTFDASAYHQ LLPSEGEFYK .LPSEGEFYK .LPSEGEFYK LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVLR.PDLN QFVL.AADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA RYGLTERRQA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_LACLE PYRB_LACLE PYRB_PSEAE PYRB_PSEFU PYRB_PSEFU PYRB_SYNY3 PYRB_TREDE PYRB_ECOLI	165 YGRTVH.SLT YGRTVHFAKP YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNL HGRTVH.SKA • 256 NAKANMKVLH	174 QALAKFDGNR RTLAKFSGNR QALAKFESNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q LALKTLGCPD MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK 266 PLPRVDEI	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR VYLISPQLLR VYLSGPEEWK VLFSGPEEWK VLFSGPSEWQ VYFSGPEYWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VVLVAPPTLL VVLVAPPTLL VVLAPPTLL VVLAPPTLL VVLAPAELA 274 ATD.VDKTPH	194 MPQYILDMLD MPAYILMLE MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PIGI.E PIGI.E PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT NYPVKEVE SSGVEWEESS YVE YVS YVK YVQ QYGVRVFT QYGVRVFT QYGVKVTT GWPATVSH PGSGKLHCHW ENGFTVREFS 293 IFARQALLAL	214 SIEEVMAEVD SIEEVVAEVD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD DLAEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQNE VVMLLRIQNE VVMLLRVQHE VVMLLRVQHE VVIMLRQRE AVLMLRVQAE IVMTLRLQKE VALIWYFTRP ••	234 RLDPSEYA RL.DPSEYA RFPDEQE.YL RFVDEME.YE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL RMNGGF RMNGGF QLERMGEQ	242 NVKA NVKA KVKG EEYHA EGYLN QLFDAKDYNA QTFDASAYHQ .LPSEGEFFK .LPSEGEFYR .FPSVREYSV .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTVERAE AYGLTVERAE AYGLTVERAE LYGLTEKRLK LFGLTJARLA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SEMA PYRB_SULSO PYRB_ARATH PYRB_BACCL PYRB_BACCL PYRB_LACLE PYRB_LACLE PYRB_PSEAE PYRB_PSEAU PYRB_MYCTU PYRB_SYNY3 PYRB_TREDE PYRB_ECOLI PYRB_ECOLI PYRB_SALTY	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA. R EVLTRLGA. R EVLTRLGA. Q LALKTLACPD LALKALGCPD LALKALGCPD MLLDTLGA. E WSLTTAGA. D DGLKIFKSVK 266 PLP RVDEI PLP RIDEI	184 FYFIAPDALA FYFIAPDALA YLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWK VJFSGPEEWK VYFSGPEWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLL VVLVAPPTLL VVLVAPPTLL VDLIAPAELA 274 ATD.VDKTPH TTD.VDKTPH	194 MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDVLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PIGI.E PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AWYFQQAGNG	204 EKGIAWSLHS EKGMAWSLHG EKGIKVVETT NYPVKEVE SSGVEWEESS YVE YVS .QYGVRVFT QYGVKVFT GYPATVSH FGSGKLHCHW ENGFTVREFS 293 IFPARQALLAL IFPAQALLAL	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .VDEAIARAD .NDDEIPELD TMDQLVATMD NADEGLKDVD DLAEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL~~ VLNSELSL~~	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VVMLLRIQNE VVMLLRVQHE VVIMLLRQRE VVIMLRQRE IVMTLRLQRE VVIMLRQAE IVMTLRLQKE VALIWYFTRP	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL RMNGGF RMNGGF QLERMGEQ	242 NVKA NVKA KVKG KIKG AARG EGYLN QLFDAKDYNA QLFDAKDYNA QTFDASAYHQ LPSEGEFFK LPSEGEFFK .LPSEGEFFYR .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SALTY PYRB_SALTY PYRB_SALSO PYRB_ARATH PYRB_BACCL PYRB_BACCL PYRB_BACSU PYRB_BACSU PYRB_PSEA PYRB_PSEA PYRB_PSEA PYRB_TREDE PYRB_ECOLI PYRB_SALTY PYRB_SERMA	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNW HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV GRENMKVLH GARENMKVLH GA.ANLKVLH	174 QALAKFDGNR RTLAKFSGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.R EVLTRLGA.R EILNTIGA.E ALLTQLGA.Q LALKTLGCPD LALKALGCPD MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK 266 PLP.RVDEI PLP.RIDEI PLP.RIDEI	184 FYFIAPDALA FYFIAPDALA YLISPELLR VYLISPELLR VLFSGPEEWK VLFSGPEEWK VLFSGPEEWK VLFSGPEEWQ VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VDLIAPAELA 274 ATD.VDKTPH ATD.VDKTPH	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EINTPGT D. EENTFGT NAEEFSKYGT PIGLEE PIGI.E PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AWYFQQAGNG AYYFQQAGNG	204 EKGIAWSLHS EKGMAWSLHG EKGIEVSSHG EKGMKVVETT NYPVKEVE SSGVEWEESS YVE YVS YVK YVK QYGVRVFT QYGVRVFT GWPATVSH PGSGKLHCHW ENGFTVREFS 293 IFARQALLAL IFAAQALLAL IFARSA.LAL	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD NADEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL VUNADLAL	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VMMLLRIQHE VVMLLRUQHE VVIMLRLQRE AVLMLRVQAE IVMTLRLQRE AVLMLRVQAE IVMTLRLQRE VALIWYFTRP ••	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHQSAVSQ RHNGAEAKTE RLSQVNN RMQGGL RMAGGL RMNGGF RMNGGF QLERMGEQ	242 NVKA NVKA KVKG KIKG AARG EEYHA EGYLN QLFDAKDYNA QLFDAKDYNA QTFDASAYHQ .LPSEGEFFK .LPSEGEFFK .LPSEGEFYK .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL.ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA RYGLTERRQA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_ARATH PYRB_BACCL PYRB_BACCL PYRB_BACSU PYRB_ACCL PYRB_PSEAE PYRB_PSEAE PYRB_PSEAE PYRB_SINV3 PYRB_TREDE PYRB_ECOLI PYRB_SERMA PYRB_SERMA PYRB_PYRAB	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL MGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNW HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV GARENMKVLH GA.ANLKVLH KAKDELRIMH	174 QALAKFDGNR RTLAKFSGNR QALAKFESNR EALTFYDVEL RILTRFRFKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK 266 PLPRVDEI PLPRUDEI PLP.RUDEI PLP.RVDEI	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR VYLISPELK VLFSGPEEWK VLFSGPEEWK VLFSGPSEWQ VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VLLAGPPTLL VDLIAPAELA 274 ATD.VDKTPH ATD.VDKTPH ATD.VDKTPH	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EINTPGT NAEEFSKYGT .GRDFEAYGE PIGLEE PVGVT PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AWYFQQAGNG AIYFROVENG	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGIEYSSHG EKGMKVVETT .NYPVKEVE SSGVEWEESS YVE YVS YVK QYGVRVFT .QYGVRVFT .QYGVRVFT .GWPATVSH PGSGKLHCHW ENGFTVREFS 293 IFARQALLAL IFARSA.LAL VFVRMALLAL	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD DADEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL~~ VVNADLAL~~ VVNADLAL~~	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VVMLLRIQHE VVMLLRUQHE VVMLLRUQHE VVMLLRUQHE VVMLRLQRE AVLMLRUQAE IVMTLRLQRE VVIMLRUQAE IVMTLRLQKE VALIWYFTRP	234 RLDPSEYA RL.DPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHQSAVSQ RHNGAEAKTE RLSQVIN RMQGGL RMAGGL RMAGGL RMAGGF QLERMGEQ	242 NVKA NVKA KVKG EEYHA EGYLN QLFDAKDYNA QTFDASAYHQ LPSEGEFFK .FPSVREYSV .LPSEGEFYR VLKKQDELRR	246 QFVLRASDLH QFVL.ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA RYGLTERRQA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_LACLE PYRB_DSEAE PYRB_PSEAE PYRB_PSEPU PYRB_SYNY3 PYRB_TREDE PYRB_ECOLI PYRB_SALTY PYRB_SEMMA PYRB_SULSO	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNU	174 QALAKFDGNR RTLAKFSGNR QALAKFESNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q LALKTLGCPD MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK 266 PLPRVDEI PLPRUDEI PLPRVDEI PLPRVDEI PLPRVDEI	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR VXLISPQLLR IYFVSPEIVK VLFSGPEEWK VLFSGPSEWQ VYFSGPEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VVLVAPPTLL VDLIAPAELA 274 ATD.VDKTPH ATD.VDKTPH HPE.VDNTKH DRK.VDKTTK	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDVLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGIEE PIGI.E PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AWYFQQAGNG AIYFRQVFNG AKYFEOASYG	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGIEYSSHG EKGMKVVETT NYPVKEVE SSGVEWEESS YVE YVS YVK YVS QYGVRVFT QYGVRVFT QYGVKVT GWPATVSH PGSGKLHCHW ENGFTVREFS 293 IFARQALLAL IFARQALLAL IFARSA.LAL VPVRMSILTK	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKD NIDDEIPELD TMDQLVATMD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL~~ VLNSELSL~~ VVNADLAL~~ VLGVI~~~~~	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQKE VVMLLRIQHE VVMLLRIQNE VVMLLRQNE VVMLLRVQHE VVIMLRVQRE AVLMLRVQAE IVMTLRLQKE VALIWYFTRP ••	234 RLDPSEYA RL.DPSEYA RFPDEQE.YL RFVDEME.YE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL RMNGGF QL.ERMGEQ	242 NVKA NVKA KVKG EEYHA EGYLN QLFDAKDYNA QTFDASAYHQ .LPSEGEFFK .LPSEGEFFK .FPSVREYSV .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA RYGLTERRQA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SALTY PYRB_SERMA PYRB_SULSO PYRB_ARATH PYRB_BACCL PYRB_BACCL PYRB_BACSU PYRB_LACPL PYRB_PSEAE PYRB_PSEAE PYRB_PSEAE PYRB_SUNY3 PYRB_TREDE PYRB_ECOLI PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_SERMA PYRB_SULSO PYRB_ARATH	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNL HGRTVH.SKA	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA. R EVLTRLGA. R EVLTRLGA. Q LALKTLACPD MLLDTLGA. E WSLTTAGA. D DGLKIFKSVK 266 PLP RVDEI PLP RIDEI PLP RIDEI PLP RIDEI PLP RIDEI PLP RIDEI PLP RIDEI	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWK VLFSGPSEWQ VYFSGPEWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLL VVLVAPPTLL VVLVAPPTLL VVLVAPPTLL VDLIAPAELA 274 ATD.VDKTPH TTD.VDKTPH HPE.VDNTKH DRK.VDKTTH TAD.VDADPR	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDVLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGIEE PIGI.E PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AWYFQQAGNG AYYFQQAGNG ALYFRQVFNG AKYFQASNG AAYFROAKNG	204 EKGIAWSLHS EKGMAWSLHG EKGIKVVETT NYPVKEVE SSGVEWEESS YVE YVS .QYGVRVFT QYGVRVFT GYPATVSH FGSGKLHCHW ENGFTVREFS 293 IFARQALLAL IFARSA.LAL VPVRMSILTK VPVRMSILTKI	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD NDDEI PELD TMDQLVATMD NADEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL~~ VLNSELSL~~ VLNSELSL~~ VLNADLAL~~ LLVGW~~~~~	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVMLLRIQHE VVMLLRIQHE VVMLLRQHE VVMLLRQPE VVIMLRQRE AVLMLRQRE AVLMLRQAE IVMTLRLQRE VXIMLRQAE	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL RMNGGF QL.ERMGEQ	242 NVKA NVKA KVKG KIKG AARG EGYLN QLFDAKDYNA QLFDAKDYNA QLFDASAYHQ LPSEGEFFK LPSEGEFFK .LPSEGEFFYR .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SALTY PYRB_SERMA PYRB_VRB_BACSU PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_BACSU PYRB_PSEAE PYRB_PSEAE PYRB_PSEAE PYRB_SALTY PYRB_SERMA PYRB_SERMA PYRB_SELSO PYRB_ARATH PYRB_ARATH	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM KARSNM HSR.VARSNM	174 QALAKFDGNR RTLAKFSGNR QALAKFEGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.R EILINTLGA.E ALLTQLGA.Q LALKTLGCPD LALKTLGCPD LALKALGCPD MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK 266 PLP.RVDEI PLP.RIDEI PLP.RIDEI PLP.RIDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR VYLISPELLR VLFSGPEEWK VLFSGPEEWK VLFSGPEEWY VYFGGPKEWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VLLAGPPTLL VDLIAPAELA 274 ATD.VDKTPH TTD.VDKTPH ATD.VDKTPH ATD.VDKTPH DRK.VDKTTK TAD.VDADPR	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EINTPGT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PVGVT PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AWYFQQAGNG AIYFRQAFNG AKYFEQASYG AAYFRQAFNG SH EKOMENG	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGIEYSSHG EKGIKVVETT .NYPVKEVE SSGVEWEESS YVE YVS YVK QYGVKVTT .QYGVKVTT .QYGVKVTT .GWPATVSH FGSGKLHCHW ENGFTVREFS 293 IFARQALLAL IFARQALLAL IFARSA.LAL VPVRMALLAL VPVRMALLAL VPVRMSILTK LFIRMALLKL LFIRMALLKL	214 SIEEVMAEVD SIEEVMAEVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD ULMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD NADEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL VLNSELSL VVNADLAL VLNGVI IYGE	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVYQTRIQRE VVMLLRIQHE VMMLLRVQHE VVMLLRIQNE VVMLLRQRE VVIMLRQRE AVLMLRVQAE IVMTLRLQRE VVIMLRQRE VVIMLRQRE VVIMLRQRE	234 RLDPSEYA RL.DPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHQSAVSQ RHNGAEAKTE RLSQVNN RMQGGL RMAGGL RMAGGL QL.ERMGEQ	242 NVKA NVKA KVKG KIKG AARG EGYLN QLFDAKDYNA QTFDASAYHQ LLPSEGEFFK .LPSEGEFFX .LPSEGEFFX LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVLR.PDLN QFVL.AADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR KYGLTVERAE AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA RYGLTERRQA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SILISO PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_LACLE PYRB_PSEAE PYRB_PSEAE PYRB_PSEAE PYRB_SILSO PYRB_SULSO PYRB_SULSO PYRB_BACCTU	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNL GARENMKVLH GARENMKVLH GARENMKVLH GARENMKVLH GARENMKVLH HANLKVLH KMKKDSILLH VMQKKAILMH RMKKGAILLH	174 QALAKFDGNR RTLAKFSGNR QALAKFESNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q LALKTLGCPD MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK 266 PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR VYLISPELLR VLFSGPEEWK VLFSGPEEWK VLFSGPSEWQ VYFGGPKEWY VLFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VLLAGPPTLL VLLAGPPTLL VDLIAPAELA 274 ATD.VDKTPH ATD.VDKTPH ATD.VDKTPH HPE.VDNTKH DRK.VDKTTK TAD.VDADPR ASELVEAKA.	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDVLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PIGI.E PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AYYFQQAGNG AYYFQQAGNG AYYFQQAGNG AYYFQQASNG SRIFKQMENG SRIFKQMENG	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT NYPVKEVE SSGVEWEESS YVE YVS YVK YVS QYGVRVFT QYGVRVFT QYGVRVFT GWPATVSH PGSGKLHCHW ENGFTVREFS 293 IFARQALLAL IFARSA.LAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VPVRMALLAL	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL VVNADLAL VLGVI IYGE LLVGW AMEGRMEHGR	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQNE VVMLLRIQNE VVMLLRVQHE VVMLLRVQHE VVMLLRVQHE VVIMLRQRE AVLMLRVQAE IVMTLRLQKE VALIWYFTRP ••	234 RLDPSEYA RL.DPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL RMNGGF QL.ERMGEQ	242 NVKA NVKA KVKG EEYHA EGYLN QLFDAKDYNA QTFDASAYHQ LPSEGEFYR .FPSVREYSV .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTVERAE AYGLTVERAE AYGLTVERAE LYGLTEKRLK LFGLTTARLA RYGLTERRQA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_SULSO PYRB_ARATH PYRB_BACCL PYRB_BACCL PYRB_LACLE PYRB_PSEPU PYRB_PSEPU PYRB_PSEPU PYRB_SULSO PYRB_SULSO PYRB_SULSO PYRB_BACCL PYRB_BACSU	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNL HSR.VARSNL HSR.VARSNL HSR.VARSNV H	174 QALAKFDGNR RTLAKFSGNR QALAKFESNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA. R EVLTRLGA. R EVLTRLGA. Q LALKTLGCPD MLLDTLGA. C WSLTTAGA. D DGLKIFKSVK 266 PLP RVDEI PLP RIDEI PLP RUDEI PLP RUDEI PLP RUDEI PLP RUDEI PLP RUDEI PLP RUDEI PLP RUDEI PAPVNRGVEI PAPVNRGVEI	184 FYFIAPDALA FYFIAPDALA YLISPELLR VYLISPQLLR IYFVSPEIVK VLFSGPEEWK VLFSGPEEWK VLFSGPSEWQ VYFSGPEYWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VVLVAPPTLL VDLIAPAELA 274 ATD.VDKTPH ATD.VDKTPH HPE.VDNTKH HPE.VDNTKH HPE.VDNTKH DCK.VDADPR ASELVEAKA. DDSLVESEK.	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDVLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGIEE PIGI.E PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AYYFQQAGNG AYYFQQAGNG AIYFFQASNG SRIFKQMENG SRIFKQMENG SRIFKQMENG	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGIEYSSHG EKGIEYSSHG SGVEWEESS YVE YVS YVS QYGVKVTT QYGVKVTT QYGVKVT GWPATVSH PGSGKLHCHW ENGFTVREFS 293 IFARQALLAL IFARSA.LAL IFARSA.LAL VPVRMSILTK LFIRMALLKL VYVRMAVLKR VFIRMAVLKR	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD NIDDEIPELD TMDQLVATMD NADEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL VINSELSL VVNADLAL VLSGV IYGE LLVGW AMEGRMEHGR ALQTNVKRGE	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VVMLLRIQNE VVMLLRQNE VVMLLRQNE VVIMLRQRE AVLMLRVQAE IVMTLRLQRE AVLMLRVQAE IVMTLRLQRE AVLMLRVQAE IVMTLRLQKE VALIWYFTRP	234 RLDPSEYA RL.DPSEYA RFPDEQE.YL RFVDEME.YE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGGL QL.ERMGEQ	242 NVKA NVKA KVKG EEYHA EGYLN QLFDAKDYNA QTFDASAYHQ .LPSEGEFFK .LPSEGEFFK .LPSEGEFYR .FPSVREYSV .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTVERAE AYGLTVERAE AYGLTVERAE LYGLTERRLA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SALTY PYRB_SALTY PYRB_SALTY PYRB_SALSO PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_BACSU PYRB_PSEAE PYRB_PSEAE PYRB_PSEAE PYRB_SALTY PYRB_SALTY PYRB_SEMA PYRB_SEMA PYRB_SALTY PYRB_SEMA PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_LACLE	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNW H	174 QALAKFDGNR RTLAKFSGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.R EILINTIGA.E ALLTQLGA.Q LALKTLGCPD LALKALGCPD MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK 266 PLP.RVDEI PLP.RIDEI PLP.RIDEI PLP.RUDEI PLP.RUDEI PLP.RVDEI PLP.RUDEI PLP.RUDEI PAPVNRGVEI PAPVNRGVEI	184 FYFIAPDALA FYFIAPDALA YYLISPELLR VYLISPELLR VLFSGPEEWK VLFSGPEEWK VLFSGPEEWK VLFSGPEEWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VDLIAPATLL VDLIAPAELA 274 ATD.VDKTPH TTD.VDKTPH HPE.VDNTKH DRK.VDKTTH HPE.VDNTKH DRK.VDKTTK TAD.VDATPR ASELVEAKA. DDSLVESEK. DGDLVEAPK.	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EINTFGT NAEEFSKYGT PIGLEE PIGLEE PIGLEE PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AYYFQQAGNG AYYFQQAGNG AYYFQQAGNG AYYFQQAGNG SRIFKQMENG SRIFKQMENG SRIFKQMENG SRIFKQMENG SRIFKQMENG SRIFKQMENG	204 EKGIAWSLHS EKGMAWSLHG EKGIKVVETT NYPVKEVE SSGVEWEESS YVE YVS .QYGVRVFT QYGVRVFT QYGVKVYT GWPATVSH FGSGKLHCHW ENGFTVREFS 293 IFARQALLAL IFARQALLAL IFARSA.LAL VPVRMALLAL LFIRMALLAL LFIRMALLAL VPVRMAULKR VFIRMAVLQC VFVRMAVLQC	214 SIEEVMAEVD SIEEVMAEVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEALARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD NADEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL VLNSELSL VVNADLAL VLGVI LLVGW LLVGW LLVGW	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVYQLRIQRE VVMLLRIQHE VVMLLRIQHE VVMLLRQHE VVMLRLQRE AVLMLRVQAE IVMTLRLQRE AVLMLRVQAE IVMTLRLQRE OVIMLRUQRE VVIMLRUQRE VVIMLRUQRE VVIMLRUQRE VVIMLRUQRE AVLMLRVQAE IVMTLRUQRE VVIMLRUQRE AVLMINTRUQAE IVMTLRUQRE OVIMUNTRUQAE	234 RLDPSEYA RLDPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHQSAVSQ RHNGAEAKTE RLSQVNN RMQGGL RMXGGF QLERMGEQ	242 NVKA NVKA KVKG KIKG AARG EGYLN QLFDAKDYNA QTFDASAYHQ .LPSEGEFFK .LPSEGEFFK .FPSVREYSV .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTLERAR AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA RYGLTEKRQA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SALTY PYRB_SALTY PYRB_SALTY PYRB_ARATH PYRB_BACCL PYRB_BACCL PYRB_BACSU PYRB_ACLE PYRB_PSEAE PYRB_PSEAE PYRB_SERMA PYRB_SERMA PYRB_SERMA PYRB_SERMA PYRB_SERMA PYRB_SERMA PYRB_SERMA PYRB_SERMA PYRB_SERMA PYRB_SERMA PYRB_SERMA PYRB_COLI PYRB_BACCL PYRB_LACLE PYRB_LACLE	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL MGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNN HSR.VARSNV HSR.VAR	174 QALAKFDGNR RTLAKFSGNR QALAKFSGNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK 266 PLPRUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PLP.RUDEI PAPVNRGVEI PAPVNRGVEI	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR VYLISPELVK VLFSGPEEWK VLFSGPSEWQ VYFSGPEWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VLLAGPPTLL VDLIAPAELA 274 ATD.VDKTPH ATD.VDADPR ASD.VEAPK ASDLVEAPK.ASDLVEAPC	194 MPQYILDMLD MPAYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDYLT D. EINPYGT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGLEE PVGVT PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AYYFQQAGNG AYYFQQAGNG AYYFQQAGNG AYYFQQAGNG SRIFKQMENG SRIFKQMENG SRIFKQMENG SRIFKQMENG SRIFQMING	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGIEYSSHG EKGIEYSSHG EKGIKVVETT .NYPVKEVE SSGVEWEESS YVE YVK .QYGVRVFT .QYGVRVFT .QYGVRVFT .QYGVRVFT .GWPATVSH PGSGKLHCHW ENGFTVREFS 293 IFARQALLAL IFARSA.LAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VFIRMAVIQC VFIRMAVIQC VFIRMAVIAC	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD DLMEVASKCD .VDEAIARAD .MDEAVESSD NIDDEIPELD TMDQLVATMD DADEGLKDVD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL VUNSELSL VVNADLAL VINSELSL VIGVI IYGE AMEGRMEHGG ALQTNVKRGE VLRGRKLGGL VLAHQGLISA	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVYQTRIQRE VVMLLRIQHE VVMLLRIQHE VVMLLRIQHE VVMLLRQRE VVMLRLQRE VVIMLRQRE AVLMLRVQAE IVMTLRLQRE VVIMLRQRE AVLMLRVQAE IVMTLRLQKE VALIWYFTRP ••• MAEKWHVVQ- AAYVISH	234 RLDPSEYA RL.DPSEYA RFPDEQE.YL RFVDEME.YE RFGERLDLYE RHAETMGLTK RHQSAVSQ RHNGAEAKTE RLSQVIN RMQGGL RMAGGL QLERMGEQ	242 NVKA NVKA KVKG EEYHA EGYLN QLFDAKDYNA QTFDASAYHQ LIPSEGEFFK .IPSEGEFFK .LPSEGEFFK LIPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVLR.PDLN QFVL.ADLA SYQVNLKVLE SYIVSLDLAN KYIVDKDLLG RYGLTLERAR AYGLNQRRYD QYGLTAERAA LYGLTEKRLK LFGLTTARLA RYGLTERRQA YFGITHDRLK SITFRKEFIE
PYRB_ECOLI PYRB_SALTY PYRB_SERMA PYRB_PYRAB PYRB_ARATH PYRB_BACCL PYRB_BACSU PYRB_LACLE PYRB_DSEAE PYRB_PSEAE PYRB_PSEAE PYRB_SINY3 PYRB_SINY3 PYRB_SINY3 PYRB_SINY3 PYRB_SINY3 PYRB_SINY3 PYRB_SINS0 PYRB_SINS0 PYRB_SINS0 PYRB_SINS0 PYRB_SINS0 PYRB_SINS0 PYRB_BACCL PYRB_BACCL PYRB_DSEAE PYRB_LACLE PYRB_DSEAE	165 YGRTVH.SLT YGRTVH.SLT YGRTVH.SLA YARTVN.SLL NGRTVR.SLA NGRTVR.SLA HSR.VARSNA HSR.VARSNA HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNM HSR.VARSNV HSR.VARSNV HSR.VARSNV HSR.VARSNL GARENMKVLH GARENMKVLH GARENMKVLH GARENMKVLH GARENMKVLH KAKDELRIMH KMKKDSIILH VMQKKAIIMH RMKSGAIILH RMKRHAIIMH LAKPDAIVMH	174 QALAKFDGNR RTLAKFSGNR QALAKFESNR EALTFYDVEL RILTRFRPKL YLLAKFKDVK EVLTRLGA.N EVLTRLGA.R EILNTLGA.E ALLTQLGA.Q LALKTLGCPD MLLDTLGA.E WSLTTAGA.D DGLKIFKSVK 266 PLPRVDEI PLPRUDEI PLPRUDEI PLPRUDEI PLPRUDEI PLPRUDEI PLPRUDEI PLPRUDEI PLPRUDEI PAPVNRGVEI PAPVNRGVEI PGPINRGVEN	184 FYFIAPDALA FYFIAPDALA FYFIAPDALA .YLISPELLR VXLISPQLLR VXLSGPEEWK VLFSGPEEWK VLFSGPEEWY VYFGGPKEWY IRVIAPATLL IRVIGPKTLI VVLVAPPTLL VVLVAPPTLL VVLVAPPTLL VVLVAPPTLL VVLVAPPTLL VVLVAPPTLL VDLIAPAELA ATD.VDKTPH ATD.VDKTPH HPE.VDNTKH DRK.VDKTTK TAD.VDADPR ASELVEAKA. DSLVESEK. DGDLVEAPK. ASDLVEAPQ. ESAVADGAQ.	194 MPQYILDMLD MPQYILDMLD MPAYILKMLE MPRHIVEELR ARKEILDEL. MKDDIKDVLT D. EENTFGT NAEEFSKYGT .GRDFEAYGE PIGIEE PKGFT PKEFQQLTLA MPEYYKVRMQ 283 AWYFQQAGNG AIYFRQVFNG AIYFRQAGNG SRIFKQMENG SRIFKQMENG SRIFKQMENG SRIFKQMTNG SVILNQVTYG	204 EKGIAWSLHS EKGMAWSLHG EKGIEYSSHG EKGMKVVETT NYPVKEVE SSGVEWEESS YVE YVS YVK YVQ .QYGVRVFT QYGVRVFT QYGVRVT GWPATVSH PGSGKLHCHW ENGFTVREFS 293 IFARQALLAL IFARQALLAL IFARSA.LAL IFARSA.LAL IFARSA.LAL IFARSA.LAL IFARSA.LAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VPVRMALLAL VFVRMAVLKR VFIRMAVQS IAIRMAVLSM	214 SIEEVMAEVD SIEEVMADVD SIEEVVPELD TLEDVIGKLD NPFEVINEVD UMEVASKCD .VDEAIARAD .WDEAVESSD NIDDEIPELD TMDQLVATMD DFDAELPAAD QLQPALEGAD SIEEYLRQAD 303 VLNRDLVL VLNSELSL VUNADLAL VLGVI LLVGW AMEGRMEHGR ALQTNVKRGE VLAHQGLISA AMSGQNTQRQ	224 ILYMTRVQKE ILYMTRVQKE VLYVTRIQKE VLYVTRIQKE VVYQTRIQRE VVMLLRIQHE VVMLLRIQNE VVMLLRQNE VVMLLRQNE VVMLRLQRE AVLMLRVQAE IVMTLRLQRE AVLMLRVQAE IVMTLRLQKE VALIWYFTRP ••	234 RLDPSEYA RL.DPSEYA RFPDEQE.YL RFVDEME.YE RHAETMGLTK RHQS.AVSQ RHNGAEAKTE RLSQVNN RMQGEL RMNGGF QL.ERMGEQ	242 NVKA NVKA KVKG EEYHA EGYLN QLFDAKDYNA QTFDASAYHQ .LPSEGEFFK .LPSEGEFFK .FPSVREYSV .LPSLREYHH VLKKQDELRR	246 QFVLRASDLH QFVL. ADLA SYQVNLKVLE SYIVSLDLAN KFIVDKDLLG RYGLTVERAE AYGLTVERAE AYGLTVERAE LYGLTVERAE LYGLTERRQA YFGITHDRLK SITFRKEFIE
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FIGURE 3. Sequence alignment of selected ATCase catalytic subunits. PALA binding residues are indicated by •, and residues proposed to be catalytically important are indicated by *¬*. Sequence numbering is based on the sequence of *E. coli* ATCase. The organisms used in the alignment were *Escherichia coli*, *Salmonella trphimurum*, *Serratia marcescens*, *Pyrococcus abyssi*, *Sulfolobus solfataricus*, *Arabidopsis thaliana*, *Bacillus caldolyticusd*, *Bacillus subtilis*, *Lactobacillus leichmannii*, *Lactobacillus* plantarum, Pseudomonas aeruginosa, Pseudomonas putida, Mycobacterium tuberculosis, Synechocystis sp., and Treponema denticola. * indicates sequences not shown for clarity.

indicated.) The positive charges of the active site complement the negative charge of the ligand. In both families, at least one residue at this binding site is contributed by

a second subunit. In E. coli ATCase, these residues are Ser 80 and Lys 84. In E. coli OTCase, Gln 82 (His 117 in human OTCase), the counterpart of Ser 80 in E. coli



FIGURE 4. Ribbon drawing of subunit of (a) *E. coli* OTCase and (b) ATCase. The bisubstrate analogues PALA or PALO, which are located in the cleft between the CP domain and the L-Asp or L-Orn domain, are shown as ball-and-stick models. The α 9a loop, present in *E. coli* OTCase adjacent to the 240s loop, is not present in *E. coli* ATCase and some other OTCases. In general, the tertiary structures of the ATCase catalytic subunit and OTCase subunit are very similar.

ATCase, forms a hydrogen bond with one of the phosphonate oxygens of the bound bisubstrate analogue PALO. Lys 86, which corresponds to Lys 84 in *E. coli* ATCase, is adjacent to both the carbonyl O of Gln 82 and the carboxy O of PALO, but not close enough to form direct bonds. However, these interactions appear to be functionally significant, since mutating Lys 86 to Gln lowers the enzyme's maximal velocity by 2 orders of magnitude.³² These side chains may be bridged by solvent molecules.

Aspartate or Ornithine Binding Site

L-Orn and L-Asp have side chains with different lengths and different charges, and their binding sites have evolved to reflect these differences (Figure 7). Several side chains at the L-Asp binding site of ATCase are positively charged, such as Lys 84, Arg 167, and Arg 229, while others such as Gln 231 are neutral. The binding site for L-Orn in OTCase has a negatively charged side chain, Asp 231, and two long hydrophobic side chains, Met 236 and Leu 125, which form a hydrophobic pocket for the methylene group of L-Orn, as well as two hydrogen-bonding side chains, Ser 235 and Asn 167.

Electrostatic Features of Active Site

Both OTCase and ATCase have a high density of charged residues at their active sites which create electrostatic potentials that can guide incoming substrates to their binding sites and assist in their binding. The electrostatic potentials of the catalytic subunits of E. coli ATCase and OTCase are shown in Figure 8. In both ATCase and OTCase, substrate binding and product release are ordered, with CP binding first, L-Asp or L-Orn binding second, carbamoylaspartate or citrulline dissociating first, and phosphate dissociating second.^{33,34} When ATCase and OTCase are unliganded, their active sites are dominated by positive electrostatic potentials that will guide their common substrate, CP, with two negative charges at physiological pH, into the CP binding pocket. After CP binds, the electrostatic potentials around the active sites of ATCase and OTCase have the opposite sign. While the active site of ATCase is still dominated by a positive potential, the electrostatic potential of the active site in OTCase has become negative. The positive potential of ATCase will help dock negatively charged L-Asp, while the negative potential of OTCase will play the same role in docking the positively charged L-Orn.

Catalytic Mechanisms

The critical step in the catalytic mechanisms of both ATCases and OTCases is nucleophilic attack of the carbonyl C of CP by an amino group. In both enzymes, the crystal structures indicate that attack is facilitated by interactions between the protein and its substrates, which increase the nucleophilicity of the amino group and the positive charge on the carbonyl C. However, the greater basicity of the δ -amino group of L-Orn requires general acid—base catalysis in OTCase, while L-Asp does not.

The group which appears to function as a general acid– base catalyst in OTCase is the sulfhydryl group of a Cys residue, which is found in a conserved HCLP motif. HCLP is replaced by HPLP in *E. coli* ATCase, which does not require a general acid–base catalyst. The S atom of this Cys in the crystal structure of the complex of the bisubstrate analogue PALO with *E. coli* OTCase is 4.3 Å from the ϵ -N of the L-Orn moiety in PALO. It thus has the potential to act as a general acid–base catalyst and to abstract a proton from the δ -amino group of L-Orn. Its basicity is increased by a hydrogen bond to the side chain of Asp 231. The Cys side chain is also close to the imidazole group of His 272, which in turn interacts with Glu 299. Although this Cys-His-Glu triad is reminiscent



FIGURE 5. Deleterious mutations found in patients with OTCD mapped on the structure of human OTCase. Mutations which produce neonatal OTCD are shown in red, those identified only in females are in blue, and those which produce late onset OTCD are in yellow.

of the catalytic triads in Cys and Ser proteases, the distance between the γ -S of Cys and the imidazole ring is too long for a strong interaction; however, a stronger interaction in some other steps of the catalytic cycle cannot be ruled out at this point.

The catalytic mechanisms of both ATCase and OTCase involve a tetrahedral intermediate (Figure 1). Gln 136 in *E. coli* OTCase, which is 4.1 Å from the carbonyl C of the CP moiety, is positioned so as to be able to stabilize this intermediate, while Gln 137 plays the same role in *E. coli* ATCase. The sequence motif NxLxxxHxxQxxD around Gln 136 is strongly conserved in OTCases, as is the corresponding motif NxGDGxxxHxxQxxD in ATCases. The similarity between these motifs suggests that both OTCase and ATCase may use a similar mechanism to stabilize the tetrahedral intermediate. However, replacement of the GDG motif in ATCase by L in OTCase reduces backbone flexibility and enables the long side chain of L-Orn to be held in place by the Leu side chain of the protein.

Subunit Interfaces

The interface between subunits in the trimers of both OTCase and ATCase is formed primarily by residues from the CP binding domains. In *E. coli* OTCase, these residues are 57–68, 72–98, and 278–317; the residues at the subunit interfaces of ATCase are analogous. Binding of substrate analogues to the active site triggers localized

conformational changes in the vicinity of residues 52 and 84 which strengthen subunit interactions; the restructuring is greater in ATCase, where it contributes to the T \rightarrow R quaternary transition,³⁵ than it is in OTCase (Figure 6). Although most residues involved in intersubunit interactions are variable, the salt bridge between Arg 57 and Glu 87 is conserved in both OTCase and ATCase, as is the interaction between Arg 59 and the carbonyl O of residue 75. These interactions are likely to be important in positioning Gln 82 in OTCase and Ser 80, Lys 84 in ATCase to interact with bound CP.

Other Protein—Protein Interfaces

Although both *E. coli* and human OTCase are trimeric in vitro, the OTCases of *Pseudomonas aeruginosa* and *Pyrococcus furiosus*, a thermophilic archaeabacterium, are dodecameric, with 23-point group symmetry. The trimers are organized tetrahedrally, with their convex surfaces in contact. However, a 6° rotation of the trimers of the *Pseudomonas* and *Pyrococcus* OTCases with respect to each other results in the intertrimer interfaces being quite different in the two proteins. In *P. aeruginosa*, a cluster of charged residues rich in Arg forms a 3-fold channel, which may bind negatively charged ions such as sulfate or phosphate.²⁶ Contacts between monomers from adjacent catalytic trimers around the 2-fold symmetry axes appear to play a role in the allosteric behavior of this



FIGURE 6. Superposition of liganded (thin line) and unliganded (thick line) catalytic subunits of (a) *E. coli* ATCase and (b) OTCase. The Protein Data Bank references for the structures are 8ATC (liganded *E. coli* ATCase), 1RAI (unliganded *E. coli* ATCase), 2ORT (liganded *E. coli* OTCase), and 1AKM (unliganded *E. coli* OTCase).



FIGURE 7. Schematic drawing showing the interaction of (a) the bisubstrate analogue PALA with active-site residues in *E. coli* ATCase and (b) the bisubstrate analogue PALO with active-site residues in *E. coli* OTCase. The residue indicated with * is from an adjacent subunit.

enzyme, since eliminating these residues eliminates allosteric regulation. In *Py. furiosus* OTCase, the Arg residues at this interface are replaced by Trp, giving it a hydrophobic character.²⁸ Since hydrophobic interactions strengthen as temperature increases, this feature of *Py. furiosus* OTCase, together with an increase in the number of electrostatic interactions within each monomer, probably accounts for its ability to retain 50% activity, even after being heated at 100 °C for as long as 1 h.³⁶

E. coli ATCase also exists as a dodecamer, however, composed of six catalytic chains and three regulatory chains, organized as two catalytic subunits and three regulatory subunits with 32-point group symmetry. This complex organization creates three unique subunit interfaces for each catalytic chain, one between catalytic subunits, and two types of interfaces between catalytic and regulatory subunits. In contrast to the prokaryotic OTCases discussed above, contacts between the catalytic trimers of E. coli ATCase in the T state involve the concave surfaces of the trimers, with residues in the 240s loops interacting, primarily through ionic or polar interactions. All subunit interfaces undergo major changes in the T \rightarrow R allosteric transition. When the transition occurs, the contact between the catalytic subunits and one of the contacts between catalytic and regulatory subunits are eliminated.

The homology between *E. coli* OTCase and ATCase raises the question of why OTCase does not associate with the regulatory subunit of ATCase, since both coexist in the cytoplasm. This interaction may be prevented by an extra helix (α 9a) present in both *E. coli* and *P. aeruginosa* catabolic OTCase which interacts with the 240s loop,



FIGURE 8. Electrostatic potential of (a) *E. coli* ATCase and (b) OTCase catalytic subunit before and after binding the first substrate CP. Potentials greater than +1 kT are shown in blue, and those less than -1 kT in are shown in red, mapped onto the molecular surface. The subunit is viewed in the same orientation as that in Figure 5. The active site is in the cleft between two domains, as indicated by the arrow. This figure was produced with GRASP.⁴¹

mainly through hydrophobic bonds, and with the 80s loop. The position of this helix, combined with sequence differences in a number of residues, would disrupt the potential interface between *E. coli* OTCase and the regulatory subunit of *E. coli* ATCase.¹⁵

Ureotelic OTCases have a C-terminus extension which folds back on the L-Orn domain and forms a ridge on the convex face of the trimer. This extension has a surprising homology with several membrane associated proteins, including two yeast mitochondrial inner membrane carrier proteins.¹⁶ In models of these carrier proteins, this sequence occurs in a loop between two transmembrane helices in a region of the molecule which has been shown to be important in carrier-specific transport. Since OTCase has been shown to be associated with the inner mitochondrial membrane,³⁷ the sequence of this extension may be a protein recognition motif which enables OTCase and other membrane-associated proteins to interact with other proteins with related functions.

Relationship between State of Assembly and Regulation

Although trimeric OTCases undergo domain closure when substrates bind, wild-type trimeric OTCases appear to be unregulated, although allostery can be induced through site-directed mutagenesis. Higher order assemblies of OTCase may or may not be regulated. Catabolic *P. aeruginosa* OTCase is regulated by the binding of negatively charged allosteric activators such as phosphate or nucleoside monophosphates at the interfaces between trimers in the dodecamer, while anabolic *Py. furiosus* OTCase, also a dodecamer, is not.

In yeast, a regulatory complex consisting of one molecule of OTCase and one molecule of arginase forms to inactivate OTCase, effectively uncoupling the biosynthetic and catabolic pathways in arginine metabolism.^{38,39} The conformational changes which promote association of OTCase with arginase have been proposed to be linked to binding of substrates at the active site.

ATCases comprised of both catalytic and regulatory subunits are highly regulated, although the details of the regulation vary between species. Chimeric enzymes have provided considerable insight into the elements of secondary structure that determine the nature of the regulation. For example, CTP stimulates the catalytic activity of *Serratia marcescens* ATCase, while CTP and UTP synergistically inhibit *E. coli* ATCase. When five divergent residues in the S5' β -strand at the junction of the allosteric and zinc domains of the regulatory chain of *S. marcescens* ATCase were replaced by the corresponding residues in *E. coli* ATCase, the chimeric ATCase acquired the allosteric properties of *E. coli* ATCase.⁴⁰

Conclusions

Structural and functional comparisons between the OT-Cases and ATCases provide an unusual opportunity to compare how two families of enzymes recognize their substrates and assemble to form large aggregates. The primary and tertiary structures of the domains that bind the common substrate CP are similar, while those of the domains that bind the second substrate, L-Asp or L-Orn, are different. The binding pockets for the second substrate are complementary to the substrates and therefore differ between OTCases and ATCases, despite some common features. The similarity in the active sites of ATCase and OTCase implies that they use similar mechanisms to stabilize the tetrahedral intermediate in the reaction mechanism. Differences in the active site, particularly replacement of the HPLP motif in ATCase by HCLP in OTCase, compensate for the difference in basicity of the α -amino group of L-Asp and the δ -amino group of L-Orn. The electrostatic properties of the active site are consistent with the ordered reaction mechanism for both enzymes, with the change of electrostatic potential in OTCase after binding the first substrate, CP, reflecting the different net charge of the second substrate, L-Asp or L-Orn. Variability in primary structure within and between the two enzyme families determines their ability to associate with other enzymes or to self-assemble to form larger aggregates. Association and aggregation of the enzymes create new properties, such as allosteric regulation, thermal stabilization, or inactivation.

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