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# Sequence analysis of cytochrome bd oxidase suggests a revised topology for subunit I

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#### Abstract

Numerous sequences of the cytochrome bd quinol oxidase (cytochrome bd) have recently become available for analysis. The analysis has revealed a small number of conserved residues, a new topology for subunit I and a phylogenetic tree involving extensive horizontal gene transfer. There are 20 conserved residues in subunit I and two in subunit II. Algorithms utilizing multiple sequence alignments predicted a revised topology for cytochrome bd, adding two transmembrane helices to subunit I to the seven that were previously indicated by the analysis of the sequence of the oxidase from E. coli. This revised topology has the effect of relocating the N-terminus and C-terminus to the periplasmic and cytoplasmic sides of the membrane, respectively. The new topology repositions I-H19, the putative ligand for heme  $b_{595}$ , close to the periplasmic edge of the membrane, which suggests that the heme  $b_{595}$ /heme d active site of the oxidase is located near the outer (periplasmic) surface of the membrane. The most highly conserved region of the sequence of subunit I contains the sequence GRQPW and is located in a predicted periplasmic loop connecting the eighth and ninth transmembrane helices. The potential importance of this region of the protein was previously unsuspected, and it may participate in the binding of either quinol or heme d. There are two very highly conserved glutamates in subunit I, E99 and E107, within the third transmembrane helix (E. coli cytochrome bd-I numbering). It is speculated that these glutamates may be part of a proton channel leading from the cytoplasmic side of the membrane to the heme d oxygen-reactive site, now placed near the periplasmic surface. The revised topology and newly revealed conserved residues provide a clear basis for further experimental tests of these hypotheses. Phylogenetic analysis of the new sequences of cytochrome bd reveals considerable deviation from the 16sRNA tree, suggesting that a large amount of horizontal gene transfer has occurred in the evolution of cytochrome bd. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Cytochrome bd oxidase; Sequence analysis; Topology

## 1. Introduction

In *Escherichia coli*, cytochrome bd is a terminal oxidase in the branched electron transport chain. It is expressed during both aerobic and anaerobic

growth conditions, but the expression level is highest when the bacterium is growing in aerobic stationary phase or in low oxygen environments [1,2] during which times it is the primary respiratory oxidase. Cytochrome bd has a remarkably high affinity for oxygen [3,4] and catalyzes the four-electron reduction of oxygen to water. When the reductant, quinol, is oxidized it releases protons on the periplasmic side of the membrane. Since protons are taken up from the

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	1				50	H19	G28			100
Pa			~~~~~M	FGL.EAID	LARIQ.FAFT	VSFUII	FPAITICLAS	YLA VLEGL	WLKT . NEEVY	RDLYHFW
sy	~~~~~~~~~~	~~~~~~~~~	~~~~~M	QDF.LSNTVA	LSRLQ.FAVT	AIFIML	WPVLTTEMGI	YLVIIEGL	WLKTRNLDYY	$\texttt{HHAR} \dots \texttt{FW}$
HNI	~~~~~~~~~	~~~~~~~~~	~~~~~M	A.L.LSPEIA	. SRMQ . FGWT	ISVEII	FASLSICLAP	FIIYFT	W.KII	.FAS.L.SIG
VcII	~~~~~~~~	~~~~~~~								~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
Rel		~~~~~~~~~~~	~~~M.FDI	~ MS FLV	LARIO FAST	T LE HEL	FUDMSTOLVE	MVA LMETL	VLVK KNEL	VI.KMAKFW
Smc	~~MGVTNTLK	PPLTTAVWRC	EESEDV. DL	ALAPE. TL.	.ARWO.FGIT	TVY.	FVPLTISLAA	LTA. GLOTA	WVRT.EKEK.	YLRATKFW
Mt	~~~~~~~~	~~~~~~~~~~~		~MNVVD	ISRWQ.FGIT	TVY.	FVPLTICLAP	LIA VMQTL	WVVT.DNPA.	WYRLTKFF
Pg	~~~~~~~~~	~~~~~~~~	~~~~~MI	MN.LDA.LVS	WSRAQ.FALT	AMY.HWL	FVPLTLCLGV	IMAIVETI	YYRNGKPE	WKRYAQFW
Сj		~~~~~~~	~~~~~	MNELSSVD	WSRAQ.FALT	ALY.HFL	FVPLTLCLSF	MIAIMETI	YVKT.KNE	.RWKKITKFW
Aca	********	~~~~~~~~~~	~~~~~	M. LD. VVE	LSRLQ.FALT	ALY.	FVPLTLEMTF	LLA IMETL	YVVTNK.E	. VYKDMTKFW
H1	~~~~~~	~~~~~~	~~~~~	M. LD. VVD	LSRLQ.FALT	ALY.	FVPLTLELSF	ILV. IMETI	YVATGK.E	. VYKDMTKFW
ECI	~~~~~~~~~~	~~~~~~~~~~~	~~~ M LDI	VE	SRLO FALT	A. MY BFL	FVPLTLEMAF	LLA IMETV	YVLSGK.Q	I YKDMTKFW
Kp	~~~~~~~~~	~~~~~~~~	~~~~.M.LDI	VE	LSRLO.FALT	AMY. FL	FVPLTLCMAF	LLA IMETV	YVLSGK.O.	IYKDMTKFW
Yp	~~~~~~	~~~~~~~	~~~~.M.FDI	VE	LSRLQ.FALT	AMY.HFL	FVPLTLCLAF	LLA IMESV	YVLSGK.Q	. IYKDMTKFW
Av	~~~~~~~~~	~~~~~~~~	~~~~~	MISESVVD	LSRLQ.FAMT	ALY.	FVPLTLGMTF	LLAIMESV	YVMTGK.Q	. VYKDMVKFW
EcII		~~~~~~~		MWDVID	LSRWQ.FALT	ALY.	FVPLTLCLIF	LLAIMETI	YVVTGK.T	. IYRDMTRFW
RC	~~~~~~~~~~	~~~~~~~~~	~~~MEFGL	VEL.	. SRLQ.FAST	AMY.EFL	FVPLTLELSI	LVA TMETV	FVMTGR.P	. IWRQMTKFW
Acta Acta	~~~~~~~~~~	~~~~~~~~	~~~~~~	MI	LARIO FALT	AMY.HFL	FUDITUGUSL	LLA. IMESL	WARFFODERU	LINEDIGEFE
Ct	~~~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~	MSAFIL	ARVO FALF	T GE HVL	FVPISLELSE	MIV LMEGL	VLETKKS	TYKOLTWFW
Tm	~~~~~~~~~~	~~~~~~~~		~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~
BsII	~~~~~~~~	~~~~~~~	~~~~~~~~~	~~~~M.	. AR . SLFGTT	MGF.	FATLGVELPL	MILVAELI	YQKT . KDD . H	YAIMAKRW
Af	~~~~~~	~~~~~~~	~~~~~	.MSGGETIID	ASWLLGLS	AL.GIYIHAV	FLSITLEFPL	VIIGLLLK	YSKSGDEDYF	KTAKIMT
StII	~~~~~~~~~~	~~~~~~~~~	~~~~~	M.EF. DAFF	LARLQ.FAFT	VSFIII	FPAITIC	. LA VTWWY	W.KVY	G*KRVIL
HS	~~~~~~~~~	~~~~~~~~~~	~~~~~	MA.LLSPEIA	. SRMQ.FGWT	15V#11	FASLSICLAP	FIIYFT	W.KDVRTNEQ	RYAR . LRS
Bn	~~~~~~~~~~	~~~~~~~~	~~~~~~~~~	MIDLD WWW	LSRF.LT	AMAX APIV	FATIGVEMPL	MFV. ISEFI	VUMTOR O	TWODATACK
ЪP				ALDED	DONTQUIANT	A	rvrbrdebsr	IDA IMESV	IVHIGK.Q.	. I WRITITIT W
	1.01									
De	TOT	NE ON	GTO GTO	WAY OF	150	G89	C DI I MUTTI	F104 E107	FLOWN FC	200
rd Sv	A RLYV. T.	NFGM	GVAT.	PMAF, OFGI	.NWA. PESES	VCD.FF	G. TVLOFFO	TMAID AG	FLGIMI FC	WDRVPP I.T
HNI	LAPFILY	.FTW.K.AV	GFVMGTVTCI	PMSF.OFGT.	.NFP.OFATI	ACELIG	G. P. LAFEA	KMARFLP, AV	FLGVLL.YG	RERVAD RT
VcII	~~~~~~~	~~~~~	. LASWGGVGI	TMSC.NLAL.	. TGR . ALCVR	VEN.VA	G PLLGYEV	MTASFMD . AT	FLGVML FG	RGRVPE WL
Ef	GNIF.LL	SF AV	GVVTCI	IQEF.QFGM.	. NWS . DYSRF	VCDIF	G.AP.LAVEA	LLASFLD.ST	FLGLWIFT	WDKM.NP.KV
BsI	GHLF.LI	NF AV	GVVTGI	LQEF . QFGL .	. NWS . DYSRF	VGDVF	G.AP.LAIEA	LLAFFMD.SI	FIGLWIFG	WDRLPKKI
Smc	GKLF.LI	NI	GVVTCI	VQEF . QFGM .	. XWS . DYSRF	VGDVF	G.AP.LAFEA	LIAFFFE.ST	FIGLWIFG	WDKLPKKI
Mt	GKLF.LI	NFAI	GVATCI	VQEF.QFGMN	WS . EYSRF	VEDVF	G.AP.LAMEG	LAASFF5.ST	FIGLWIFG	WNRL. PRLV
Pg	QKLF.GI	NFAI	GVATel	ILEF.EFGT.	.NWS.NYSLF	VeDIF	G.AP.LAIEG	ILASEMD.AT	FIAVME FG	WNKV.SKGF
Aca	G. KLF.GI	NF. AL	GVT TEV	TMEF EFGT	NWS YYSHY	VEDIF	G AP LATEA	LLASFLS ST	FVGLEF FG	WDRU. SKGK
Hi	GKLF.GI	NFAL	GVTTCI	IMEF.OFGT.	. NWS . YYSHY	VGDIF	G.AP.LAIEA	LLASFLS.ST	FVGLFFFG	WDRL SKGK
StI	GKLF.GI	NLAL	GVGTCL	TMEF . QFGT .	. NWS . YYSHY	LCDIS	G.AP.LSIXG	VMSEFXE.AT	FVGLFFFG	WDRL SKVQ
EcI	$\texttt{G.} \dots \texttt{KLF} \cdot \texttt{GI}$	$\mathtt{NF} \ldots \ldots \mathtt{AL}$	GVATCL	TMEF.QFGT.	.NWS.YYSHY	VCDIF	G.AP.LAIEG	LMASFLD.ST	FVGLFFFG	WDRMGKVQ
Kp	GKLF.GI	NFAL	GVATCL	TMEF . QFGT .	.NWS.YYSHY	VGDIF	G.AP.LAIEG	LMAEFLE.ST	FVGLFF FG	WDRLGKVQ
Yp	GKLF.AI	NFAL	GVATCL	TMEF . QFGT .	. NWS . YFSHY	VCDIF	G.AP.LAIEG	LMAEFLE.ST	FVGLFFFG	WDRLTKHQ
AV	GKLF.GI	NFAL	GVTICI	TMEF.QFGT.	. NWA . YYSHY	VCDIF	G.AP.LAIEG	LTASFLS.ST	FIGMFFFG	WDRL.SKIQ
RCII	G TLF GI	NFAL	GVAICL	TMEF.QFGT.	NWS.FISNI	VEDIF	G.AP.LAMEA	LMASFLD.ST	FVGLFFFG	WORL. NKIQ
VcI	G KLF.GI	NFAL	GVATCL	TMEF.OFGT.	.NWS.YYSHY	VEDI	G.AP.LATEA	LVADELD, ST	FVGLFF. FG	WDRL SKRO
Aqa	TTLF.AI	NF AA	GVVACI	VLEF.EFGT.	.NWS.EYSKT	VCDIF	G.AP.LAIEA	IFAFFLE.SV	FLGVLLFG	RDRVSP.K.F
Ct	IRIFT.L	$\texttt{TFV} \dots \dots \texttt{V}$	GVVTCL	MQIF.SFGA.	. NWS . RFAEY	TCNVF	G.M.FLGSEG	MFAFFLE.SG	FLGVLLFG	RYKV.S.KKM
Tm	~~~~~~~	~~~~~	.VATCL	TMEF.QFGT.	.NWS.YYSHY	VGDIF	G.AP.LAIEA	LVASFLS.ST	FVGLFFFG	WDRLSKRQ
BSII	TKAQAV	LL	GVAIPTC.	TIAGTQLAL.	. LWPG . FMEV	ICRVM	S.LP.FQIE.	IYA5FV5.AL	FMSIYV. YA	ADRL.SP.AM
SFTT	SCORSISSOS	NFCROLPDOP	GAVTer	DUDN DI	QAWP	ACC IT	AFAP.LALE.	LLADANDIAT	LV.LFIVILG	RIRTSYSI
Hs	3606313363	F WVKVFAV	GEVMGTVTEL	PVKN.EL	NEP OFATT	ACELIC	G. PLATEN	KMADELD AV	FLOVIL VC	REPUAD PT
Stc	AKGYAI	TVAV	GV.VTCT	TITELQLL	LL. GRHLET	ACHVI	.ALPLF.IO.	VFASFFS.AI	FLSIYFYT	WNRFK . NKWT
Вр	GTLF.GI	NF AL	GVAT~~	~~~~~~~~~	~~~~~~~~	~~~~~~~~		~~~~~~~~~	~~~~~~~	
	201	<b>S14</b> 0		P154	250					300
Pa	HFFA. TVMVA	IGTLISTFWI	LASN SWMQ	Трос		FE	IV DGRVI .	. PVDWLAVIF	NPSFPY	
sy	HYLA.TILVA	IGANLSTFWI	LSAN. SWLQ	TRAGG		IF.	.V. DGKFV.	. VQDYFAAIA	NP.FMVN	
HNI	YVLS.SVLVG	VGAWLSGFWI	LVVN AWMQ	TPRG	• • • • • • • • • • •	YE	MVTRNGMEVA	KLTDPVAAFL	TPRMPW	
VCII	HILS. TVLVA	VGTSLSAFWI	LVLN. SWMH	TRAG		YE	VI.DGVVH.	. VTSWKEVIF	NPSMPY	•••••
Rel	HALC TWLVS	FGTIMSSEWI	LTAN SEMO	FD VG	ETT KNG	RAE	MV. DEVAV.	IS.	NP	K.V
Smc	HLAC. IWMVS	IGTLLSAYFT	LAAN SWMO	HE.VG.	. YRINEEKG	RAE.	LT. DFWOV		NTTLN	
Mt	HLAC.IWIVA	IAVNVSAFFI	IAAN SFMQ	HPVG	AHYNPTTG	RAE	LSSIV.	VLLTN	NT	
Pg	HLSA.TWLTI	IGASLSAVWI	LIAN AWMQ	EPVGMT	FNPDTM	RNE	M TDFWAL .	VF	SS.TA	I
Cj	HLLS. TWCVA	IGSNLSAFWI	LVANGWMQ	YPVGMS	FNPDTA	$\texttt{R} \ldots \texttt{N} \ldots \texttt{E} \ldots$	MQSFFEV.		SP.VA	I
Aca	HLLA . TYCVA	FGSNLSAMWI	LVAN GWMQ	SP	VGSEFNFETM	RME	M TSIMDLW	$\dots \dots \mathbf{L}$	NP.IA	Q
Hi	HLLA. TYCVA	FGSNLSAMWI	LVAN GWMQ	AP	TGSEFNFETV	RME	M TNFLDLW	L	NP.VA	· · · · · · · Q · ·
SCI EcT	HMCV TWEVA	LGSNLSALWI	LVAN CHMO		SDENFETM	RME	MV.SFSEL.	V.L	NP.VA	QV.
Kn	HMAV, TWPVA	LGSNLSALWI	LVAN. CWMO	NE. TA	SDENFEIM	RM F	MV SPORT	V.L	NP VA	QV.
Yp	HLAV. TWLVA	LGSNFSALWI	LVAN GWMO	NR. IA.	SDFNFETM	RME.	ML. SFSEL	V.T.	NP.VA	vv
Av	HLAV. TWLVA	LGSNLSALWI	LVAN GWMO	HE.VG	AEFNFETM	RME	LV. DFGAL .		NP.VA	ov
EcII	HLLV. TWLVA	FGSNLSALWI	LNAN GWMQ	¥₽	TGAHFDIDTL	RM E	M TSFSEL .	VF	NP.VS	QV.
Rc	HMLV. AWGVA	IGSNFSALWI	LIANGWMQ	NGVG	AVFNPMTM	RM E	LV. DFFAV.	$\ldots \ldots \mathbf{L} \cdot \mathbf{F}$	NP.VA	QA.
vcI Acr	MLVV . XXXXX	AXXXXXXXXXXX	XXXX XXXX	XX	XXXXFNYQTM	KME	M TSFAEVV	L	NP.VA	Q
Aqa Ct	HEFS ACMIA	LGAHMSAFWI	UCAN SWMO	TR 50	VENUMENC	MINE O	AILASFFDAV	VNYS	TPY	
Tm	HLVV. TWLVA	LGSNFSALWT	LVAN, GWMO	NR. VG	SEFNFETM	RM	MV. SFADV		NP.VA	Q
BsII	RIVA.VFFVL	VGAAASAV	LITNVHAFEG	TEAG	FKILNG	K.I.TD	.V. DPWAA	F.F	NP.SF	
Af	AILA.VYWIF	AALSG V	LIMSVNSWLV	APWGTGPIAK	SIYPFMPEFG	GLAADAQK	LVILKILAIA	SGMPIQAIIQ	NPEVAGKVGV	ILTDPYVA
StII	HFLS.TCMVA	LGTLMSTFWI	LASNSWMH	TPQDL		KFT	TV.R*SR	WTGS~~	~~~~~~~~	
Hs	YVLS.SVLVG	VGAWLSGFWI			~~~~~~~~~~	~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~
Stc	HMIIGL.PVV	SGGMLSAF	FITSVNSFMN	Т <mark>Е</mark> АG	FQMKDG	RMIHVD~~~~	~~~~~~~~~	~~~~~~	~~~~~~~	~~~~~
							the second real real real real real real real real			

Fig. 1. Alignment. These were created using PILEUP in the GCG software package with gap creation and extension penalties of 3.0 and 1.0, respectively, followed by manual adjustment. VC23 is a fragment that must come from either VcII or VcIII, but which one is not known.

Da	301 P	H186	A TAFFU C	ACA AWH	350		A TR K	MI.SMAN WMA	↓ Q-loop	Start 400
sy	S	FLHMFFAT.L	ET SMFVIG	GISAWC	ILTGR.QPQ.		FFAR	SLQVIL.VVV	MAVAPLQIFI	G H. LSA . E
HNI	M	YVHMMNASVI	SVALLVAG	VS.AYLVW.	KKPDA	D		ALKLAV.VLL	LVSAPFQAVH	GDAYGRH.VE
VcII Ff	WVEF S	LAUTLLASAL	T. ASFLIAG	IS.AYQ	VLRNAKH	Q	ASM PT	GLKVAVSVAA	LAI.PVQILV	GDLHGLNTLE
BsI	WVE.F	. PHVIFGALA	T.GAF.FIAG	VS. A FK	LLKKK	EV PFFK	QSF.KLAMIV	GL.CAG.	LGV.GLS	GHMQAEHLME
Smc	F	HSFSAAFL	TGGAF . MV . G	IAAFH	LMRKK	HIPVMR	TSL.RL	GLVTLA	VGGL.LTAVS	GDTLGKVMYE
Mt	F	. THTVSGALL	TAGTE	.AVSAWW	LVRSSTT	HADSDTQAM.	Y.RPATIL	GC.WVAL.AA	TAGLLFT	GDHQGKLMFQ
cj		LHTIGSGYV	I.SALF.VMG	ISAWF	ML	GRHIIEAK	KSL.VVGASF	GL.VCS	IFLFFS	GDESAYRVTQ
Aca	SKF	. LETLSAGYV	S.AAFF.VLA	ISSYY	LLKGR	DIGFAK	RSFS.VASTF	GI.ISVVS	LLIM	GDESGYEIGY
Hi	SKF	. LETLSAGYV	T.GAFF.VLA	ISSYF	LLKGR	DFEFAK	RSFS.VAATF	GF.IASI.S	VLIL	GDESGYDIGK
EcI	KFV	TVASGYV	T.GAMF.ILG	IS.AWY	MLKGR	DFA FAK	RSFA.IAASF	GM.AAVL.S	V.IV.L	GDESGYEMGD
Кp	KFV	HTVASGYV	T.GAMF.ILA	ISSWY	MLKGR	DFAFAK	RSFA.IAASF	GM.AAILS	V.IV.L	GDESGYEMGD
Yp Av	KFV		T.GAMF.ILG T.GAVE VLA	IS.SYY	LLKKR	DIPFAK	RSFA.IAASF	GL.ASVLS	V.IV.L	GDESGYEMGD
EcII	KF	. VETVMAGYV	T.GAMF.IMA	ISAWY	LLRGR	ERNVAL	RSFA.IGSVF	GT.LAIIGT.	LQL	GDSSAYEVAQ
Rc	KFV	HTVSAGYV	T.ASIF.VIG	VSAWY	LLRGR	HIDLAR	RSIA.VASAF	GL.AASL.S	V.IV.L	GDESGYEATH
Ada		. UPTVASAYT	T.GAIF.VAG	IS.AYY	ILQGR	DIEFAR	ESF.RIAVTI	GM.IASL	LOILA	GDESGYKLGD
Ct	RFT	HVVLGAWL	S.G.IFLVLS	VS.AHY	LRKERHK	DFAN	Q	GL.KISMFCA	FLVLALQLWS	ADVTARGVAK
Tm	KFV	HTVAAGYT	T.GAMF.ILG	IS.AYY	LLKGR	DVAFAR	RSFA. IAASF	GM.ASVLS	V.IV.L	GDESGYELGE
Af	IFNPFAAISA	LUALFAAF	SVGVS	IALLAFS	LY.	. YTGGE K	RNL KAAKVA	SLVILVLFL.	IOPTILGHEM	GRESAQMLIE GDGVVE
StII	~~~~~~~~~	~~~~~~~~~	~~~~~~~~	~~~~~~	~~~~~~~~	~~~~~~		~~~~~~~		~~~~~~~
Hs	~~~~~~~	~~~~~~~~~~	~~~~~~~~~~~	~~~~~~~	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~		~~~~~~~~~~	~~~~~~~~~	~~~~~~~~~~	~~~~~~~
Bp	~~~~~~~~~		~~~~~~~~	~~~~~~~	~~~~~~~~~	~~~~~~~	~~~~~~~~		~~~~~~~~	~~~~~~
Pa	401 K251	AMECHUDNS	SGE PT	DI.TI.	450 EGW PD	MORFET	PERVET	289	KUSLTEDIDA	
Sy	QVSVHQPAKL	AAMEALWETV	PAKTP	A	. AWSVVALPN	DKAEKN	DWELSI	FGALSYILEL	KPQLDKPIQG	LKDWAPVDRP
HNI	DTQPOKF	AAMBAHYETG	SADLHLLAF.	PK	SLDALTD	PRTE.N	LFTVSL	FG.IGSFLAS	GGDFDAEVIG	LNEY EENP
VCII	G. OPMAR	MAMOGVWQTE	RGA	PA	FALPN AWTLTAW	A DER	DFALGI	EN.LASLI.L	THDMINGE1VG YNKLSGSVDG	LDAFAP.DHP
BsI	SQPMKM	AASEGLWEDS	G.D	PA	.AWT.AF	.ATIDTK	NEKSSNEIKV	FYALS.YLA.	YQKFSGSVKG	МК
Smc	QQPMKM	AAABALW.DG	. EK	PA	. PFSVFAY	.GDVD.K	GHNKV.ALEV	FGLLS.FLA.	HSDFESYVPG	IND
MC Pa	KOPMKL	AAMPALYDSG	OTDKDGLT	ADGKGLPL.	.NFSVLTV	.GRQNNCDSL PAKETPODDK	EA.FLFNVSV	RVLP.FLA.	TRNPSGYVPG	INNILEGGYV
cj	TQPMKL	AAMEGVY . QG	E.HRAGL.	VP	FGILN	P.KKT.IDNN	ESVFLFDITI	FYALS.ILG.	NRDPNSFVPG	IEDLIYGN
Aca	AQPTKL	AAMEGEW	HTQ.P.A	PA	. AWNMIIV	PNQAEQ	KND. FSLQI	FYIAG.VIV.	TRSFDKQFSG	LIDL
StI	VOKTEL	MANDAEF	ETH.P.A.	PA	. PFLPVAI	PDODKO	ENH. LAIOI	YALG. IIA.	TRSIDKEIIG	LKDL
EcI	VQKTKL	AAIBAEW	ETQ.P.A	PA	.AFTLFGI	PDQE.E	ETNK.FAIQI	FYALG.IIA.	TRSVDTPVIG	LKEL
Kp	VQKTKL	AAIBAEW	ETQ.P.A	PA	. AFTLFGI	PDQ.RR	RRT. FAIQI	PFALG.IIA.	TRSVDKQVTG	LKAL
YP AV	VOKAKL	AAIBAEW	ETQ.PP ET.HPA	PA	.AFTLFAI	PNQETM PNEEEO	ENR. FAIQI RTD. FAVKI	WVLG.IIA.	TRSLDTPVIG	IKDL
EcII	VQPVKL	AAMEGEW	QTE . P A	PA	. PFHVVAW	PEQDQE	RN. AFALKI	PALLG.ILA.	THSLDKPVPG	LKNL
Rc	NQRMKL	AAIBGMW	DTE.E.A	PA	.SFNLFGI	PDQEAR	ET.K.YAIKI	PYVMG,LIG.	TRSLTTEMPG	IKDL
Aqa	TQPLKL	AMMEDKW	ETESG. A.	.GLEIVP	.AFILFGL	PNQKEG	IAIKI	EKLLS.ILA.	YHDPDAKVYG	IKDLVOT
Ct	HQPAKL	AAFDGVF	КТQ	GHTPI	Y.LLGIV.	DMK . K	E RVIGIPI	PSGLSLLV	HRNAKTPVTG	L.D
Tm	VQRVKL	MAIDSEW	HTE.P.A	PCUADI	AFTLFGI	PNQEEM	RTD. YAIKI	PFALG.DIA.	TRSLD~~~~	
Af	MNPTKF	MMMD NAK	ET	.FYNPM.I	ALVAYGD	PSR	ERVR.WAIEI	PIVGF	D.EFERQCNS	LGDAELGDLA
StII	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~		~~~~~~~~~	~~~~~~~	~~~~~~		~~~~~			*******
Stc	~~~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~	~~~~~~	~~~~~~~~	~~~~~~~
Вр	~~~~~~		~~~~~~	~~~~~~~	~~~~~~~~~	~~~~~~~			~~~~~~~~~	~~~~~~~
	501				550					600
Pa	NST.V									VF
SY HNT	RMVGL					• • • • • • • • • • •	• • • • • • • • • • • •	•••••	• • • • • • • • • • • •	IY
VcII	. PVAP									LF
Ef BSI	T.V T.L.	OAEY	KRLVE	K. Y. K	G.DDK	• • • • • • • • • • •	NY	••••	•••••	YPP.VN P.P.VK
Smc	<b>T</b>	N	KALQE	QF	GPGD		Y			KPIVP.V.
Mt Pa	KADGTTAT		IRDLQQEYQQ GRRAIMALND	RF	GDMEAALOHV	SVIDEN FP	YFGY.S		чот	KNDIVPPVC
cj	ESKGI	EPMQNRIDR	GKIAIQTLKD	YKLAKE N	NDTIAMANHK	SILETHFK	DFGY.G	. Y	LEK.	. PSDTIPPVA
Аса ні	QERN	LERVRS	GIQAY ALLQ	QLREEKK	ANGQASEETK	AKFDKVQK	DLGF GLLLK	RYTDNVVD	ATEEQIKQA	A ADTIPKVA
StI		HEERFRN	GMKDY . ELLE	QXRA	GSTDQA VR	DQFNRM. KK	DLGY . GLLLK	RYTPNVTD	ATEAQIQQA	T.KDSIPRVG
EcI	MVQ	HEERIRN	GMKAY . SLLE	QLRS	GSTDQA VR	DQFNSM KK	DLGY .GLLLK	RYTPNVAD	ATEAQIQQA	T.KDSIPRVA
кр Үр		HEVRIRN	GIQAY . SLLE	QLRG	GNTDPAVR	DAFNKAKQ	DLGY.GMLLK	RYTENVAD	.ATEEQIQLA	A.QDSIPAVA
AV		HEARIRN	GMVRYG . LLE	ELRA	GNKSPEKIA.	.AFNEVKD	DLGY .GLLLK	KYTPNVVD	ASEEQIKQA	A.KDTIPSVA
Rc		AEGRIRS	GKMAWL.LMQ GVIAYDALL.	QIRAQ	AKGDVAPEVK	QAFRGLEG DTFEAHSA	DLGY.GMLLS DLGY.AMLL.	KIAPDMN	HVTAAQY.QA LATDAOISEA	AMKGAIPQVA AWK.TVPOVA
VcI	R	HEHL.LRIRN	GMVAY . QLLE	RLQA	GDASVETQ	RKFEQT NH	DLGY .GLLLK	RYTDTITD	ANEAQIQQA	A . DDSMPTVW
Aqa Ct	rQ	KIAK	GE	EVF	GE . PKDEWPNVA	DELPELWL FVFO	שPR	QFAGRQSL	YITEEEIP.P	1WIP
Tm	~~~~~~~~~~~~		~~~~~~~	~~~~~~~~~~			~~~~~~	~~~~~~~~~~~~		
BSII Af	GQLGIT.MDA	AIATAKOV	GVKVGSE. F	AF	. PRDEWPPL. WNTE	F			KAESR	IH
StII				· · · · · · · · · · · · · · · · · · ·						
	~~~~~~~~~~	~~~~~~~~~		~~~~~~~~~		~~~~~~		~~~~~~~	~~~~~~~	~~~~~~~
HS Stc									~~~~~~~	~~~~~~~~~~
HS Stc Bp				~~~~~~~~~~~~	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~		~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~		~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

Fig. 1 (continued).

cytoplasmic side to make water [5-8], an electrochemical gradient results that is available for various processes such as the production of ATP, membrane transport and flagellar motion [9-11]. Sequence alignments clearly categorize the cytochrome bd oxidases as unique and not homologous to the superfamily of heme-copper terminal oxidases that includes cytochrome c oxidase [12,13]. In contrast to

Da	601 WSF			Q-loop end	1 1 M393 650	M TLVCVWSL	WT.PWP	GO	DK LEN SK	700
Sy	YSF				RINVAIGLE	FAALMAVTVL	QWLR.	GK	LKPEIISQQK	
HNI	WSF				. RFWVGLGFL	FIGL.ALW.G	GYLTYR.	G.	.RLTEST	
VcII	TLFWSF		• • • • • • • • • • • •		. RVVVGVGVL	M.LLVS.WFG	AWRVWR.	KPSLV	.KPLPK	к
BsI	TTFWSF				. RIOVGAG.V	VMIL.AAL	GGLWLNRRK .	KL	.ENS	KW
Smc	. AYWGF				.RW0IGFGMA	SFSLGLL	GL.WLTRKRF	LLPPALRTGE	DEVPHLVLLK	KPLGARLTRM
Mt	VTYWSF			•••••	. RMSIGL.MA	IPVLFALI	AL.WLTR	G.	GQIPN	QRW
cj	LTFYSF				.HINVALGSF	FFLLFIV	TLYLTMAN	DIEKFRKV.		
Aca	PTFWSF				. RVMMATGG .	.AILLLM	LLAFVQNVR.	KTVGS		
Hi	PNFWAF			• • • • • • • • • •	. RADIAAGG.	.LIALLT	FGAFVQNLR.	NKVTQ	· · · · · · · · · · · · · · · · · · ·	· · · · · · · · · · · · · · · · · · ·
EcI	PLIXAI				.RINVACG.	FLLLAII	ALSFWSVIR.	N.RIGE	K	K
Kp	PLYFAF				.RINVACG	VLMLL II	ALSFWSVIR.	NRIGE	к	к
Yp	PLYFAF			· · · · · · · · · · · ·	.RINVACG	FLMLLII	GLAFYNVVR.	GRIGE	K	К
AV EcII	PVFWSF				.RADVGAG	LLLLVM	LIALVOTLR.	GKIDO	HR	K
Rc	PLFWSF				.RINVGAG	FFMLALI	GYMFFTS.	NFRGGR	FP	т
VcI	PLFWSF			• • • • • • • • • • •	.RIOVGCGF.	.IMLFVF	GAALLQTCR.	QRITH	• • • • • • • • • • •	• • • • • • • • • • •
Aqa Ct	TY				. RGOVFLG.	MVLLA.	SLGF1FTVQD A.F.	TIEQ		KKSWSCK .KG
Tm	~~~~~~~	~~~~~~~	~~~~~~~~~~		~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~~~~~~~	~~~~~~~	~~~~~~~~	~~~~~~~	~~~~~~~
BsII	TL F				. NAWVGVG	.MLLILYSII	GVVWRK	• • • • • • • • • • •	VLK	KDRFPT
AI StII	AAYYT'. KIAF	GVIGFVSAIA	LFAHFRKLPL	LSSLVDRILG	RRAGLILPIG	VFL				
Hs	~~~~~~	~~~~~~		~~~~~~	~~~~~~	~~~~~~~~	~~~~~~~	~~~~~~~	~~~~~~	
Stc	~~~~~~~~	~~~~~~~~	~~~~~~~~	~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~~	~~~~~~	
ЪÞ										
	701		G440 0	3447 W451	750					800
Pa	AFLRLTLL	MGPSGLI	AILAGØFTTE	MGRQPWVVY.	GL.MRTA	DASSA.QSVT	QMSLT	LLTFV.VVYF	LSF.GVG.I.	GWMMRLV
SY	WLLRAWVF	AAPLGYL	AVETGWIVRC	VGROPWIVY.	GE.MRTA	E. SASN.LP	PGEILF.SLT	GLSVM.YIVF	LIATLY	.F.G. SRII
VcII	PYMYALIG	MTFSGWV	ATIAGWYVTE	IGROPWLVS.	GV.LRTA	EAVT P.VA	SSSVGI.SLT	L.YL.IT.Y	VVL.LVAYVH	TL.FYHAR.
Ef	MLWIVALC	. TFA. PFL	antt <mark>gø</mark> lvte	LGRYPWTVY.	G.LFTIE	QSVSPNVS	VASLIT.SNV	${\tt I} \ldots {\tt YFLLF}$	AGLGSV.MVY	$\texttt{LVI} \dots \texttt{LEL}$
BsI	YLRIM.IAL.	ISF. PF. L	ANSAGUIMTE	IGROPWTVM.	G.LMTTA	QSVSPNVT	AGSLL.FS.I	IAFGVMYMI.	LGAL . LVF	LFIREI
Mt	FSWLAL.	LTM. PAPFL	ANSAGOVETE	MGROPWVVVP	NPTGDOL . VR	LTVKAGVSDH	SATVVATSL.	LMFTLVY	AVLAVI.WCW	LLKRYI
Pg	.RWFHMIAI.	VCMPLAWV	ASQS <mark>GW</mark> IVAE	VGROPWTIQ.	DLLPVQ	AAVS.KLE	AGSVI.	ITFFVFLVLF	. SALLVAELN	IMRKAIKK
Cj	.LWVCL.	LSIPLGY. I	AAEAGOIVAE	VGROPWAIQ.	DLLPVH	IAAT.QL	.GKVNVQ	ISFWIFAVLF	. TALLIAEVK	IMLTQIKK
Aca Hi	I PLULKVIJW	GLPLPW I	ALECGOFLAE	YGRODWATY	EILPVG	VSAS.KLA	TGDLWF.SIG	L.IC. ALY	LAFITVEMY	LIFKYG
StI	WLLRAALY	OFFICIAL ST			1111DIDI IO	101101112011	100000000000			Dan to to the first
		.GIPLPWI	AVEAG0 FVAE	YCROPNAI	GEVLPTA	VVNS.SLT	VGDLLF . SMS	L.ICGLY	. TLFLVAELF	LMFKFA
EcI	WLLRAALY	.GIPLPWI .GIPLPWI	AVEAGNFVAE AVEAGNFVAE	YGRQPWAI YGRQPWAI	GEVLPTA	VVNS.SLT VANS.SLT	VGDLLF.SMS AGDLIF.SMV	L.ICGLY L.ICGMY	. TLFLVAELF . TLFLVAELF	LMFKFA
Ec I Kp	WLLRAALY	.GIPLPWI .GIPLPWI .GLPLPWI	AVEAGWFVAE AVEAGWFVAE AVESGWFVAE	YGROPWAI YGROPWAI YGROPWAI	GEVLPTA GEVLPTA GEVLPTA	VVNS.SLT VANS.SLT VANS.SLT	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV	L.ICGLY L.ICGMY L.ICGLY	. TLFLVAELF . TLFLVAELF . TLFLVAELF	LMFKFA LMFKFA LMFKFA
EcI Kp Yp Av	WLLRAALY WLLAAAFY WLLRAALY .PWLLKFALY	.GIPLPWI .GIPLPWI .GLPLPWI .GIPLPWI .SLPLPWI	AVEAGOFVAE AVEAGOFVAE AVESGOFVAE AVEAGOFVAE ATQTGOFVAE	YGROPWAI YGROPWAI YGROPWAI YGROPWAI HGROPWTIG.	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.VLPTH	VVNS.SLT VANS.SLT VANS.SLT VANS.SVT LSAS.SLS	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGEILF.SMA TGDL.WGSLI	L.ICGLY L.ICGMY L.ICGLY L.ICGLY ALIAFY	. TLFLVAELF . TLFLVAELF . TLFLVAELF . TLFLIAEMY . TLLLVVEMY	LMFKFA LMFKFA LMFKFA LMFKFA LMIRFA
Eci Kp Yp Av Ecii	WLLRAALY WLLAAAFY WLLRAALY .PWLLKFALY WVLKMALW	.GIPLPWI .GIPLPWI .GLPLPWI .GIPLPWI .SLPLPWI .SLPLPWI	AVEAGWFVAE AVEAGWFVAE AVESGWFVAE AVEAGWFVAE ATQTGWFVAE AIEAGWFMTE	YGROPWAI YGROPWAI YGROPWAI YGROPWAI HGROPWTIG. FGROPWAIQ.	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.VLPTH DILPTY	VVNS.SLT VANS.SLT VANS.SLT VANS.SVT LSAS.SLS SAHS.ALT	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGEILF.SMA TGDL.WGSLI TGQLAF.SLI	L.ICGLY L.ICGMY L.ICGLY L.ICGLY ALIAFY MIVGLY	. TLFLVAELF . TLFLVAELF . TLFLVAELF . TLFLIAEMY . TLLLVVEMY . TLFLIAEVY	LMFKFA LMFKFA LMFKFA LMFKFA LMIRFA LMQKYA
EcI Kp Yp Av EcII Rc	WLLRAALY WLLAAAFY WLLRAALY .PWLLKFALY WVLKMALW WALRVAVF	.GIPLPWI .GIPLPWI .GLPLPWI .GIPLPWI .SLPLPWI .AIPVPWI	AVEAGNFVAE AVEAGNFVAE AVEAGNFVAE AVEAGNFVAE ATQTGNFVAE AIEAGNFMTE AAETGNFVAE	YGROPWAI YGROPWAI YGROPWAI YGROPWAI HGROPWTIG. FGROPWAIQ. FGROPWAIQ.	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.VLPTH DILPTY G.LLPTA	VVNS.SLT. VANS.SLT. VANS.SLT. VANS.SVT. LSAS.SLS. SAHS.ALT. LSVS.NLS.	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGEILF.SMA TGDL.WGSLI TGQLAF.SLI IW.DVV	L.ICGLY L.ICGMY L.ICGLY L.ICGLY ALIAFY MIVGLY LTLAGFVTLY	. TLFLVAELF . TLFLVAELF . TLFLVAELF . TLFLIAEMY . TLLLVVEMY . TLFLIAEVY . TVLLVIEIR	LMFKFA LMFKFA LMFKFA LMFKFA LMFIRFA LMQKYA LMLAAI
EcI Kp Yp Av EcII Rc VcI Aqa	WLLRAALY WLLAAAFY WLLRAALY WLLKFALY WVLKMALW WALRVAVF KPWVLKAALW RRWLLKLFFY	.GIPLPWI .GIPLPWI .GLPLPW.I .SLPLPW.I .SLPLPW.I .AIPVPW.I .S. .SIPLP.IV	AVEAGMFVAE AVEAGMFVAE AVEAGMFVAE AVEAGMFVAE ATQTGMFVAE AIEAGMFMTE AAETGMFVAE ANILGMIVAE	YGRQPWAI YGRQPWAI YGRQPWAI HGRQPWAI FGRQPWTIG. FGRQPWTVD. VGRQPWVVY.	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.VLPTH DILPTY G.LLPTA Y.ILKTK	VVNS.SLT VANS.SLT VANS.SLT VANS.SVT LSAS.SLS SAHS.ALT LSVS.NLS DAASP.LP	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGDLIF.SMA TGDL.WGSLI TGQLAF.SLI IW.DVV AGQIL.TSII	L.ICGLY L.ICGMY L.ICGLY L.ICGLY ALIAFY MIVGLY LTLAGFVTLY LFSSIY	.TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLIAEMY .TLFLIAEWY .TVFLIFIR FIVFLIF.LG	LMFKFA LMFKFA LMFKFA LMFKFA LMQKYA LMLAAI LMVQKVIKGP
EcI Kp Yp Av EcII Rc VcI Aqa Ct	WLLRAALY .WLLRAALY .WLLRAALY .WVLKMALW .WVLKMALW .WALRVAVF KPWVLKAALW RRWLLKLFFY ILWILSF	.GIPLPWI .GLPLPWI .GLPLPWI .SLPLPWI .SLPLPWI .AIPVPWI .S .SIPLPIV .SVLCPEL	AVEAGMFVAE AVEAGMFVAE AVESGMFVAE ATQTGMFVAE ATQTGMFVAE AAETGMFVTE AAETGMFVTE ANILGMIVAE CNEIGMISTE	YGRQPWAI YGRQPWAI YGRQPWAI HGRQPWTIG. FGRQPWAIQ. FGRQPWTVD. VGRQPWTVD. VGRQPWVVY.	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.ULPTA G.LLPTA  G.LLPTA G.LLKTK	VVNS.SLT VANS.SLT VANS.SLT LSAS.SLS SAHS.ALT LSVS.NLS DAASP.LP DATSPIVN	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGELLF.SMA TGDL.WGSLI TGQLAF.SLI IW.DVV AGQIL.TSII AGQ.IWQSLI	L.ICGLY L.ICGLY L.ICGLY L.ICGLY ALIAFY MIVGLY LTLAGFVTLY LFSSIY LFSSIF	.TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLIAEMY .TLLLVVEMY .TLFLIAEVY .TVLLVIEIR FIVFLIF.LG ICLLSVF.VS	LMFKFA LMFKFA LMFKFA LMFKFA LMQKYA LMLAAI LMVQKVIKGP LLLKKI
EcI Kp Yp Av EcII Rc VcI Aqa Ct Tm BsII	WLLRAALY .WLLRAALY .WLLRAALY .PWLLKFALY .WVLKMALW .WALRVAVF KPWVLKAALW RRWLLKLFFY ILWILSF .WLL.IIF	.GIPLPWI .GLPLPWI .GLPLPWI .SLPLPWI .SLPLPWI .AIPVPW.I .SIPLP.IV .SVLCPE.L	AVEAGMFVAE AVEAGMFVAE AVESGMFVAE ATQTGMFVAE ATQTGMFVAE ALEAGMFMTE AAETGMFVAE ANILGMIVAE CNEIGMISTE	YGRQPWAI. YGRQPWAI. YGRQPWAI. HGRQPWAI. FGRQPWAIQ. FGRQPWAIQ. YGRQPWVVY. VGRQPWVVY. TGRQPWVVY.	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.ULPTA G.LLPTA G.LLPTA G.LLKTK H. LLKTS	VVNS.SLT VANS.SLT VANS.SLT LSAS.SVT LSAS.SLS SAHS.ALT LSVS.NLS DAASP.LP DATSPIVN	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGELLF.SMA TGDL.WGSLI TGQLAF.SLI IW.DVV AGQIL.TSII AGQ.IWQSLI TGSIGV	L.ICGLY L.ICGMY L.ICGLY L.ICGLY ALIAFY MIVGLY LTLAGFVTLY LFSSIY LFSSIY LFSSIY	.TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLIAEMY .TLFLIAEMY .TLFLIAEVY .TVLLVIEIR FIVFLIF.LG ICLLSVF.VS 	LMFKFA LMFKFA LMFKFA LMFKFA LMQKYA LMLAAI LMVQKVIKGP LLLKKI VILLYYF
EcI Kp Yp Av EcII Rc VcI Aqa Ct Tm BsII Af	WLLRAALY .WLLRAALY .WLLRAALY .WVLKFALY .WVLKAALW .WALRVAVF KPWVLKAALW RRWLLKLFFY ILWILSF .WLL.IIF G	.GIPLPWI .GLPLPWI .GLPLPWI .SLPLPWI .SLPLPWI .SLPLPWI .SIPLPIV .SVLCPE.L .MTAGPFSLI AAVPS	AVEAGMFVAE AVEAGMFVAE AVEAGMFVAE AVEAGMFVAE ATEAGMFVAE ATEAGMFMTE AAETGMFVAE ANILGMIVAE CNEIGMISTE GIEFGMIFAC VLGMYVRE	YGRQPWAI. YGRQPWAI. YGRQPWAI. FGRQPWAI. FGRQPWTIG FGRQPWTVD. YGRQPWVVY. YGRQPWVVY. TGRQPWVVY.	GEVLPTA GEVLPTA GEVLPTA G.VLPTH DILPTY G.LLPTA G.LLKTK HLLKTS GLLYP.E	VVNS.SLT VANS.SLT VANS.SLT VANS.SVT LSAS.SLS SAHS.ALT LSVS.NLS DAASP.LP DATSPIVN DVVTT	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGEILF.SMA TGDL.WGSLI TGQLAF.SLI IW.DVV AGQIL.TSII AGQ.IWQSLI TGSIGV .GRSF.EFA	L.ICGLY L.ICGLY L.ICGLY ALIAFY MIVGLY LTLAGFVTLY LFSSIY LFSSIY LFSSIY LFLF.FTFVY VFMSVIIAAI	.TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLIAEMY .TLFLIAEMY .TLFLIAEWY .TLFLIAEWY .TLFLIAEWY .TLFLIAEWY .TLFLIF.LG ICLLSVF.VS 	LMFKFA LMFKFA LMFKFA LMFKFA LMQKYA LMLAAI LMVQKVIKGP LLLLKKI VLLYYF FVATRGYRYL
EcI Kp Yp Av EcII Rc VcI Aqa Ct Tm BsII Af StII	WLLRAALY .WLLRAALY .WLLRAALY PWLLKFALY .WVLKMALW .WALRVAVF KPWVLKAALW .RWLLKAFFY ILWILSF .WLLIIF 	GIPLPW.I GIPLPW.I GIPLPW.I SLPLPW.I SLPLPW.I SLPLPW.I SIPLP.IV SIPLP.IV SVLCPE.L MTAGPFSLI AAVP.S	AVEAGMFVAE AVEAGMFVAE AVESGMFVAE AVESGMFVAE ATQTGMFVAE AIEAGMFWTE AAETGMFWTE AAETGMFWAE CNEIGWISTE GIEFGGIFAC GIEFGGIFAC	YGRQEWAI. YGRQEWAI. YGRQEWAI. YGRQEWAI. GRQEWAIQ. FGRQEWAIQ. FGRQEWAIQ. GRQEWVYY. VGRQEWVYY. YGRQEWVYY.	GEVLPTA GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.LLPTA G.LLPTA 	VVNS.SLT VANS.SLT VANS.SUT LSAS.SLS SAHS.ALT LSVS.NLS DAASP.LP DATSPIVN DVVTT	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGEILF.SMA TGDL.WGSLI TGQLAF.SLI TGQLAF.SLI AGQ.IWQSLI TGSIGV GRSF.EFA	L.ICGLY L.ICGLY L.ICGLY L.ICGLY ALIAFY MIVGLY LTLAGFVTLY LFSSIY LFSSIF LFLF.FTFVY	.TLFLVAELF TLFLVAELF TLFLVAELF TLFLIAEMY TLLLVVEMY TLLLVVEMY TLFLIAEVY FIVFLIF.LG ICLLSVF.VS AVLGAAV.VY AAFGMV.SMY	LMF KFA LMF KFA LMF KFA LMF KFA LMF KFA LM QKYA LML AAI LMVQKVIKGP LLL KKI VLL YYF FVATRGVRYL
EcI Kp Yp Av EcII Rc VcI Aqa Ct Tm BsII Af StII Hs Stc	WLLRAALY .WLLRAALY .WLLRAALY .PWLLKFALY .WALRVAVF KPWVLKAALW RRWLLKLFFY ILWILS.FF .WLL.IIF .WLL.IIF	GIPLPW.I GIPLPW.I GIPLPW.I SLPLPW.I SLPLPW.I SLPLPW.I SLPLPW.I SLPLP.IV SVLCPE.L MTAGPFSLI AAVP.S	AVERGMEVAE AVERGMEVAE AVERGMEVAE AVERGMEVAE AIEAGMEVAE AIEAGMEVAE AIEAGMEVAE ANILGWIVAE GIEFGWIFAC VLGMEVAE	YGRQEWAI. YGRQEWAI. YGRQEWAI. YGRQEWAI. GRQEWAIG. FGRQEWATG. FGRQEWATG. FGRQEWATG. YGRQEWATY. YGRQEWATY. YGRQEWATY.	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.VLPTH DILPTY G.LLPTA Y.ILKTK HLLKTS GLLYP.E	VVNS.SLT VANS.SLT VANS.SLT VANS.SUT LSAS.SLS SAHS.ALT LSVS.NLS DAASP.LP DAASP.VN DVVTT ELVTV.VGY.	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGDLIF.SMV AGELIF.SMA TGDL.WGSLI IW.DVV AGQIL.TSII AGQ.IWQSLI TGSIGV GRSF.EFA	L. ICG LY L. ICG LY L. ICG LY ALI AFY MIV GLY L. TLAGFVTLY L FSIY L FSIY L FSIY L FSIY L FSIY	TLFLVAELF TLFLVAELF TLFLVAELF TLFLIAENY TLLLVVENY TLLLVVENY TVLLVIFIR FIVFLIF.LG ICLLSVF.VS AVLGAAV.VY AAFGMV.SMY	LMF KFA LMF KFA LMF KFA LMF KFA LM IRFA LM IRFA LM QKYA LML AAI LMVQKVIKGP LLL KKI VLL YYF FVATRGYRYL
EcI Kp Yp Av EcII Rc VcI Aqa Ct Tm BsII Af StII Hs Stc Bp	. WLLRAALY . WLLRAALY . WLLRAALY . PWLLKFALY . WVLKMALW . WALRVAVF KPWVLKAALW RRWLLKLFFY ILWILSF . WLLIIF 	GIPLPW.I GIPLPW.I GIPLPW.I SLPLPW.I SLPLPW.I SLPLPW.I SLPLPW.I SLPLPW.I SLPLPW.I SLPLPW.I SLPLP.IV SVLCPE.L MTAGPFSLI AAVP.S	AVERGMEVAE AVERGMEVAE AVERGMEVAE AVERGMEVAE AIEAGMEME AIEAGMEME AIEAGMEME ANILGWIVAE CNEIGMISTE GIEFGWIFAC VLGMEVRE	YGRQEWAI. YGRQEWAI. YGRQEWAI. HGRQEWAI. GRQEWAIG FGRQEWATG FGRQEWATG GRQEWATG GRQEWATY YGRQEWATY YGRQEWATY YGRQEWATY YGRQEWATY	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.VLPTH DILPTY G.LLPTY Y.ILKTK HLLKTS GLLYP.E	VVNS.SLT VANS.SLT VANS.SLT VANS.SUT LSAS.SLS SAS.ALT LSVS.NLS DAASP.LP DATSPIVN DVVTT ELVVV.VGY.	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGDLIF.SMA TGDL.WGSLI IW.DVV AGQIL.TSII AGQ.IWQSLI TGSIGV .GRSF.EFA	L. ICG LY L. ICG LY L. ICG LY ALI AFY MIV GLY LTLAGFVTLY L FSIY L FSIY L FSIY L FSIY L FSIY L	TLFLVAELF TLFLVAELF TLFLVAELF TLFLIAEMY TLLLVVENY TLLLVVENY TVLLVIFIR TVFLIF.LG ICLLSVF.VS AVLGAAV.VY AAFGMV.SMY	LMF KFA LMF KFA LMF KFA LMF KFA LM IRFA LM QKYA LML AAI LMVQKVIKGP LLL KKI VLL YYF FVATRGYRYL
EcI Kp Yp Av EcII Rc VcI Aqa Ct Tm BsII Af StII Hs Stc Bp	. WLLRAALY . WLLRAALY . WLLRAALY . WULKFALY . WVLKFALY . WVLKFALY . WVLKALY FWWULKJEFY ILWILSF 	GIPLPWI GIPLPWI GLPLPW.I SLPLPW.I SLPLPW.I SLPLPW.I SLPLPW.I SUPLPW.I SVLCPE.L MTAGPFSLI AAVP.S	AVEROMFYAE AVEROMFYAE AVEROMFYAE AVEROMFYAE AVEROMFYAE ATOTOMFYAE AILECOMFYAE AILECOMFYAE AILECOMFYAE CONSTANTION CONSTANTION CONSTANTION	YGRQWAI. YGRQWAI. YGRQWAI. HGRQWAIG FGRQWATG GGRQWATG GGRQWATG GGRQWATG GGRQWATG GGRQWATG GGRQWATG GGRQWAI GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQWAI. GGRQ	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.VLPTH JLLPTA Y.ILKTK HLLKTS GLLYP.E	VVNS.SLT VANS.SLT VANS.SLT UANS.SVT LSAS.SLS SAHS.ALT LSVS.NLS DATSPIVN DVVTT ELVTV.VGY.	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGELLF.SMV TGDL.WGSLI TGDL.WGSLI TGQLAF.SLI AGQ.LWQSLI TGSIGV .GRSF.EFA	L.ICGLY L.ICGLY L.ICGLY L.ICGLY L.ICGLY MIVGLY LTLAGFVTLY LTLAGFVTLY LTLAGFVTLY LTLAGFVTLY LFSIF LFSIF	TLFLVAELF .TLFLVAELF .TLFLVAELF TLFLVAELF TLFLVAENY .TLLLVVEMY .TVLLVIENT FIVFLIF.LG FIVFLIF.LG FIVFLIF.LG AVLGAAV.VY AAFGMV.SMY	LMF KFA LMF KFA LMF KFA LMF KFA LM KFA LM QKYA LML ANI LMVQKVIKGP LLL KKI VLL YYF FVATRGYRYL
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EcI Kp Yp Av EcII Rc VcI Aqa Ct Tm BsII BsII Hs Stc Bp Pa	. WLLRAALY WLLRAALY .WLLRAALY .PWLLKPALY .WVLKMALW .WALRVAVF KPWVLKAALW .WLL.IIF 	GIPLPWI GIPLPWI GIPLPWI SIPLPWI SLPLPWI SLPLPWI SIPLPWI SIPLP.IV. SIPLP.IV. SUPLPE.L THEG.RE	AVERGMFYAE AVERGMFYAE AVERGMFYAE AVERGMFYAE ATQTGMFYAE ATQTGMFYAE AILGMFYAE AILGMFYAE GIEFGMIFAC VLGMYVRE 	YGRQUWAI. YGRQUWAI. YGRQUWAI. GRQUWAI. GRQUWAI. GRQUWTG FGRQUWTU GRQUWTU GRQUWTU TGRQUWTU TGRQUWTY.	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.VLPTH JLPTY 	VVNS.SLT VANS.SLT VANS.SLT LSAS.SLS SAHS.ALT LSVS.NLS DATSFIVN DATSFIVN LSVVTT ELVTV.VGY HAQAADRDOD	VGDLF.SMX AGDLF.SMV AGDLF.SMV AGELF.SMV TGDL.WGSLI TGQLAF.SLI IW.DVV  TGGL.WGSLI  TGSIGV  TGSIGV  GRSF.EPA   863 KRN	L.ICGLY L.ICGMY L.ICGLY L.ICGLY L.ICGLY LICGLY MIVGLY UTLAGFVLY LFSIY LFSIY LFSIY LFSIY	TLFLVAELF TLFLVAELF TLFLVAELF TLFLIAEMY TLFLIAEWY TLFLIAEVY TVLLVIFIR FIVFLIF LG ICLSVF VS AVLGAAV.VY AAFGMV.SMY	LMF KFA LMF KFA LMF KFA LMF KFA LM KFA LM CKYA LML AAI LMVQKVIKGP LLL KKI VLL YYF FVATRGYRYL
EcI Kp Yp Av EcII Rc VcI Aqa Ct Tm BsII BsII Hs Stc Bp Pa Sy	WLLRAALY WLLRAALY WLLRAALY PWLLKPALY WVLKMALW WALRVAVF KPWVLKAALW WALRVAVF KPWVLKALS.F .WLL.IIF .WLL.IIF .WLL.IIF 	GIPLPWI GIPLPWI GIPLPWI SLPLPWI SLPLPWI SLPLPWI SIPLPWI SIPLP.IV SVLCPE.L MTAGPFSLI AAVPS THEG.RE TLPAPRG.SE	AVERGMEYAE AVERGMEYAE AVERGMEYAE AVERGMEYAE ATCIGNEYAE AICIGNEYAE AICIGNEYAE AICIGNEYAE AICIGNEYAE AICIGNEYAE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE CREISHISTE	YGRQWAI. YGRQWAI. YGRQWAI. HGRQWAI. HGRQWAI. HGRQWAI. GRQWATVJ. VGRQWATVJ. VGRQWAVVY. VGRQWVVY. VGRQWVVY. NGRQWATVJ. STRARDISAA	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.VLPTH DLPTY G.LLPTA G.LLFTA LLKTS 	VVNS.SLT VANS.SLT VANS.SLT VANS.SLT UANS.SVT SAHS.ALT DASP.LP DATSPIVN DATSPIVN UVTT ELVIV.VGY.	VGDLF.SMV AGDLIF.SMV AGDLIF.SMV AGELIF.SMV TGDL.WGSLI TGDLAF.SLI IW.DVV 	L.ICGLY L.ICGMY L.ICGLY L.ICGLY L.ICGLY MIVGLY MIVGLY LTLAGFVLY LTLAGFVLY LFSIY LFSIY LFSIY	TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLVAENT .TLFLVAENT .TLFLVAENT .TVLLVIEIR FIVFLIF.LG ICLLSVF.VS 	LMF KFA LMF KFA LMF KFA LMF KFA LM KFA LM RFA LM QKYA LML AAI LMVQKVIKGP LLL KKI VLL YYF FVATRGVRYL
EcI Kp Yp Avv EcII Rc VcI Aqa CtI Tm BsII Hs StII StII StII Bs Stc Bp Pa Sy HNI VcII	. WLLRAALY WLLRAALY WLLRAALY WLLKPALY .WVLKMALW WVLKMALW WVLKMALW WLLKLFY ILWILSFY ILWILSFY G G G G 	GIPLPWI GIPLPWI GIPLPWI SIPLPWI SLPLPWI SLPLPWI SIPLPIV SULCPE.L 	AVERGMEYAE AVERGMEYAE AVERGMEYAE AVERGMEYAE AVERGMEYAE ATC1GMEYAE AIEGMEYAE AIEGMEYAE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CNEIGMISTE CN	YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. GRQWAI. GRQWAI. GRQWAI. GRQWAI. GRQWAI. YGRQWAI. YGRQWYY. YGRQWYY. YGRQWYY. YGRQWYY. YGRQWYY. YGRQWYY. YGRQWYY. YGRQWYY. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI.	CEVLPTA .GEVLPTA .GEVLPTA .GEVLPTA .GULPTA .GULPTA .GULPTA .GLLPTA 	VVNS.SLT VANS.SLT VANS.SLT VANS.SVT LSAS.SLS SAHS.ALT DATSPIVN DATSPIVN UVTTT ELVTV.VGY HAQAADRQD	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGDLIF.SMV AGELLF.SMV TGDL.WGSLI TGQLAF.SLI IW.DVV AGQLL.TSII AGQ.IWQSLI TGSIGV .GRSF.EFA 	L.ICGLY L.ICGLY L.ICGLY L.ICGLY L.ICGLY MIVGUY JTLAGFVIL LFSIY LFSIY LFSIY UFMSUIIAAI	TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLVAELY .TLFLVAENY .TLFLVAENY .TVLLVIEIT FIVFLIF.LG ICLLSVF.VS ANFGHV.SMY	LMF KFA LMF KFA LMF KFA LMF KFA LM TRFA LM QKYA LML AAI LMVQKVIKGP LLL KKI VLL YYF FVATRGYRYL
EcI Kp Yp Av EcII Rc Ct Tm BSII Af StII Hs Stc Bp Pa Sy HNI VcII Ef	.WLLRAALY .WLLRAALY .WLLRAALY .WLLKPALY .WVLKMALW .WALRVAVF .WVLKAALW RRWLLKLFPY ILWILSF .WLL. IIF 	GIPLPWI GIPLPWI GIPLPWI SIPLPWI SLPLPWI SLPLPWI SIPLPIV SIPLPIV SIPLPIV SUCCPE.L MTAGPFSLI AAVPS SIPLPIV SLCGUZE SLGUZE SLGUZE SPSSTKA DYEAK	AVERGEFVAE AVERGEFVAE AVERGEFVAE AVERGEFVAE ATQTSFVAE AILGONFVAE AILGONFVAE AILGONFVAE AILGONFVAE AILGONFVAE GIEFGENFFAC VLGENFVAE ASLMGTVTKH ASLMGTVTKH AL.AKEEPF.	YGRQWAI. YGRQWAI. YGRQWAI. GRQWYIG FGRQWYIG FGRQWYIV YGRQWYVY YGRQWVYY YGRQWVYY YGRQWVYY YGRQWVYY YGRQWVYY YGRQWYYY TGRQWYIY SALDYFDK.GV	GEVLPTA GEVLPTA GEVLPTA GEVLPTA GLPTA GLLPTA GLLPTA ,Y.ILKTK GLLPTA ,Y.ILKTK GLLYS GILYPS GILYPS 	VVNS.SLT VANS.SLT VANS.SLT VANS.SVT LSAS.SLS. SAHS.ALT LSVS.NLS. DASP.LP DATSPIVN ELVTV.VGY. HAQAADRDQD	VGDLF.SMS AGDLF.SMV AGDLF.SMV AGELLF.SMA TGDL.WGSLI TGQLAF.SLI AGQL.TSII AGQL.TSII AGQL.WGSLI TGSL.GV  GRSF.EFA  GRSF.EFA  B663 KRN	L.ICGLY L.ICGMY L.ICGLY L.ICGLY L.ICGLY LTLAGFVTLY LTLAGFVTLY LFSIIF LFSIIF LFSIIF	TLFLVAELF TLFLVAELF TLFLVAELF TLFLIAEMY TLLLIAEMY TLFLIAEWY TVLLVIEIR FIVFLIF.LG ICLLSVF.VS ANGANV.VY AAFGMV.SMY	LMF KFA LMF KFA LMF KFA LMF KFA LM TRFA LM QKYA LML AAI LMVQKVIKGP LLL KKI VLL YYF FVATRGYRYL
EcI Kp Yp Av EcII Rc VcI Aqa Aqa Ctt Tm BsII StII StII StI Bp Pa Sy HNI VcII Ef BsI	.WLLRAALY .WLLRAALY .WLLRAALY .WLLKAALY .WVLKMALW .WVLKMALW .WVLKAALW .WWLLAALW .WWLLAALW .WWLL.IIF 	GIPLPWI GIPLPWI GIPLPWI SIPLPWI SLPLPWI SLPLPWI SIPLPWI SIPLP.IV. SIPLP.IV. SUPLPE.L THEG.RE TLPAPRG.SE SLGVQE SLGVQE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SLGVPE SL	AVERGEFVAE AVERGEFVAE AVERGEFVAE AVERGEFVAE ATOTGEFVAE ATOTGEFVAE AIELGEFFAE GIEFGEFFAE GIEFGEFFAE GIEFGEFFAE TNPGGAGQK. ASLMCTVTKH SSA.GFX	YGRQUWAI. YGRQUWAI. YGRQUWAI. GRQUWAI. FGRQUWTG FGRQUWTG GRQUWTV YGRQUVY. YGRQUVY. YGRQUVY. TGRQUVY. TGRQUVY. STOPARPLSAA ETNRRPAELA ALDPFDK.GV	GEVLPTA GEVLPTA GEVLPTA GULPTA G.VLPTH LLPTA 	VVNS.SLT VANS.SLT VANS.SLT VANS.SLT LSAS.SLS SAHS.ALT DATSPIVN DATSPIVN DATSPIVN HAQAADRDQD	VGDLF.SMX AGDLF.SMV AGDLF.SMV AGELLF.SMV AGELLF.SMV AGELLF.SMV AGELLF.SMV AGELF.SMV AGELF.SMV AGELF.TSII AGE.WGSLI 	L.ICGLY L.ICGMY L.ICGLY L.ICGLY L.ICGLY LICGLY MIVGULY LTLAGFVLY LFSIY LFSIY LFSIY LFSIY	TLFLVAELF TLFLVAELF TLFLVAELF TLFLIAEMY TLFLVVEMY TLFLIAEVY TVLLVIFIR FIVFLIF LG ICLSVF VS AVLGAAV.VY AAFGMV.SMY	LMF KFA LMF KFA LMF KFA LMF KFA LM KFA LM CKYA LML AAI LMVQKVIKGP LLL KKI VLL YYF FVATRGYRYL
EcI Kp Yp Av EcII Rc Ct StII Afa StII StII StII Pa Sy HNII VCII BSII Smc Kt	.WLLRAALY .WLLRAALY .WLLRAALY .WLLKFALW .WVLKMALW .WALKVAALW .WALKVAALW RRWLLKLEFY .WLL.IIF .WLL.IIF .WLL.IIF .WLL.RG.P.V. RNG.PD.L R.G.E.L R.G.E.L KGG.P.V. RKGP.V.	GIPLPWI GIPLPWI GIPLPWI GIPLPWI SLPLPWI SLPLPWI SLPLPWI SIPLP.IV. SVLCPE.L 	AVERGMEYAE AVERGMEYAE AVERGMEYAE AVERGMEYAE ATQTGMEYAE ATQTGMEYAE AIEGGMEYAE AIEGGMEYAE AIEGGMEYAE GIEFGMIFAC VLGWYVRE CONTINUE SALGOVTKH SSA.GRW AL- CONTINUE KL.KKENEP. LE.H	YGRQUWAI YGRQUWAI YGRQUWAI HGRQUWAI HGRQUWIG. FGRQUWITUD. 	GEVLPTA GEVLPTA GEVLPTA GEVLPTA G.VLPTH DLPTY G.LLPTA 	VVNS.SLT VANS.SLT VANS.SLT VANS.SLT UANS.SVT SAHS.ALT LSAS.SLS. DASSP.LP DATSPIVN DATSPIVN UVVTT. ELVIV.VGY.	VGDLF.SMV AGDLF.SMV AGDLF.SMV AGELF.SMV AGELF.SMV AGELF.SMV AGELF.SMV AGELF.SMV AGGL.TSII AGQ.IWQSLI TGSIGV .GRSF.EFA 	L.ICGLY L.ICGMY L.ICGLY L.ICGLY ALIAFY MIVGUVLY LTLAGFVLY LFSIY LFSIY LFSIY	TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLVAENT .TLFLVAENT .TLFLVAENT .TVLLVIEIR .TVLLVIEIR .TVLLVIEIR 	LMF KFA LMF KFA LMF KFA LMF KFA LM TRFA LM QKYA LML AAI LMVCKVIKGP LLL KKI VLL YYF FVATRGVRYL
EcII Kpp Av EcIII Rc CtVcI Mr BSIII HS StII HS StII HS StII HS StII F BSII SMC F BSII SMC Mt Pa Q Ci	. WLLRAALY WLLRAALY WLLRAALY .WLLKPALY .WVLKMALW .WALRVAVF .WVLKAALW RRWLLKLFFY ILWILS. F G G G G G 	GIPLPWI GIPLPWI GIPLPWI GIPLPWI SIPLPWI SIPLPWI SIPLPWI AIVPOI SIPLP.IV SULCPE.L 	AVERAMEYAE AVERAMEYAE AVERAMEYAE AVERAMEYAE AILEANNEYAE AILEANNEYAE AILEANNEYAE AILEANNEYAE AILEANNEYAE AILEANNEYAE SILEANNEYAE SILEANNEYAE ASLMGTVIKH SSA.GRW AL	YGRQWAI. YGRQWAI. YGRQWAI. YGRQWAI. GRQWTIG FGRQWTVD YGRQWVY. YGRQWVY. YGRQWVY. YGRQWVY. YGRQWVY. YGRQWVY. YGRQWVY. YGRQWVY. YGRQWYY. YGRQWYY. YGRQWYY. YGRQWYY. YDPPSQE.Y STDPPSQE.V STDPPSQE.V	GEVLPTA GEVLPTA GEVLPTA GVLPTH G.VLPTH G.LLPTA G.LLPTA G.LLPTA G.LLPTA G.LLPTA G.LLPTA G.LLATS G.LLATS G.LLATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS G.LEATS	VVNS.SLT VANS.SLT VANS.SLT VANS.SVT SAHS.ALT LSAS.SLS. DASP.LP DATSPIVN DVVTT. ELVIV.VGY. 	VGDLLF.SMS AGDLIF.SMV AGDLIF.SMV AGDLIF.SMV AGDLLF.SMV AGDLLF.SMV AGDLLF.SMV AGDL.F.SMV TGDL.WGSLI TGDL.AF.SLI AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQIL.TSII AGQILF.SMV AGQILF.SMV AGQILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGILF.SMV AGGIL.TSII AGGIL.SMV AGGIL.SMV AGGIL.SMV AGGIL.SMV AGGIL.SMV AGGIL.SMV AGGIL.SMV AGGIL.SMV AGGIL.SMV AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AGGIL AG	L.ICGLY L.ICGLY L.ICGLY L.ICGLY L.ICGLY MIVGUY UTLAGFVL LTLAGFVL LFSSIY LFSSIY LFSSIY LFSSIY	TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLVAELF .TLFLVAENT .TLFLVAENT .TLFLVAENT .TVLVIENT .TVLVIENT .TVLVIENT 	LMF KFA LMF KFA LMF KFA LMF KFA LM TRFA LM QKYA LML AAI LMVQKVIKGP LLL KKI VLL YYF FVATRGVRYL
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TLFLVAELF TLFLVAELF TLFLIAEW TLLLVVEMY TLFLIAEW TVLLVIEIR TVLLVIEIR TVLLVIEIR AAFGMV.SMY	LMF KFA LMF KFA LMF KFA LMF KFA LM TRFA LM QKYA LML AAI LMVQKVIKGP LLL KKI VLL YYF FVATRGYRYL

Fig. 1 (continued).

the heme–copper oxidases, cytochrome bd oxidases do not pump protons [14]. The fact that the enzyme does not pump protons may contribute energetically to its high affinity for oxygen and high catalytic efficiency [15]. In general, relatively little is known about what advantages using a cytochrome *bd* terminal oxidase instead of a heme-copper oxidase confers on an organism. In *E. coli*, cytochrome *bd* may be im-

Table 1The reported sequences for cytochrome bd

Organism	Abbreviation	Domain	Classification	Q	Ref.
E. coli	EcI	Bacteria	D. Proteobacteria (Sc. gamma)	Yes	a
	EcII			Yes	b
A. vinelandii	Av	Bacteria	D. Proteobacteria (Sc. gamma)	Yes	с
H. influenzae	Hi	Bacteria	D. Proteobacteria (Sc. gamma)	Yes	d
A. actinomycetemcomitans	Aca	Bacteria	D. Proteobacteria (Sc. gamma)	Yes	e
K. pneumoniae	Кр	Bacteria	D. Proteobacteria (Sc. gamma)	Yes	f
S. typhimurium	StI	Bacteria	D. Proteobacteria (Sc. gamma)	Yes	g
	StII			-	h
Y. pestis	Yp	Bacteria	D. Proteobacteria (Sc. gamma)	Yes	i
V. cholerae	VcI	Bacteria	D. Proteobacteria (Sc. gamma)	Yes	j
	VcII			_	j
	VcIII			-	j
P. aeruginosa	Ра	Bacteria	D. Proteobacteria (Sc. gamma)	No	k
R. prowazekii	Rp	Bacteria	D. Proteobacteria (Sc. alpha)	-	1
R. capsulatus	Rc	Bacteria	D. Proteobacteria (Sc. alpha)	Yes	m
B. pertussis	Вр	Bacteria	D. Proteobacteria (Sc. beta)	_	n
C. jejuni	Ċj	Bacteria	D. Proteobacteria (Sc. epsilon)	Yes	0
M. tuberculosis	Mt	Bacteria	D. Gram-positive (Sd. High GC)	No	j
S. coelicolor	Smc	Bacteria	D. Gram-positive (Sd. High GC)	No	р
B. subtilis	BsI	Bacteria	D. Gram-positive (Sd. Low GC)	No	q
	BsII			No	r
S. carnosus	Stc	Bacteria	D. Gram-positive (Sd. Low GC)	_	s
E. faecalis	Ef	Bacteria	D. Gram-positive (Sd. Low GC)	No	j
C. trachomatis	Ct	Bacteria	D. Chlamydia	No	t
P. gingivalis	Pg	Bacteria	D. Bacteroides and Cytophagales	Yes	j
Synechocystis sp. strain PCC6803	Sy	Bacteria	D. Cyanobacteria	No	u
T. maritima	Tm	Bacteria	D. Thermotogales	-	j
A. aeolicus	Aqa	Bacteria	D. Aquificaceae	Yes	v
H. salinarium	Hs	Archaea	F. Halobacteriaceae	No	W
Halobacterium sp. NRC-1	HNI	Archaea	F. Halobacteriaceae	No	Х
	HNII			No	х
A. fulgidus	Af		F. Archaeoglobaceae	Yes	У

The abbreviations denote the different cytochromes bd, and are used in the text and in succeeding figures. Yp1 and Yp2 refer to two non-overlapping fragments. The classification follows that of Woese in [104] and [105]. The abbreviations used in the classification stand for Division (D.), Family (F.), Subdivision (Sd.) and Subclass (Sc.). Q indicates whether or not the sequence contains a 60-amino-acid region towards the C-terminal end of the Q-loop. (-) indicates that this portion of the sequence is not available. The sequence references are as follows: a GenBank: ECOCYD, D90713, ECAE000176, [71-73]; b GenBank: S63811, D90713, ECAE000176, [71,72, 87, 106]; <sup>c</sup>GenBank: AVICYDAB, [25]; <sup>d</sup>GenBank: HIU32787, [107]; <sup>e</sup>Actinobacillus Genome Sequencing Project, personal communication; <sup>f</sup>GenBank: KPCYDAB, [108]; <sup>g</sup>Genbank: AF001503, [17]; <sup>h</sup>GenBank: SYTRES, [109]; <sup>i</sup>These sequence data were produced by the Y. pestis Sequencing Group at the Sanger Centre and can be obtained from ftp.sanger.ac.uk/pub/pathogens/yp; <sup>j</sup>Sequence data were obtained through early release from The Institute for Genomic Research at www.tigr.org and/or through NCBI at www.ncbi.nlm.nih.gov.; <sup>k</sup>GenBank: PACIOAB, [22]; <sup>l</sup>GenBank: RPCYDB, RPZ82486, [110,111]; <sup>m</sup>http://capsulapedia.uchicago.edu/ capsulapedia/Searches/BLAST.shtml; <sup>j</sup>GenBank: MTCY01B2, [112]; <sup>n</sup>These sequence data were produced by the *B. pertussis* Sequencing Group at the Sanger Centre and can be obtained from ftp.sanger.ac.uk/pub/pathogens/bp. °These sequence data were produced by the C. jejuni Sequencing Group at the Sanger Centre and can be obtained from ftp.sanger.ac.uk/pub/pathogens/cj; <sup>p</sup>These sequence data were produced by the S. coelicolor Sequencing Group at the Sanger Centre and can be obtained from ftp.sanger.ac.uk/ pub/S\_coelicolor/sequences; <sup>q</sup>GenBank: D83026, [113,114]; <sup>r</sup>GenBank: AF008220, [113,114]; <sup>s</sup>GenBank: STAPTSIA, [115]; <sup>1</sup>Chlamydia Genome Project, personal communication; <sup>u</sup>GenBank: D90904, [116]; <sup>v</sup>GenBank: AE000736, [105]; <sup>w</sup>GenBank: HSTBP, [117]; <sup>x</sup>GenBank: AF016485; <sup>y</sup>Genbank: AF2297, [68].

										100
Pa	1 ~~~~~MMEY	AL	LOHYWWFLVS	LLGALLVFLL	G31 50 FVOGCOS	FLFSLG	KDELT	OKMMVNS.TG	RKWE	100
Cj	~~~~~MFF	GLELEG	LQIYWWLILS	LLGGLLVFMF	FVQGCQT	LIDELS	KDELE	KTMLVNS.LG	RKWE	
Yp2			~~~~~~~~	~~~~~~~~		~~~~~~~~	~~~~~~~	~~~~~~	~~~~~~	~~~~~~~
VC23 VCI	~~~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~~~~
StI	~~~~~MIDY	EVL	.RFIW.WL	LVGILLIGFA	VTDGFDMCVG	MLTRFLG	RNDTE	RRIMINS.IA	PHWDGNQVW.	
Kp	~~~~MIDY	EVL	.RFIW.WL	LIGILLIGFA	VADGFDMCVG	MLTRFLG	RNDTE	RRIMINA.IA	PHWDGNQVW.	
EcI	~~~~~.MIDY	EVL	.RFIW.WL	LVGVLLIGFA	VTDGFDMCVG	MLTRFLG	RNDTE	RRIMINS . IA	PHWDGNQVW.	• • • • • • • • • • • •
VcIII	~~~~~~	EV	~~~SS.W	GFA	ITDGFDMCVG	A LVPIIG	KNDIE	RRVMINS.IA	PHWDGNOVW.	
Hi	~~~~~MIDY	EFL	.RFIW.WV	LVIVLLIGFS	VTDGFDMCVT	ALLPVIG	KKEVE	RRIMINT.IA	PHWDGNQVW.	
EcII	~~~~ <b>MFDY</b>	ETL	.RFIW.WL	LIGVILVVFM	ISDGFDMCIG	CLLPLVA	RNDDE	RRIVINS.VG	AHWEGNQVW.	
Aca	~~~~~MFDY	EFL	.RFVW.WI	LVCVLLIGFA	VTDGFDMCV.	LSLLPFTG	KKEVE	KRIMINT.IA	PHWDGNQVWF	FIAMILVLAA
Rc	~MILHELLSY	DLL.	.RVIW.WV	LLGVLLIGLA	ATDGFDMCVA	ALNPFVA	KSDAE	RRVVINT. IG	PVWEGNOVW.	
Tm				~~~~~~~~	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~~~~~	~~~~~~~	~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~~
Ef	~~~~~.MSTL	QL	LW.FV	LIGVLFSGFF	FLEGFDFCVG	MAVQTLA	HNDDE.K	DQVVAT IG	PVWDGNEVW.	
BSI	~~~~~ M	F T.	LHDLW.FI	LVAVLEVGEE	FLEGFDFCVG	MATRFLG	HNELE.R	RVLINT.IG	PFWDANEVW.	
Mt	~~~~~~~	~~~~~MV	LOELW.FG.	VIAALFLGFF	ILEGFDFCVG	.MLMAP. FA	HVGMGDPETH	RRTALNT.IG	PVWDGNEVW.	
Rp	~~~~~~	~~~~~~~	~~~~~~~	~~~~~~~	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~~~~~~	~~~~~~~	~~~~NS.IA	PFWDGNETWL	v
Pa	~~~~~~~~~~	~MGID	LPLIW.AV	IIIFGIMMYV	VMDGFDLCIG	MLYPF.F	KDSGD	RDVMMNT.VA	PVWDGNETWL	V
VCII	MEDLE	~MMQY	LPEIY.LL	LLGFTVFMYA	VLDGYDLEVG	IL.LP.R	NDVAQ	RDRMIAS.IG	PFWDANE'IWL	V
Ada	~~~~~	~~~~~MEL	LPVIW.FV.	LLGFIIAMYA	ALDGFDLCVG	IVYPFLA	KDEEE	KRILLNS.IG	PVWDANEVWL	I
Ċt	~.MEFSLAT.	.IL	. PVVW. YV	ILCIAVFAYS	LGDGFDLCLS	TIY.FLS	KDEKE	RRLLLNS.IG	PVWDGNEVWF	v
HNI	MTDPLIPVDT	YLVDS	LPEVWFGA	VV FALGMY	IV.GFDFCIG	MLYA	. TRTDEHERE	LDTFL . AAFG	PVWDANEVWI	VAF
BsII	~~~~~MVQM	EIST.DALIA	ISIIWGFVF.	. I YA	VMATMDFCAG	FWSMIYLN	KEHMKATD	IANRFLS	PTWEVINVFI	VA
	1.01		577		150					
Pa	FTFTTL	VTFGGALFAS	FLFYSTSFG	GAYWVWM	LILECEIIO	AVSY . EYOSK	HGNVW.GRK	TYOTI	FING VLAPV	LLGTAV. STF
cj	LGFTTL	VLFGGAAFAA	FPLFYSTSFG	GAYWAWL	.CILFCFILQ	AVAY.EYRKK	. ENNVY . GSK	TYEIFL	KING.YLGVF	LIGVAV.SSF
Yp2	~~~~~~~			~~~~~~	~~~~~~~	~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~
VC23 VCI	~~~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~	~SLSGLIPPI.	LEGVAEGN L
StI	L	ITAGGALFAA	WEMVYAAAF.	SGFYVAM I	. LVLASLFFR	PVGL.DYRSK	IEDPRWR.NM	.WDWGV	FIGNF.VPPL	VIGVAFGN.L
Kp	L	ITAGGALFAA	WPMVYAAAF.	SGFYVAMI	. LVLASLFFR	PVGF . DYRSK	IEDNRWR.NM	.WDWGI	FVGSF.VPPL	VIGVAFGN.L
EcI Vn1	L	ITAGGALFAA	WEMVYAAAF.	SGFYVAMI	. LVLASLFFR	PVGF.DYRSK	IEETRWR . NM	.WDWGI	FIGSF.VPPL	VIGVAFGN.L
VcIII	L	ITAGGALFAA	WELVYATSF.	SGFYLAM I	. VTLAALWI.R	PVGL, DYRSK	TESTKWR NN	.WD	SASGE . IPPV	LEGVAEGN L
Hi	L	LTAGGAIFAA	WEIVYAVSF.	SGFYIAL V	. LVLAALFLR	PLGF . EYRAK	IDNPTWR.SV	.WDWGL	FAGGF . VPAL	VFGVAFGN . L
EcII	$\ldots \ldots L$	ILAGGALFAA	WERVYAAAF.	SGFYVAMI	.LVLCSLFFR	PLAF . DYRGK	IADARWR.KM	.WDAGL	VIGS.LVPPV	VFGIAFGN.L
Aca	LFFRPVGFEL	LTAGGAMFAA	WELVYATSF.	SG		YRAK	IDNPTWR.KA	.WDWGL	FIGG.SAPSL	VSRV*WEN.L
AV RC	L	ITAGGALFAA ILCCCATFAA	WELVYATAF.	SGMYWAL.L	LVLFGLFFR	PVGF . DYRSK	LENKKWR.DM	.WDWAL	LL.QVRLPAL	LFGVAFAN L
Tm	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~~~~~~~~~~~	~~~~ATSF.	SGSYLAM I	. VTLCALWLR	LVGL . DYRSK	IESTKWR.NN	.WDLAI	SASGF . IPPV	IFGVAFGN.L
Ef	L	LTAGGAMFAS	FEYWYASLF.	SGYYLILF	TI.LFGLIIR	GVSF.EFRHN	MPEGKRR . RM	.WNWTL	SIGSFLVP.F	FFGILFIS.L
BsI	L	LTGAGAIFAA	FENWYATM.L	SGYYIPF	VIVLLALMGR	GVAF.EFR	GKVD . HL	KWVKVWDWVV	FFGS.LIPPF	VLGVLFTT.L
Mt	Ľ	ITAGGATFAA	FREWIATUF	SALVIPL I.	AT LEGMILE	GVAF.EIRVK	CKID DP	KWRTGADEGI	ALCSWI. PAL	LWGVAFGN.I
Rp	L	GGGGLFAA	FFLAYSILMS	AL.YIPII.L	MLLGLIFR	GVAF . EFRFK	AHIGH.RC	IWDYSF	HF.GSMLAVF	CQGLMLGT . F
Pa	L	GGAALFGA	FPLAYAVVLS	AL.YLPLI.F	MLVGLIFR	GVAF . EFRFK	AKPAKQH	IWDKAF	IG.GSLVATF	FQGVALGA . F
VcII	L	. AVGILLIA	FFTAHSLIFT	EL.YLPTA.L	MLIALIMR	GVAF . DFRAK	AK ADH . KD	HWDLCF	KI.GSLLAAL	TQGYMIGR Y
aga Aga		AGGALFAA	FEVAVATION	GL VLPVI L	ILFMI.TLR	AVSF.EFR.	EN. ANK KL	WINIAF	GV.GSFLAAL	LEGLTLON V
Ct	I	MFAG. LFAG	FETAYGTLL .	SIFYMPI	WTMVMLYIFR	GCSL . EFRSK	AE SNRWKL	FWDVLF	SISGMSI.SF	FLGTLAGN.L
HNI		GTMLLAA	FPRVYSRLLA	DNYLLALGFV	VALVFR	GLG.PELREQ	REDER	.WKRYTDYAF	. VGGSVFAPL	LLGMLAGRWL
BsII	• • • • • • • • • •	IVVALFSF	FPGATFV	LGTVL.LIPG	SMILLLLAIR	S.GFLVFSNT	AKERK	TLRYISG.	. ISGFIIPAI	LILV.LPV
	201				250					200
Pg	FTGSSFVVNK	MAMFDLSGGN	QIVSAWQPFN	GWQLRGLEAV	LNLWNVVLGL	AVFFLARV	SALLYF. INN	IDDES.LYAA	AKR	RLWANTVAFL
Cj	FSGSEFILNE	H	NFVS.WQN	PLHGLELL	LNPFNYLLGL	ALVFLARL	LGAAYF.MNN	INDEN.IKIR	AMK	KLMINSILFL
Vc23	~~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~~	~~~~~~~~~~~	~NPCGWLDGI	VSLTMLVT	QGATYLQMR.	TRGERHLR	SRKAAQI	SALVMSV
VcI	MHRLPFSL	NA	LL.MV DYH	GSFIDL	ITPFSVLSGG	IGV. LMALV	OGSAWLTLK .	TSDILHKK	ARLTAOI	SVLCLFG
StI	LQGVPFHV	DE	YLRLYXT	GNFFQM	LKPXGLLTGI	VSV.GMI.IT	QGATYLXXR.	TVGELHLR	ARATSQI	AALVTLV
Kp	LOGVPFHV	DE	YLRLYYT	GNFFQL	LNPFGLLAGI	VSV.AMI.LT	QGATYLOMR .	TVGELHLR	TRSVSTV	PALVTLI
Yp1	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~				~~~~~~~~~~~	vsv.GM1.11	QGATTLQMR.		1KA1AQV	
VcIII	LQGVPF	Q	. LS~~~~~~	~~~~~	~~~~~~		~~~~~~	*****	~~~~~	~~~~~~~~~~
H1 FCII	LQGVPFHF	NE	LTQV. TYT	GSFFEL	LNPFALLCGV	ISLS. MLVT	HGANWLOMK .	TTEALRDR	ARTVSQIG	SIVTLI
Aca	LHGVTLEL		LQQV. QYT	GTFFGL	LNPFALLCGV	ISLA. MLTT	HGANWLOMK .	TTSELRAR	ACVISOVG.	ATVTLI
Av	FLGLPFRL	DE	TMR.T. HFE	GSFFSL	LHPFALLAGV	VSLS. MLCA	HGGSWLMLR.	TEGDLYER	SCKATRL	SAIVFLG
Rc	LOGVPFTL .	DE	TL.LP. VYP	GNPLTKLLGL	LNPFALFVGV	VSL.SMH.IA	HGAAWLVLK.	TEGAVQAR	ARRIGSW	AGVLTIV
Ef	VQGMP.L.		N	GNMHAQFTDY	FNLFSIVGG.	VAL. TLLCYL	HGMNYIALK.	TEGPIRER	ARNYAEILYG	VLYIGLVV
BsI	FRGMP I	DA	DM	.NIHAHVSDY	INVYSILGG.	VTV.TLLCFQ	HGLMFITLR.	TIGDLQNR	ARKMAQKIMG	VVFVAVL
Smc M+	VHGVEI VRGLP V	DR	DLEYV	GSVWDL	LNPYALLGGL	VTL.TLFTF.	HGTVFTALK.	TVGEIRER	ARTLA	. LRVGLVTAV
Rp	V	.QG	IVIDGR	.QFAGGSFDF	LTPFSVMTGI	ALIF.GYALL	.GATWLILK.	TENKTO	DWAYKSAL	YILFYV
Pa	I	.EG	IPVENR	.SFAGGSLDW	IAPFPLFCGL	ALIV.AYTLL	.GCTWLIMK	. TEGRLQER	MHDLARPLAL	.VLL
VcII	VVGF	.ES F C	AP EAY	A.FA.	VLSAL	CVAA.AYVYI	. GGAWLVLK .	TEGELQ . V	VPRVGRV	KQDGWR
Aqa	IKGLPVKLVE	KELYGEVVKT	HMICA. DOD	CSYTGLLINI	LDPYALLVAL	.LTV.SFVAM	HGAIYAAYV.	TNGDLSHR	AASLAKKL.	WFNS
Ċt	LVGFPI	APDT	sŶ.	SSLSWKLF.	FRPYPVLCGL	FVV.TAFAL.	HGISFALMK.	. TTEG . LHER	LKNKFSY.	VLSSYLVLYL
HNI Bsit	FAGATLPVVL THG.GF.IFK	T DGT	T	G	PNAYSET OF	VAVSIV	TG. FLAAK.	TDSGLASE	LRSYG YRAYR¥	VGAAATV
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Fig. 2. Cytochrome bd subunit II alignment. Created using the same parameters as in Fig. 1.

portant during the transition between anaerobic and aerobic growth conditions, presumably scavenging deleterious molecular oxygen and other reactive oxygen species from the cell [16]. Other intriguing roles of cytochrome *bd* are also slowly coming to light. For example, in the alimentary tracts of young chickens, non-virulent strains of *Salmonella typhimurium* must have a functional cytochrome *bd* in order to

	301				350					400
Pa	IFFLAYIAFL	LTTEGFAV	N	PVSKEVYMEP	YKYLYNFLD.	MPAVLAVFL.	LGVILV.LG.	GI.GLTLLRK	GFKRGIWLHG	TGTVLTVLAL
ci	PFFLGFLAWI	FLKDGFSV	DTN	GVVSMSA	NLYLYNFLNO	M IFAVLLV	IGVILVLLG.	MVQG.TK	GCSKAIFTLG	LGTVLTVFAL
Yp2	AFLLAGIWLV	KGIDGFVITS	VLD.TAAESX	PMRKEVAHQA	GAWLINFNKY	PILWALPA	LGVILPLF	TILLS	RFEKGAWAF.	LFSSLTIACV
Vc23	~~~~~~~	~~~~~~		~~~~~~~	~~~~~~~~	~~~~~A	LGVSMPLL	SVLAS	RLDKGGLAF .	LTSSLGNAGV
VcI	LFIIGG.FMV	HGMNGYLIVS	SLD.YNAISN	PLNKVVFQQA	GAWLTNFERY	PWMWFA.P.	MGGLMMA M	GVFLSA	KWKNDAITF.	VCASVTNACI
StI	CIALAGVWVM	YGIDGYVVTS	AIDHHTA.SN	PLTKEVARET	GAWLVNFNNA	PILW.LV.PA	LGVVLPLL	TILTSR	. MEKGAWAF .	LFSSLTLACI
Kp	CFALAGVWVY	YGIDGYVVKS	VMD.HTGPSN	PLTKEVAREA	GAWMVNFNNM	PALW.AI.PA	LGPWLPLL	TVISTK	. ADKGAWAF .	LFSSLTLACI
EcI	CFALAGVWVM	YGIDGYVVKS	TMDHYAA . SN	PLNKEVVREA	GAWLVNFNNT	PILW.AI.PA	LGVVLPLL	TILTAR	. MDKAAWAF .	VFSSLTLACI
Yp1	~~~~~~~~~~	~~~~~~~	~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~~~	******	~~~~~~~
/cIII	~~~~~~~	~~~~~~~~~	~~~~~~~~~	~~~~~~	~~~~~~~	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~		~~~~~~~	~~~~~~~~~	~~~~~~~~~~
H1	AFVLAGVW.L	YSKDGYVVTS	TIDHF.APSS	PMNKEVAVET	GAWFRNFNEM	PILW IFPA	LAVVAALL.	NAAFS	KANRCGFAF.	FFSALTMAGV
FGII	CFLLAGYWLW	VGIDGFVLLA	Q.DA.NGPSN	PLMKLVAVLP	GAWMNNFVES	PVLW. IFPL	LGFFCPLL	TVMAI	YRGRPGWGF.	LEASLIGEGV
Aca	APVLAGVWLS	F. KDGFVVTS	VIDH.NAPSN	PIGKEVAVQA	GAWFNNIKEM	PILW. LFPV	LAVGGALL.	NAIPS	KANKCGFAF .	LOTELATICA
RC RC	TENI NOUNILA	ECIDAVOEVE	ADDD LCDCM	DITERNAR	CENTDAYOTE	PL. IQPAPL	LGLVG. GAL	INT MP	L WCCWAV	TASMICIECU
Tm	CEVAAGEWUO	H TROUMING	ATDONAA SN	PLDSEVVR.G	GSWIDNIQIK	F WIAVAFA	D. AVDGDGGA	VVD. PIK	.D. NSGNAV.	TASHIGITGV
Ff	FAV LM	V FKT	DEVE KN	F AVT	T.T	LTT.ATV	VI.TVIA N.V.	GVEKBK	FMLAF	LASGLELANT
BST	AFA AL	SAVOT	D	MF T		REGETTIPLA	VIJVICEMLA	AVETRKKKDG	WTFG M	TGAGLALT
Smc	LALA. FLL	WTOA	DSGDA KS	. I VA		VAVAAL	VAALMA, NOA	G	EGWSE	ALSGVTIVAA
Mt	GFGL	WTOL AY	GKDWT	WLVLAVAGCA	0A		VL	. VW. RRVSDG	WAF.	MCTLIVVAAV
Rp	ALFMG.L.VS	LSAPFLNNYI	NHRWFS	M	PN.I.Y.YL	SII. PIITV	LI.FIKLI.	KAIKO	K. KEVKPF.	IY. TILLFL
Pa	AI.IG.V.VS	LWTPLAHAEI	AARWFS	L	PN.L. FWFL	P.V. PIL.V	LVTFYALL	RSVAN	N DHVKPF .	VLTLVLIF
VcII	R~~~~~~~	~~~~~~~~~	****	~~~~~~~~~	~~~~~~~		~~~~~~~~~	~~~~~~~~~~	~~~~~~~~	~~~~~~~~~
Sy	TLAGA.VFIT	ISTPAFSEEA	RAQLFT	A	PL.VYIF.	AAIPLVGL	LFIGL.LL	RSLYL	R EENTPI.	IWTFLVFS
Aqa	ALLYLIVH	ILTMIYHPLL	IKNYFT		.R.MFIF.	PALPIV	IVAFITII	VALNR	QKYSLAF.	WSSTAMIF.
Ct	SLLIATI.L.	.GMPQT	LG	VCCRIEGA	PG.IPAY	PLII	LLSVVTLSCC	. YAEKRAV	SIGKYGKAF.	VLSCINL
HNI	AY . LGGVVVL	LGT		VVATDA	GGAASAVLSL	PVAAVVA	LSIVAGLGG.	SVLARRGRYR		LASALALP.T
BsII	GPISLL	FAVCIMVT		MRNEA	N.WLYSGMMN	DFSWI.IASF	ITFVIA.GIA	LFLPNKSFGQ	NIGKPRLALV	AIGIQYF
					150					501
<b>D</b> -	401		WDI O		450					501
Pg	401 LLVAGWNDTS	W.YPST	YDLQ	SSLTIENASS	450 SHFTLKVM	SYVS.LLIP	FVLAYIFYA.	WRALD.I	RKITKKEM	501 EQDDHVY
Pg Cj Vp2	401 LLVAGWNDTS LSSIGLGQSA LLTAGYY	W.YPST F.YPSL	YDLQ SDLQ	SSLTIENASS SSLTLKNASS	450 SHFTLKVM SYYTLSVM.	SYVSLLIP AYVSLLVP	FVLAYIFYA. FVLAYIIYV.	WRALD.I WNAMDKV	RKITKKEM KITREEI	501 EQDDHVY~~~~ ANDDHAY~~~~
Pg Cj Yp2	401 LLVAGWNDTS LSSIGLGQSA ILTAGXX	W.YPST F.YPSL .XFPFVMPSS MEPEVMPSS	YDLQ SDLQ TMPN L. NPA	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTMWDATS	450 SHFTLKVM SYYTLSVM SLLTLKVMT. SOVTLELMT	SYVSLLIP AYVSLLVP IVAIIFVP	FVLAYIFYA. FVLAYIIYV. IILLYTSWCY	WRALD.I WNAMDKV XKMF VK MF	RKITKKEM KITREEI GRIDKEFI CR LDDKFI	501 EQDDHVY~~~~ ANDDHAY~~~~ ENNKHSLY~~~
Pg Cj Yp2 Vc23 Vc1	401 LLVAGWNDTS LSSIGLGQSA ILTAGXX IFTAGFA LLTAGFA	W.YPST F.YPSL .XFPFVMPSS .MFPFVMPSS MFPFTMPSS	YDLQ SDLQ TMPN LNPA F FPS	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTMWDATS HSLTLWDATS	450 SHFTLKVM SYYTLSVM SLTLKVMT. SQVTLELMT. SEPTILLIMT	SYVSLLIP AYVSLLVP .IVAIIFVP .VVAVVMVP CVAFVMIP	FVLAYIFYA. FVLAYIIYV. IILLYTSWCY IILGYTIWSY	WRALD.I WNAMDKV XKMF YKMF PT.ME	RKITKKEM KITREEI GRIDKEFI GRLDDKFI GR.LDKOYI	501 EQDDHVY~~~~ ANDDHAY~~~~ ENNKHSLY~~~ EDNKNSLY~~~
Pg Cj Yp2 Vc23 VcI StI	401 LLVAGWNDTS LSSIGLGQSA ILTAGXX IFTAGFA ILTAGFA	W.YPST F.YPSL .XFPFVMPSS .MFPFIMPSS .MFPFIMPSS	YDLQ SDLQ TMPN LPPS FEPS TMMN.A.	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTLWDATS SLAWWDATS	450 SHFTLKVM SYYTLSVM SLTLKVMT. SQVTLELMT. SERTLNIMT. SOMTLN.LM.	SYVSLLIP AYVSLLVP IVAIIFVP VVAVVMVP GVAFVMLP TWVA.AVLVP	FVLAYIFYA. FVLAYIIYV. IILLYTSWCY IILGYTIWSY IILFYTAFSY IILIYTSWCY	WRALD.I WNAMDKV XKMF YKMF. RTMF. WKMF.	RKITKKEM KITREEI GRIDKEFI GRLDKEYI GRLDKQYI GRIAREHI	501 EQDDHVY~~~~ ANDDHAY~~~~ ENNKHSLY~~~ ERNHHSLY~~~ ESNTHSLY~~~
Pg Cj Yp2 Vc23 VcI StI Kp	401 LLVAGWNDTS LSSIGLGQSA ILTAGXX IFTAGFA ILTAGFA ILTAGIA	W.YPST F.YPSL XFPFVMPSS MFPFVMPSS MFPFIMPSS MFPFVMPSS	YDLQ SDLQ TMPN LNPA FEPS TMMNA	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTMWDATS SLAMWDATS SLAMWDATS	450 SHFTLKVM. SYYTLSVM. SUTLKVMT. SQVTLELMT. SQNTLN.IM. SQNTLN.LM. STLTLN.VM.	SYVSLLIP AYVSLLVP VAIIFVP VVAVVMVP GVAFVMLP TWVA.AVLVP TYVA.IVFVP	FVLAYIFYA. FVLAYIIYV. IILLYTSWCY IILGYTIWSY IILFYTAFSY IILLYTSWCY IILLYTWCY	WRALD.I WNAMDKV XKMF YKMF WKMF WKMF.	RKITKKEM KITREEI GRIDKEFI GRLDDKFI GRLDKQYI GRIAREHI GRITREDI	501 EQDDHVY ANDDHAY ENNKHSLY ESNTHSLY ESNTHSLY EXNTHSLY
Pg Cj Yp2 Vc23 VcI StI Kp EcI	401 LLVAGWNDTS LSSIGLGQSA ILTAGXX ILTAGFA ILTAGIT ILTAGIA	W.YPST F.YPSL .XFPFVMPSS .MFPFVMPSS .MFPFIMPSS .MFPFVMPSS .MFPFVMPSS	YDLQ TMPN LNPA FEPS TMMNA. TAMNA.	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTLWDATS .SLAMWDATS .SLTMWDATS	450 SHFTLKVM SYYTLSVM. SLLTLKVMT. SQVTLELMT. SQMTLN.LM. STLTLN.VM. SOLTLN.VM.	SYVSLLIP AYVSLLVP VAVIFVP VVAVVMVP GVAFVMLP TWVA.AVLVP TYVA.IVFVP TWVA.VVLVP	FVLAYIFYA. FVLAYIIYV. IILLYTSWCY IILGYTIWSY IILFYTAFSY IILIYTSWCY IILLYTAWCY IILLYTAWCY	WRALD.I WNAMDKV XKMF YKMF WKMF WKMF WKMF.	RKITKKEM KITREEI GRIDKEFI GRLDDKFI GRIAREHI GRIAREHI GRITKEDI	501 EQDDHVY ANDDHAY EDNKHSLY ERNHHSLY ERNTHSLY ERNTHSLY ERNTHSLY
Pg Cj Yp2 Vc23 VcI StI Kp EcI Yp1	401 LLVAGWNDTS LSSIGLGQSA ILTAGXX IFTAGFA ILTAGFA ILTAGIA ILTAGIA	W.YPST F.YPSL .XFPFVMPSS .MFPFIMPSS .MFPFVMPSS .MFPFIMPSS .MFPFVMPSS	YDLQ SDLQ TMPN LNPA FEPS TMMNA. TAMNA. TMMNA.	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTLWDATS .SLAMWDATS .SLTMWDATS	450 SHFTLKVM SYYTLSVM. SLUTLKVMT. SQVTLELMT. SERTLNIMT. SQMTLN.LM. STLTLN.VM. SQLTLN.VM.	SYVSLLIP AYVSLLVP IVAIIFVP GVAFVMLP TWVA.AVLVP TVVA.IVFVP TWVA.VVLVP	FVLAYIFYA. FVLAYIIYV. IILLYTSWCY IILGYTIWSY IILFYTAFSY IILIYTSWCY IILLYTTWCY IILLYTAWCY	WRALD.I WNAMDKV XKMF YKMF WFMF WKMF WKMF	RKITKKEM KITREEI GRIDKEFI GRLDDKFI GRIAREHI GRITREDI GRITREDI	501 EQDDHVY ANDDHAY EDNKHSLY ERNHHSLY ERNHHSLY ERNTHSLY ERNTHSLY
Pg Cj Yp2 Vc23 VcI StI Kp EcI Yp1 VcIII	401 LLVAGWNDTS LSSIGLGQSA ILTAGXX ILTAGFA ILTAGFA ILTAGIA ILTAGIA	W.YPST F.YPSL .XFPFVMPSS .MFPFVMPSS .MFPFIMPSS .MFPFVMPSS .MFPFVMPSS	YDLQ SDLQ TNPA FPPA TMMNA. TMMNA. TMMNA.	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTMWDATS SLAMWDATS SLAMWDATS SLTMWDATS	450 SHFTLKVM SYTLSVM SLLTLKVMT. SQVTLELMT. SQNTLN.LM. SQLTLN.VM. SQLTLN.VM.	SYVSLLIP AYVSLLVP VAIIFVP VAVVMVP GVAFVMLP TWVA.AVLVP TWVA.IVFVP TWVA.VVLVP	FVLAYIFYA. FVLAYIIYV. IILLYTSWCY IILGYTIWSY IILIYTSWCY IILIYTSWCY IILLYTAWCY	WRALD.I WNAMDKV XKMF. YKMF. WKMF. WKMF. WKMF.	RKITKKEM KITREEI GRIDKEFI GRLDDKFI GRLDKQYI GRIAREHI GRITREDI GRITKEDI	501 EQDDHVY ANDDHAY ENNKHSLY ESNTHSLY EKNTHSLY EKNTHSLY
Pg Cj Yp2 Vc23 Vc1 StI Kp EcI Yp1 VcIII Hi	401 LLVAGWNDTS LSSIGLQSA ILTAGX ILTAGFA ILTAGFA ILTAGIA ILTAGIA ILTAGIA IITAAVS	W.YPST F.YPSL .XFPFVMPSS .MFPFIMPSS .MFPFIMPSS .MFPFIMPSS 	YDLQ SDLQ HPA FPS TMMNA. TMMNA. TMMNA.	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTWWDATS HSLTLWDATS SLTMWDATS SLTMWDATS QSLLMWDSTS	450 SHFTLKVM. SYYTLSVM. SLITLKVMT. SQVTLELMT. SQTTLN.LM. STLTLN.VM. SQLTLN.VM. SELTLTLML.	SYVSLLIP AYVSLLVP VVAITFVP .VVAVMVP GVAFVMLP TWVA.AVLVP TYVA.IVFVV IFAVVFVV	FVLAYIFYA. FVLAYIIYV. IILJYTSWCY IILFYTAFSY IILJYTSWCY IILLYTSWCY IILLYTAWCY IILLYTWCY IALAYTIWSY	WRALD.I WNAMDKV XKMF YKMF. WKMF. WKMF. WKMF. SKMF.	RKITKKEM KITREEI GRIDKFI GRLDKFI GRLDKQYI GRIAREHI GRIAREDI GRITREDI GRILANFI	501 EQDDHVY ANDDHAY ENNKHSLY ERNHHSLY ERNTHSLY ERNTHSLY DKNKHSLY
Pg Cj Yp2 Vc23 Vc1 StI Kp EcI Yp1 VcIII Hi EcII	401 LLVAGWNDTS LSIGLQSA ILTAGKA ILTAGFA ILTAGFA ILTAGFA ILTAGIA ILTAGIA ILTAGIA ILTAGIA IITAAVS IFTAGIT	W.YPST F.YPSL XFPFVMPSS .MFPFVMPSS .MFPFVMPSS .MFPFVMPSS .MFPFVMPSS 	YDLQ SDLQ TMPN FPPA FPA FPA TMMNA. TAMNA. TMMNA. SHPE SHPE VSPI	SSLTIENASS SSLTLKNASS VSLTWWDATS HSLTMWDATS HSLTLWDATS SLATWWDATS SLTWWDATS QSLLMWDSTS	450 SHFTLKVM SYYTLSVM SULTLKVMT. SQVTLELMT. SQVTLELMT. SQMTLN.LM. STLTLN.VM. SQLTLN.VM. SELTLTLML. SQLTLSIML.	SYVSLLIP AYVSLLVP .IVAIIFVP .VVAVVMVP .GVAFVMLP TWVA.VLVP TYVA.IVFVP TWVA.VVLVP IFAVVFVV .VIVLIFLP	FVLAYIFYA. FVLAYIIYU. IILLYTSWCY IILGYTIWSY IILGYTIWSY IILIYTSWCY IILAYTTWCY IILAYTTWCY IILAYTWCY IILAYTWSY IVLLYTWSY	WRALD.I WNAMDKV XKMF. YKMF. TMF. WKMF. WKMF. XKMF. SKMF. XKMF.	RKITKKEM KITREEI GRLDKEFI GRLDKCFI GRLDKQYI GRIAREHI GRITREDI GRITREDI GRLDANFI GRLDANFI GRLDANFI	501 EQDDHVY ANDDHAY EDNKHSLY ERNHHSLY ERNTHSLY EKNTHSLY EKNTHSLY EKNTHSLY DKNKHSLY DKNKHSLY
Pg Cj Yp2 Vc23 VcI StI Kp EcI Yp1 Hi EcII Hi EcII	401 LLVAGWNDTS LSIGLGQSA ILTAGXX ILTAGFA ILTAGIA ILTAGIA ILTAGIA IITAGIT IFTAGIT ILTAAIA	W.YPST XPPFVMPSS MFPFVMPSS MFPFVMPSS MFPFVMPSS MFPFVMPSS MFPFVMPSS LFPFVMPSS LFPFVMPSI	YDLQ TNPA LNPA FEPS TMMNA. TAMNA. TAMNA. SHPE SHPE SHPE	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTIWDATS SLTMWDATS SLTMWDATS SSLTMWDATS SSLLMWDSTS SSLLMWDSTS	450 SHFTLKVM. SLITLKVMT. SQVTLEIMT. SQUTLN.IM. STLTLN.VM. SQLTLN.VM. SELTLILM. SQLTLN.VM. SSLTLTLML.	SYVSLLIP AYVSLLVP .IVAIIFVP .VVAVMVP .GVAFVMLP TWVA.AVLVP TYVA.IVFVP IFAVVFVV VILVFLE .FFLSLIFVV	FVLAYIFYA. FVLAYIIYV. IILYTSWCY IILYTSWCY IILYTAFSY IILIYTSWCY IILYTWAY IALAYTWCY IALAYTWSY IVLLYTWSY IVLLYTWSY ILSYTWAY	WRALD.I WNAMDKV XKMF WKMF WKMF WKMF SKMF YKMF YKMF	RKITKKEM KITREEI GRLDKFI GRLDKYI GRLAKYI GRITREDI GRITREDI GRLDANFI GRMTTFTL GRMTTFTL GRSSFI	501 EQDHVV ENNKHSLY EDNKHSLY ENNKHSLY ENNTHSLY EKNTHSLY EKNTHSLY DKNKHSLY DKNKHSLY DKNKHSLY
Pg Cj Yp2 Vc1 StI Kp EcI Yp1 VcIII Hi EcIII Aca Av	401 LLVAGWNDTS LSSIGLQSA ILTAGXX ILTAGFA ILTAGIT ILTAGIA ILTAGIA IITAAVS IFTAGIT ILTAAIA ILTAAFA	W.YPSL XFPFVMPSS MFPFVMPSS MFPFVMPSS MFPFVMPSS MFPFVMPSS MFPFVMPSS LFPFVMPSS MFPFVMPSS MFPFVMPSS CSRSVMPSS	YDLQ SDLQ TNPA FPA FPS TAMNA. TAMNA. TAMNA. TAMNA. SHPE SHPE SHPE SHPE SHPE	SSLTIENASS SSLTLKNASS VSLTWUDATS HSLTLWDATS HSLTLWDATS SLATWUDATS SLTWUDATS SSLTLWDSTS SSLTLWDSTS SSLTLWDAYS	450 SHFTLKVM. SYYTLSVM. SULTLKVMT. SQUTLLNT. SQUTLN.UM. STLTLN.VM. SQLTLN.VM. SQLTLN.VM. SQLTLSIML. SKLTLTLM. SKLTLLM.	SYVSLLIP AYVSLLVP .IVAIIFVP .VVAVMVP .GVAFVMLP TWVA.AVLVP TWVA.IVFVP TWVA.IVFVP 	FVLAYIFYA. FVLAYIIYU. IILLYTSWCY IILFYTAFSY IILFYTAFSY IILLYTAWCY IILLYTAWCY IILLYTWSY IVLLYTUSY ILLSYTWSY ILLSYTWSY ILLSYTWCY	WRALD.I WNAMDKV. XK. MF. RT. MF. RT. MF. WK. MF. WK. MF. SK. MF. YK. MW. YK. MW.	RKITKKEM KITREEI GRLDKEFI GRLDKQYI GRLDKQYI GRITREDI GRITREDI GRLDANFI GRLDANFI GRIDSSFI GRIDSSFI GRLDSVTI	501 EQDDHYY ENNRHSLY ERNRHSLY ERNRHSLY ERNRHSLY ERNRHSLY RRNENLY DKNRHSLY EDIKNSLY EDIKNSLY
Pg Cj Yp2 Vc23 StI StI Kp EcI Hi EcII Aca Av Rc	401 LLVAGWNDTS LSSIGLGGSA ILTAGYA ILTAGYA ILTAGIA ILTAGIA ILTAGIA ILTAGIA ILTAGIA ILTAGIA ILTAGFA ILTAGFA ISTYGLS	W.YPST F.YPSL .XFPFVMPSS .MFPFIMPSS .MFPFVMPSS .MFPFVMPSS 	YDLQ SDLQ TNPA FEPS TMMN. A. TMMN. A. TMMN. A. SHPE SHPE SHPE L.V.SP.	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTLWDATS SLAMWDATS SLTMWDATS SSLTLWDATS SSLTLWDATS SSLTLWDATS SSLTIWDATS SSLTIWDAYS	450 SHFTLKVM. SLUTLKVMT. SQVTLELMT. SQMTLN.LM. SQLTLN.VM. SQLTLN.VM. SQLTLN.VM. SQLTLITLML. SKLPLITLM. SQKTLGIML. SQMTLF.IM.	SYVSLLIP AVVSLLVP VAIIFVP GVAFVMLP TWVA.AVLVP TWVA.VVLVP 	FVLAYIFYA. FVLAYIIYV. IILLYTSWCY IILSYTTWSY IILIYTSWCY IILLYTSWCY IILLYTWCY IILLYTWCY IILLYTWCY ILLSYTIWAY IILSYTIWAY IILSYTWAY	WRALD.I WNAMDKV XKMF. YKMF. WKMF. WKMF. SKMF. SKMF. YKMW. YKMW. YKMW. XKMF.	RKITKKEM KITREEI GR LDOKFI GR LDOKYI GR LARCHI GR IAREHI GR ITREDI GR ITKEDI GR MTTETL GR MITETL GR LDANFI GK LNDQTI GK VREEDI	501 EQDDHVY ENNKHSLY EDNKKSLY ERNIHSLY ERNIHSLY EKNTHSLY EKNTHSLY DKINKHSLY DLINSLY EDINSLY EANPHGLY SRIPNA.Y
Pg Cj2 Vc23 Vc1 StI KpI EcII Aca Aca Rc Tm	401 LLVAGWNDTS LSSIGLQSA ILTAGXA ILTAGFA ILTAGFA ILTAGIA ILTAGIA IITAAVS IFTAGIT IITAAVS IITAGFA ISTYGLS	W.YPST F.YPSL XFPFVMPSS MFPFIMPSS MFPFIMPSS MFPFVMPSS MFPFVMPSS LFPFVMPSS LFPFVMPSS CSRSVMPSS MFPFILPSS	YDLQ SDLQ TNPA FPPS TMMNA. TMMNA. TMMNA. SHPE SHPE SHPE SHPE SHPE SHPE SHPE S	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTWWDATS SLAMWDATS SLAMWDATS SLTMWDATS SSLTMWDATS SSLTLWDSTS SSLTIWDATS SSLTIWDAYS SSLTIWDAYS	450 SHFTLKVM. SLJTLKVMT. SQVTLELMT. SQVTLELMT. SQMTLN.LM. STLTLN.VM. SCLTLN.VM. SQLTLSIML. SQKTLSIML. SQKTLGIML. SQMTLF.IM.	SYVSLLIP AYVSLLVP .IVAIIFVP .WVAVMVP .GVAFVMLP TWVA.AVLVP TWVA.VVLVP 	FVLAYIFYA. FVLAYIIYV. IILYTSMCY IILFYTAFSY IILIYTSMCY IILIYTMCY IILLYTMCY IILLYTMSY IVLLYTLMSY ILLSYTIMAY IILGYTLMCY IILGYTLMCY	WRALD.I WNAMDKV XKMF RTMF. WKMF. WKMF. WKMF. SKMF. YKMK. YKMF. WRMW. 	RKITKKEM KITREEI GRIDKFI GRLDKYI GRIAREHI GRITREDI GRITREDI GRITKEDI GRLDANFI GRLDANFI GRLDASFI GRLDSSFI GK.LNQTI GKVREDI	501 EQDHYY ENNCHAY ENNCHASLY ERNTHSLY ERNTHSLY ERNTHSLY ERNTHSLY DKNKHSLY DKNKHSLY EANPHGLY SRNPNA, Y
Pg Cj Yp2 Vc23 Vc1 StI Kp EcI Yp1 VcIII Hi EcII Aca Acc Rc Tm	401 LLVAGWNDTS LSSIGLQSA ILTAGXA ILTAGFA ILTAGFA ILTAGIA ILTAGIA ILTAGIA IITAAVS IITAAJA ILTAGFA. ISTVGLS	W.YPST F.YPSL XFPFVMPSS MFPFIMPSS MFPFIMPSS MFPFIMPSS MFPFVMPSS LFPFVMPSS MFPFVMPSS MFPFVMPSS MFPFLMPSS MFPFLMPSS MFPFLMPSS LFPFVMPSL CSRSVMPSS	YDLQ SDLQ TMPA FEPS TMMN.A. TAMN.A. TAMN.A. SHPE SHPE SHPE I.DPA I.DPA.SA TIGS.EGF	SSLTIENASS SSLTLKNASS VSLTMWDATS HSLTMWDATS HSLTIWDATS SLATWOATS SLTIWDATS SSLTIWDATS SSLTIWDATS SSLTIWDATS SSLTIWDATS SSLTIWDATS SLTIWDATS	450 SHFTLKVM. SLITLKVMT SQVTLELMT. SQMTLNLM STLTLN.VM. SQLTLN.VM. SQLTLSIML SQLTLSIML SQLTLSIML SQLTLFLML SQLTLFLML SQLTLFLML SQLTLFLML SQLTLFLML	SYVSLLIP AVVSLLVP .VVALIFVP .VVALVAVMVP .GVAFVMLP TWVA.AVLVP TWVA.VVLVP 	FVLAYIFYA. FVLAYIIYV. IILYTSWCY IILFYTAFSY IILFYTAFSY IILIYTSWCY IILLYTAWCY IILLYTIWAY ILLSYTIWAY IILSYTIWAY IILSYTSWY FVLAYTAWSY	WRALD.I WNAMDKV XKMF YKMF WKMF WKMF SKMF XKMM YKMW YKMW YKMW YKMW YIF.R	RKITKKEM KITREEI GR LDKFI GR LDKFI GR LDKYI GR IAREHI GR ITREDI CR LDANFI GR ITREDI CR LDANFI GR IDSSFI GK LNDQTI KK I.SQTA	501 EQDDHY ANDDHAY ENNKHSLY ERNIHSLY ENNTHSLY ERNIHSLY DKINKHSLY EDINSLY EDINSLY EANPHGLY SRIPNA, Y
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Fig. 2 (continued).

suppress growth and colonization by virulent *S. ty-phimurium* strains [17]. Also, increased production of cytochrome *bd* in *Klebsiella pneumoniae* elevates the level of nitrogen fixation by the organism [18]. Although immunological studies have indicated for some time that cytochrome *bd* is relatively wide-spread among the Gram-negative bacteria [19], the lack of sequence data has hampered studies on cytochrome *bd*.

The two-dimensional topology of cytochrome *bd* has been predicted based on Kyte–Doolittle [20] and Goldman–Engleman–Steitz [21] hydropathy plots of the amino acid sequence [22–26]. Subunit I was predicted to contain seven transmembrane helices with the N-terminus located in the cytoplasm and the C-terminus in the periplasm. Subunit II was predicted to have eight transmembrane helices with both termini found in the periplasm.

Partial proteolysis [27] and monoclonal antibody binding [28] studies found that a large, hydrophilic domain on the periplasmic side of the membrane [29] is necessary for quinol oxidation. This domain, known as the Q-loop, is located in subunit I, and covalent modification with a photo-reactive quinol analogue indicates that it contributes at least in part to the quinol binding site [30]. Proximity mapping using an artificial protease has demonstrated that the Q-loop is adjacent to a portion of the subunit II polypeptide located between the first two transmembrane spans [31]. Hence, this region of subunit II must also be located on the periplasmic side of the membrane.

Other approaches have also provided information about the protein topology. Based on thiol reactivity with Ellman's reagent [32], which reacts only with cysteines that are solvent accessible [33], none of the cysteines in the protein are solvent accessible. This would be consistent with a model in which the endogenous cysteines are all located in buried transmembrane regions of the protein [31]. The gene fu-



Fig. 3. Kyte–Doolittle hydropathy profiles. (A) *E. coli* cytochrome *bd*-I and (B) *B. subtilis* cytochrome *bd*-I. A window of 19 residues was used. Asterisk indicates transmembrane helices newly added to topology.

sion approach, using  $\beta$ -galactosidase [23] and alkaline phosphatase [26] fusions has provided considerable information about the topology of each of the two subunits. However, it has been noted that certain elements of these data do not fit the predictions based on the hydropathy profile for subunit I from *E. coli* [23,26].

The three-dimensional structure of cytochrome bd is known only at a very rudimentary level. It is a heterodimeric [34] integral membrane protein composed of subunits I and II, which are 58 and 43 kDa, respectively [35,36]. It contains three prosthetic groups: heme  $b_{558}$ , heme  $b_{595}$  and heme d. Hemes  $b_{558}$  and  $b_{595}$  are protoporphyrin IX while heme d is a chlorin [37].

Heme  $b_{558}$  is the initial electron acceptor from quinol [38]. Heme  $b_{558}$  is low-spin, six-coordinate and is located entirely within subunit I [39]. It has been shown that this low-spin heme has histidine/methionine ligation, with H186 in subunit I (I-H186) [40] and I-M393 [41] as the two axial ligands.

Hemes  $b_{595}$  and d appear to form a heme-heme binuclear center where the oxygen chemistry occurs [42,43]. Heme  $b_{595}$  is high-spin, five-coordinate and I-H19 has been proposed to be its axial ligand [40,44,45]. Heme d is high-spin and appears to be virtually always five-coordinate [45], even though this heme binds O<sub>2</sub>, CO and cyanide [46–52]. A protein-based axial ligand for heme d has remained enigmatic. Although electron nuclear double resonance (ENDOR) studies indicate that the ligand is not nitrogenous when heme d is oxidized [53], electron paramagnetic resonance (EPR) work suggests that when heme d is reduced the ligand is nitrogenous [43]. Another EPR study, on oriented bilayers, indicated that hemes  $b_{558}$  and d are oriented at an angle of 90° with respect to the plane of the membrane while heme  $b_{595}$  is at an angle of 60° [54].

Progress using site-directed mutagenesis as a probe of structure and function of cytochrome bd has been slow because the relatively few sequences that have been available until recently, are closely homologous, leaving a large number of apparently conserved residues, the mutagenic targets of choice. Recently, however, a substantial number of sequences encoding cytochrome bd have become accessible from numerous bacteria as well as several archaea. In this report, these sequences are used to re-evaluate the topology of subunit I of cytochrome bd, assigning it nine transmembrane helices instead of the previous seven. This revised topology is compatible with most of the available structural data, and suggests that all three of the heme prosthetic groups are located near the periplasmic side of the membrane. On the periplasmic edge of one of the new proposed transmembrane spans is a newly revealed conserved region of subunit I, containing the sequence GRQPW. This is the most conserved region of the protein and it is an obvious candidate for participating in either the binding of quinol, or possibly, heme d. Additionally, phylogenetic analyses suggest that cytochrome bd has been horizontally transferred between prokaryotes a number of times, producing an evolutionary tree substantially different from the canonical one based on 16sRNA.



Fig. 4. Topological model of cytochrome *bd*-I subunit I from *E. coli*. The shaded boxes show the location of predicted transmembrane helices. The periplasm and cytoplasm are denoted by 'out' and 'in', respectively. Completely conserved residues are shown with reverse contrast. *LacZ* and *PhoA* gene fusions with high activity are indicated. At the end (C-terminus) of helix VI and at the beginning of helix VII, the start and end, respectively, of the Q-loop are delineated with broad lines. The region of the Q-loop missing in several sequences is encircled.

# 2. Experimental procedures

#### 2.1. Sequence analysis

Homology searches were performed with the BLAST 2.0 program [55] accessible at the National Center for Biotechnology Information (URL: http:// www.ncbi.nlm.nih.gov) or using BLAST [56] in the GCG package (Wisconsin Package Version 9.0, Genetics Computer Group (GCG), Madison, WI). The TBLASTN method was used for all searches. Sequences were obtained from GenBank [57], The Institute for Genomic Research (TIGR), or other services (see Table 1). All sequences were inspected for frameshift errors and corrected when possible. Multiple sequence alignments of the cytochrome *bd* sequences were performed using the program Pileup in GCG. Gap creation and extension penalties used were 3.0 and 1.0, respectively. At certain regions, the alignments had to be adjusted manually using the sequence editor in GCG. The resulting alignments were submitted to two different algorithms for predicting transmembrane helices in membrane proteins based on multiple sequence alignments: PHDtopology [58–61] (URL: http://www.embl-heidelberg.de/ predictprotein/predictprotein.html) and TMAP [62] (URL: http://www.embl-heidelberg.de/tmap/). Hydropathy profiles of single sequences were created using the Kyte–Doolittle algorithm [20] in the program GREASE [63]. Plots of amino acid location on a transmembrane helix were made using the program HelicalWheel in GCG.

To estimate the evolutionary distances, phylogenetic trees were created using four programs in the Phylip package [64,65]. SEQBOOT was used to bootstrap the sequences and create 100 data sets. Then, PROTDIST and the Dayhoff PAM matrix were used to create a distance matrix for the each randomly ordered data set. Next, NEIGHBOR was used to construct neighbor-joining trees [66] from the distance matrix. Finally, CONSENSE was used to select to determine the consensus tree. The trees were plotted with TreeView [67].

# 2.2. Sequencing

Sequencing and synthesis of all oligonucleotide primers used for sequencing was done by the Genetic Engineering Facility at the University of Illinois (Urbana, IL).

#### 3. Results

#### 3.1. Sequence analyses

The cytochrome *bd* sequences available are shown in Table 1. There are 22 complete and eight partial sequences for subunit I. For subunit II, there are 20 complete and eight partial sequences. Twenty-six different organisms are represented. Five organisms contain multiple cytochrome bd sequences. In addition, the complete genome of Archaeoglobus fulgidus contained a second subunit I sequence (Genbank: AF2296) [68] with some homology to subunit I. This sequence was not included in this analysis, however, because its C-terminus is shortened by over 100 residues and it is highly divergent. It is intriguing that no subunit II homologue was found in the A. fulgidus genome. Despite biophysical evidence to the contrary [69], a cytochrome bd sequence was not found in the complete genome of Helicobacter pylori [70].

The sequence for *E. coli* cytochrome *bd*-I has been reported three times. The two genomic sequences of *E. coli* recently reported [71,72] provide a sequence



Fig. 5. Topological model of cytochrome bd-I subunit II from E. coli. See Fig. 4 for details.



Fig. 6. Helical wheels of transmembrane regions of subunit I (*E. coli* bd-I). (A) helix III (E99, E107); (B) helix VII (R391, M393). Hydrophobic residues are boxed.

for cytochrome *bd*-I differing in three amino acids from the cloned sequence initially deposited [73]. All three amino acids are located in subunit I. With the genomic amino acid denoted on the left and the original sequence on the right followed by the residue number, they are ML121, FL213 and ML481. The cloned sequence was reexamined, confirming in part the original sequencing of these genes. Residues 121 and 481 in subunit I are, in fact, leucines. Residue 213 in subunit I, though, is a phenylalanine, indicating either that the original submission contained a sequencing error at this position or that a mutation was acquired at some point in the laboratory. An alignment of the cytochrome *bd* sequences indicates that 20 residues in subunit I (Fig. 1) and two in subunit II (Fig. 2) are completely conserved. The heme ligands I-H19, I-H186 and I-M393 are the only conserved histidines and methionines (other than the initiating methionines). As noted previously for Pabd (*Pseudomonas aeruginosa*) [22], the C-terminal third of the Q-loop, approximately from I-L310 to I-P385, is also not present in a number of other sequences (Table 1).

The new topology prediction is based on multiple sequence alignments of the 22 complete sequences available for subunit I and the 20 for subunit II. Fig. 3 illustrates the differences in Kyte–Doolittle hydropathy profiles between individual sequences. The use of multiple sequences for the topology prediction allows the algorithm to see beyond these variations between sequences and produce a more accurate result. The algorithm predicts the location of transmembrane helices and whether loops are cytoplasmic or periplasmic. The predicted topologies for subunits I and II are shown in Fig. 4 and Fig. 5, respectively. Two new transmembrane helices are predicted in subunit I. There is a transmembrane helix beginning at I-W55 and ending with I-T69 and the N-terminus is now located in the periplasm. Also, there is a transmembrane helix beginning with I-R424 and terminating at I-W441, relocating the C-terminus of subunit I to the cytoplasmic side of the membrane. Additionally, transmembrane helix II in subunit II is highly unusual in that it is predicted to be some 32 amino acids long. It was manually truncated at 24 residues for Fig. 5.

Four highly conserved charged residues are located within transmembrane helices. I-E107 is completely conserved in all sequences and only two turns away from I-E99 on the same face of helix III (Fig. 6A). In helix VII (Fig. 6B), I-R391 is found on the opposite side of I-M393, a ligand for heme  $b_{558}$ . I-R391 is an asparagine in one sequence (Fig. 1) and histidine in two others, conserving a nitrogen group capable of hydrogen bonding. The transmembrane helices in subunit II do not contain conserved residues, except II-P76.

Unrooted phylogenetic trees were made using the largest continual stretches of good sequence alignment where data are available from the most organisms. For subunit I (Fig. 7), residues 63 to



Fig. 7. Unrooted phylogenetic tree for subunit I. For sequences that are known to have or not have the C-terminal portion of the Q-loop, 'Q' or 'No Q', are respectively appended to the name. Residues 63 to 144 (*E. coli* cytochrome *bd*-I numbering) were used, the largest region of good alignment. The Q-loop region was not used for tree creation.

144 were used. For subunit II (Fig. 8), residues 51 to 214 were used. There are some expected groupings, such as that of the gamma proteobacteria clustering together, as do most of the Gram-positive bacteria, but there are also significant exceptions. For example, the Gram-negative *P. aeruginosa* and one of the *S. typhimurium* sequences are found in a completely different region. Also, the archaeon *A. fulgidus* groups with *Staphylococcus carnosus* and one of the *Bacillus subtilis* sequences. Furthermore, the extremely thermophilic bacterium *Thermotoga maritima* is found in the



Fig. 8. Unrooted phylogenetic tree for subunit II. Residues 51 to 214 (*E. coli* bd-I numbering) were used, the largest region of good alignment. Sequences known to have or not have the C-terminal portion of the Q-loop have 'Q' or 'NO Q', respectively, appended to their name.

midst of the gamma subclass of Gram-negative bacteria.

### 4. Discussion

#### 4.1. Topology

Information from *LacZ* and *PhoA* gene fusions is complementary and defines the topology of the protein. The previously proposed topology does not agree entirely with the *LacZ* and *PhoA* fusions [26] reported previously for subunit I of cytochrome *bd* from *E. coli*. In contrast, the revised topology proposed in the current work agrees well with the gene fusion data. The previous topology placed the C-terminus of subunit I on the periplasmic side, leaving the two active *LacZ* fusions in the C-terminal tail unexplained. In the new topology for subunit I, the *LacZ* fusions with high activity are found entirely on the cytoplasmic side of the membrane. In the old topology, the highly active *PhoA* fusion in the loop between helices II and III was located in the cytoplasm [26]. In the revised topology no PhoA fusions with activity are located on the cytoplasmic side of the membrane.

The revised topology remains consistent with results from chymotrypsin digestion [27] that localized the Q-loop to the periplasmic side of the membrane. It also is in accord with proximity mapping using an artificial protease [31] which indicated that loop I–II in subunit II is close to and on the same side of the membrane as the Q-loop.

The topology prediction algorithms used are good at predicting the number and general location of transmembrane helices, with a reported accuracy of 86% [61]. It must be recognized, however, that the ends of the helices predicted are still imprecise and can shift several residues either way depending on which sequences are input to the program. In light of this, the following discussion will describe residues as roughly located in the cytoplasmic, middle or periplasmic third of the transmembrane helices.

One of the most interesting consequences of the revised topology is that it locates H19 in subunit I, the ligand for heme  $b_{595}$ , in the periplasmic third of the membrane. If H19 is in the periplasmic third of the membrane, then heme d must also be in this region, since heme  $b_{595}$  and heme d appear to share a binding pocket within the protein [42,43]. This situation, if correct, would be similar to that of cytochrome c oxidase [74,75], where the dioxygen-reactive site is located near the periplasmic side of the prokaryotic membrane (intermembrane space for the mitochondrial oxidase). Since the protons required in the chemistry of making water come from the opposite side of the membrane (bacterial cytoplasm), this necessitates at least one pathway for protons to reach the active site. Cytochrome c oxidase has at least two putative channels that allow protons access to its active-site, the heme-copper binuclear center [74-77]. In principle, the network of proton-conducting channels in cytochrome bd can be less complex than those in the heme-copper oxidases, since cytochrome bd does not pump protons.

It has been suggested [24] that a protonation site is located close to heme  $b_{595}$  which may be the immediate source for substrate protons, based on the sensitivity of the heme  $b_{595}$  EPR signal to pH [78] and the pH-dependency of its reaction with nitrite [79]. Although subunit II does not have any conserved, hydrophilic transmembrane helices, helical wheel plots of transmembrane helix III in subunit I suggest that one face of this helix has appropriately positioned protonatable residues. The completely conserved E107 (*E. coli* numbering) is two helical turns directly below E99 (which is a glutamine in only one sequence (Fig. 1)). It is conceivable that the two glutamates participate in a proton-conducting channel to the oxygen-reactive active site (heme d/heme  $b_{595}$ ) from the cytoplasm. Also, T26 (subunit I, *E. coli* numbering), which is located in the middle of helix I below H19, is also highly conserved and could be part of a proton-conducting channel.

# 4.2. The quinol binding site

It has been demonstrated experimentally that the N-terminal portion of the Q-loop is somehow involved in quinol binding ([29,80]). The current sequence alignments indicate there are seven sequences of cytochrome *bd* in which 75 residues are missing at the C-terminal portion of the Q-loop. Hence, this part of the Q-loop probably is not important for quinol binding. The revised topology locates the highly conserved GRQPW region (Fig. 1), also on the periplasmic side of the membrane, close to the end of the new proposed transmembrane helix VIII in subunit I. Thus, this GRQPW region might contribute, along with the first part of the Q-loop, to a quinol oxidation site.

R391 in subunit I (E. coli numbering) is the only highly conserved, positively charged residue within the membrane. It is located on the opposite face of the putative transmembrane helix VII from M393 (Fig. 6B), which is the axial ligand for heme  $b_{558}$ [41]. The proximity to heme  $b_{558}$  along with the sequence location of R391 at the end of the Q-loop suggests that it could participate in quinol binding or electron transfer from quinol. Semiquinones have been shown to have a functional role in other proteins [81-83] and the positive charge of R391 could help stabilize a semiquinone anion species during turnover. A thermodynamically stable semiquinone has been observed in E. coli cytochrome bd [84]. Alternatively, this arginine might interact with the propionic acid groups of heme  $b_{558}$  as is the pattern observed in cytochrome c oxidase [75,85,86]. Mutagenesis experiments should clarify the role of R391.

# 4.3. The roles of multiple cytochrome bd oxidases

The adaptive responses of bacteria and archaea to a variety of growth conditions by using branched respiratory pathways and multiple terminal oxidases are well-documented [9,11]. Several bacteria have been found to contain more than one cytochrome bd (Table 1). The second cytochrome bd from B. subti*lis*, although related to the other low (G+C)-content Gram-positive bacterium S. carnosus, is significantly divergent from the other bacterial sequences (Figs. 7 and 8). The incomplete genome from Vibrio cholerae reveals two partial but unique genes encoding overlapping regions of subunit I. Remarkably, V. cholerae contains three different incomplete genes encoding subunit II, indicating that there are three different cytochrome bd oxidases in V. cholerae. The two sequences encoding subunit I in A. fulgidus are located adjacent to each other in the genome and actually overlap a few bases. Although they are in different positive reading frames it is conceivable that they form a functional heterodimer, in which case the missing subunit II in A. fulgidus is substituted by a modified version of subunit I (AfbdI). It will be interesting to see the biophysical properties of any cytochrome bd oxidase from this archaeon. Relatively little is known, however, about why a microbe specifically uses multiple cytochrome bd oxidases [87]. Except for Halobacterium salinarium NRC-1 pNRC100 which has two identical sequences due to an inversion sequence [88], all these organisms contain divergent cytochrome bd sequences. There is a second cytochrome bd encoded in E. coli (cytochrome *bd*-II), that is also capable of oxygen reduction coupled to quinol oxidation. Cytochrome bd-II in E. coli is encoded by AppY [89,90]. However, expression of this protein has been achieved only under unusual conditions. Transcriptional activation of AppY was induced by a plasmid encoding a 3.4-kb region of DNA from the alkaliphilic Bacillus firmus OF4 in an E. coli strain lacking the respiratory oxidases that allow respiratory growth under normal conditions, (cytochrome bd-I and cytochrome  $bo_3$ ) due to genomic deletion [87]. It is worth noting that in E. coli, cytochrome bd-II exhibits higher sensitivity to cyanide inhibition than does the well characterized cytochrome bd-I [87], suggesting a functional distinction. It seems likely that multiple cytochrome bd oxidases found in the same organism probably have different functional roles.

# 4.4. Phylogeny

Over time, naturally occurring single amino acid

mutations tend to conserve only those amino acids essential for structure and function. Alignments of highly divergent sequences reveal conservation of residues that are indispensable. Larger changes in proteins are also possible, though, since lateral gene transfer can move even entire genes directly between organisms. In such cases, phylogenetic trees derived from those proteins will be different from the true evolutionary lineage of the organism. The 16sRNA phylogeny was the first to elucidate the three domains in the tree of life to be archaea, bacteria and eukaryotes and has been widely held as the standard phylogeny. Recent genomic data, however, has raised a considerable number of objections to partitioning the tree of life in this way [91-93]. It is therefore useful to compare the cytochrome bd phylogenetic trees with that of 16sRNA to further test its applicability as a general model.

It should be noted that the phylogenetic trees were created using residues outside the Q-loop (Fig. 4). It is of interest, therefore, that sequences possessing the complete C-terminal region of the Q-loop cluster entirely within two branches of the subunit I tree (Fig. 7) and almost entirely within one branch of the subunit II tree (Fig. 8). Moreover, organisms that do not have the sequence encoding the full C-terminus of the Q-loop dominate the rest of the tree. Since the phylogenetic trees were made without using the Q-loop region of the sequences, this provides independent support for the validity of the phylogenetic interpretation.

The phylogenetic analysis suggests that lateral gene transfer of cytochrome bd has occurred on several occasions. In support of this conclusion, a recent study of the E. coli strain MG1655 genome [94] predicted that the genes encoding cytochrome bd-II were transferred laterally into the genome. The cytochrome bd phylogenetic trees indicate that although most organisms of the gamma subclass contain a cytochrome bd similar to the two cytochrome bd sequences in E. coli, some of them (S. typhimurium, V. cholerae) also contain at least one other cytochrome bd sequence that is more closely related to those found in the cyanobacteria and the archaeal halobacteria. Although the phylogenetic tree based on subunit I sequences was created without using the Q-loop region of sequence, this separation of the gamma subclass is supported by the lack of the C-terminal portion of the Q-loop in P. aeruginosa cytochrome bd (this portion of the sequence is not available for StbdII), in contrast to all the other cytochrome bd sequences from the gamma subclass of proteobacteria. Since the only cytochrome bd sequence known from P. aeruginosa clusters within this divergent group, this further predicts that complete sequencing of its genome will reveal a second cytochrome bd more closely related to the E. coli cytochrome bd sequences. It is worth noting that the *P. aeruginosa* cytochrome *bd* is proposed not to contain heme d, but, to utilize heme b instead [22]. This may prove to be a common feature of this grouping. Utilization of different heme groups for the same function has been extensively observed in the heme-copper oxidases [11].

Cytochrome *bd* sequences from the more ancient bacteria and archaea also provide ample evidence of lateral gene transfers. The ancient hyperthermophilic bacterium T. maritima is found in the middle of the gamma subclass of proteobacteria in the tree based on subunit I (Fig. 7). Likewise, the most ancient bacterium on the tree, Aquifex aeolicus, instead of clustering close to the archaea as expected, is found with C. *jejuni*, an epsilon subclass proteobacterium, and P. gingivalis, a member of the cytophagales. The archaeal halobacteria sequences are more related to the cyanobacteria and to some of the Gram-negative sequences than to the archaeon A. fulgidus. Similarly, A. fulgidus exhibits greater similarity to the low (G+C)-content Gram-positive bacteria than to the archaeal halobacteria sequences. This can only be explained by there having been a substantial amount of horizontal transfer [95] of cytochrome bd genes between domains, similar to other phylogenetic analyses of proteins that have placed archaeal branches among those of the low (G+C)-content Gram-positive bacteria [96]. The mode of horizontal gene transfer is, perhaps, more clear in the archaeal halobacteria, since it has been suggested that the plasmid on which the cytochrome bd sequences of Halobacterium sp. NRC-1 are found may be particularly susceptible to transfer between both archaea and bacteria [97].

As more sequence data are made available, though, it is becoming apparent that phylogenetic analysis of a single protein often fails to completely support the 16sRNA phylogeny, particularly if the enzyme studied is metabolic (cytochrome bd) or biosynthetic in function as opposed to informational (16sRNA) [96]. Often, lateral transfer of genes is predicted to have occurred and models are clearly emerging that the contents of genomes are highly dynamic. For example, in the 100 million years that E. coli has been evolving, approximately 1400 kb of DNA has been transferred into and 1400 kb has been lost from its genome [94,98]. The size, but not the contents, of the genome has remained relatively constant. Along these same lines, the phylogenetic trees reported here for cytochrome bd reveal no clear separation between the bacteria and archaea, in agreement with [91-93], but in contrast to what would be expected if the canonical 16sRNA tree were observed [99,100]. The trees are consistent, however, with the annealing theory of genomes, which states that the last common ancestor implied by the phylogenetic trees was actually a number of organisms with very high rates of horizontal gene transfer [101].

Phylogenetic analyses of the heme–copper oxidases have been used to show that a mutual ancestor of the archeal and bacterial enzymes was present before atmospheric oxygen became abundant, i.e., before photosynthesis arose [102,103]. Due to the apparent high degree of lateral gene transfer of cytochrome bd between organisms, however, the phylogenetic analyses presented here are unable to provide further evidence either for or against this intriguing hypothesis. It is hoped that as more sequences become available, studies of the phylogeny of cytochrome bd will be able to contribute to this debate.

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