# On the Membrane Topology of Vertebrate Cytochrome P-450 Proteins\*

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Hydropathy profiles of 34 aligned cytochrome P-450 sequences were compared to identify potential transmembrane segments. Eleven regions with the potential to cross a membrane in at least some P-450 sequences were detected. The known sidedness of several residues and peptides was used to eliminate some of these regions from consideration. Further arguments based on the location and orientation of the heme relative to the membrane excluded others. This process of elimination was continued until only two regions remained. These two segments, present in the first 66 amino acids of the P-450 NH<sub>2</sub> termini, are proposed as the only transmembrane peptides of vertebrate microsomal P-450s. Mitochondrial P-450s may have a different membrane association. The three-dimensional structure of cytochrome  $P-450_{cam}$  was examined for the location of conserved charged residues. These residues occurred mainly on the opposite surface from the substrate-binding site and along the edges of the flat triangular P-450<sub>cam</sub>. A model is proposed for vertebrate microsomal P-450s that is similar to P-450<sub>cam</sub>. The substrate-binding site faces the membrane, the heme is parallel to the membrane surface, and two NH2-terminal transmembrane segments anchor the protein to the bilayer.

Cytochrome P-450 is a superfamily of monooxygenase proteins present in all the kingdoms of living organisms. The most studied forms come from mammals and bacteria. In bacteria, the known P-450 proteins are soluble, while in vertebrates they are membrane bound. One bacterial P-450 has been crystallized, and the three-dimensional structure is known to 1.6-Å resolution (2, 3). No three-dimensional structures are known for the membrane-bound forms, however, more than 40 distinct vertebrate P-450 sequences have been determined. These sequences contain information that can be used to predict the membrane topology of cytochrome P-450.

The present understanding of protein structure dictates that a protein segment in a lipid bilayer must assume a secondary structure for thermodynamic reasons. There are only two structural possibilities, helix and  $\beta$ -sheet. Cogent arguments have been presented in a recent review, that  $\beta$ structure is likely in a membrane only when it forms part of an aqueous pore (4), as in matrix porin. Integral membrane proteins surrounded entirely by lipid are not candidates for transmembrane  $\beta$ -structure. These proteins (including cytochrome P-450) most likely have their transmembrane segments in the form of helices. An accurate prediction of the membrane-spanning helices of cytochrome P-450 proteins would be a valuable step toward understanding P-450 structure. With this in mind we have aligned 33 vertebrate P-450 sequences and the bacterial P450CIA1<sup>1</sup> (P-450<sub>cam</sub>) sequence by the method of Needleman and Wunsch (5) as modified by Gotoh (6). In a previous study, the phylogenetic relationships and the evolution of these cytochrome P-450s were reported (7). Here, the sequence alignment is analyzed for structural information relevant to the membrane topology of vertebrate P-450 proteins. A model that has only two transmembrane segments at the P-450 NH<sub>2</sub> terminus is proposed. Analysis of the conservation of amino acids in six sets of cytochrome P-450s suggests several regions that may be involved in interaction with NADPH-cytochrome P-450 reductase. One of these regions contains a very highly conserved tryptophan that could participate in electron transfer between these two proteins.

## MATERIALS AND METHODS

Alignment of P-450 Sequences—The cytochrome P-450 proteins used and the methods of aligning them are described in detail elsewhere (7). The alignment is shown as Fig. 1.

Identification of Potential Transmembrane Regions in Cytochrome P-450-Cytochrome P-450 amino acid sequences were converted to sequences of numbers corresponding to the hydrophobicity scales of Engelman et al. (4) or Kyte and Doolittle (8), as listed in Table I. Gaps were given the value 0. During the conversion the sequence was scanned for complementary charges with 2 or 3 residues between them. Such residues would appear on the same side of an  $\alpha$ -helix and could form charge pairs. Because paired charges could more easily be accommodated in a membrane, the numeric values of these amino acids were reduced by half. For each position in the sequence, a window varying from 15 to 24 amino acids (exclusive of gaps) was summed to obtain the hydropathic index. Of these 10 sums, only the lowest value was saved. A printout was made of the window starting position, window width, and hydropathic index at the minimum value. Sequential files with extension .prn were used to store this information for each sequence. Lotus 1-2-3 was used to import these files and make the graphs in Fig. 2. Potential transmembrane segments were identified by comparing these graphs for negative valleys that occurred with some regularity in several or many of the P-450s.

Conservation of Amino Acids in Cytochrome P-450 Sequences— The sequence alignment shown in Fig. 1 was analyzed by computer to determine the maximum number of identical amino acids at each position along the length of the alignment. The resulting data were depicted as histograms, with *tall bars* representing highly conserved positions and *low bars* representing poorly conserved positions and/

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 $<sup>^1\,</sup>A$  new nomenclature has been adopted for use in the cytochrome P-450 field. The reader is referred to Reference 1 for a detailed account.

TABLE I Hydropathic index scales of Goldman, Engelman, and Steitz (GES) and Kyte and Doolittle (KD)

	GES	KD	
	-3.7	-2.0	
Met (M)	-3.4	-1.9	
Ile (I)	-3.1	-4.5	
Leu (L)	-2.8	-3.8	
Val (V)	-2.6	-4.2	
Cys (C)	-2.0	-2.5	
Trp (W)	-1.9	0.9	
Ala (A)	-1.6	-1.8	
Thr (T)	-1.2	0.7	
Gly (G)	-1.0	0.4	
Ser (S)	-0.6	0.8	
Pro (P)	0.2	1.6	
Tyr (Y)	0.7	1.3	
His (H)	3.0	3.2	
Gln (Q)	4.1	3.5	
Asn (N)	4.8	3.5	
Glu (E)	8.2	3.5	
Lys (K)	8.8	3.9	
Asp (D)	9.2	3.5	
Arg (R)	12.3	4.5	

or gaps in the alignment (Fig. 3). Six different sets of aligned P-450 sequences were examined in this manner: all 34 sequences, all vertebrate sequences (*numbers 1-33* in Fig. 1), all sequences of P-450s found in the endoplasmic recticulum (*numbers 1-31* in Fig. 1), and P-450s of the methylcholanthrene (P450I) and phenobarbital (P450II) families taken together (*numbers 1-23* in Fig. 1) or as separate groups (*numbers 15-23* and *1-14* in Fig. 1, respectively). The appearance of these plots is reminiscent of a city skyline, and therefore we call them skyline plots.

### **RESULTS AND DISCUSSION**

Cytochrome P-450 Membrane Topology-Models proposed for vertebrate cytochrome P-450 structure generally contain 6-10 transmembrane segments (9-12), although recently two models were proposed with only one membrane segment (13, 14). These segments are assumed to be  $\alpha$ -helical or a mixture of  $3_{10}$  helix and  $\alpha$ -helix. The recent availability of many P-450 sequences and better methods for predicting membrane helices prompted a closer examination of this model. To begin, 34 cytochrome P-450 sequences from eight protein families were aligned (7), as shown in Fig. 1. Next, hydropathic index plots were made for each sequence. These plots were computed using a variable window width and compensation was made for charge pairs. Because these plots were made from aligned sequences, with the gaps included, the resulting graphs were all of the same length and could be compared directly (Fig. 2). By inspecting the graphs 11 regions were identified with negative valleys (hydrophobic sequences) in several or many P-450 sequences. These regions are shaded in Fig. 1. The exact boundaries and each segment's hydropathic index (both Engelman, Steitz, and Goldman's scale (4) and Kyte and Doolittle's scale (8) were used) are given in Table II. The hydropathy scales and the one-letter amino acid code are given in Table I. The regions between the shaded areas in Fig. 1 contain many charged residues (printed in *bold type*). Consequently, these zones are poor candidates for transmembrane segments.

The 11 shaded regions were considered as potential transmembrane segments. All true membrane-spanning segments were assumed to be among these 11, however, it was not assumed that all 11 would span the membrane. Each segment was considered along with additional information bearing on its location relative to the membrane. Finally, by a process of elimination based on logic and a synthesis of findings from electron paramagnetic resonance (EPR) spectroscopy, x-ray crystallography, quantitative peptide antibody binding studies, chemical modifications, fusion protein experiments, and secondary structure prediction, only 2 of the 11 regions were predicted to be transmembrane segments.

The first segment is clearly the strongest candidate for a membrane-spanning segment. The Goldman, Engelman, and Steitz values for all sequences except  $P-450_{cam}$  and the two mitochondrial  $P-450_{scc}$  sequences range from -25 to -50 with an average value of -39 (see Table II, segment 1). The suggested cutoff value for considering a segment to be a potential transmembrane segment is -20 (4). All models of P-450 topology predict this region is a transmembrane segment (9-14). We concur. As discussed later, the mitochondrial sequences may have a different membrane topology.

Chemical modification studies on rabbit P450IIB1 (LM2) have shown that the NH<sub>2</sub>-terminal methionine and Lys<sup>384</sup> (alignment position 466) were labeled by fluorescein isothiocyanate (FITC)<sup>2</sup> from the cytoplasmic surface of rabbit liver microsomes (15-17). The interaction with NADPH-cytochrome P-450 reductase was inhibited when either of these residues was modified. Since the interaction between these two proteins is a cytoplasmic phenomenon and since FITC has two negative charges, making it unlikely to penetrate the microsomal membrane (18), these two residues were identified as cytoplasmic. Therefore, rabbit P450IIB1 and probably all microsomal P-450s, if a common topology is assumed, have their NH<sub>2</sub>-terminal residues on the cytoplasmic face of the endoplasmic reticulum (ER). If the first hydrophobic segment (S1 in Fig. 1) is a transmembrane segment as we propose, then at least a portion of the P-450 molecule following S1 will be present in the ER lumen.

Additional studies on this same P-450 indicate that Ser<sup>128</sup> (alignment position 168) can be phosphorylated by the purified catalytic subunit of cAMP-dependent protein kinase in vitro (19). Phosphorylation of rabbit liver microsomes by this kinase labels a protein with electrophoretic mobility equivalent to phosphorylated P-450<sub>LM2</sub>. Peptide maps (and the corresponding autoradiograms) of the phosphorylated microsomal protein and purified P-450<sub>LM2</sub> were the same after treatment with trypsin,  $V_8$ -protease or CNBr (20). These results strongly suggest that the labeled microsomal protein was P-450<sub>LM2</sub> and that phosphorylation occurred at the same site in the purified and microsomal forms. In fact, the sequence of  $P-450_{LM2}$  has only one site specific for cAMP-dependent protein kinase (Arg-Arg-X-Ser-X, where X represents an hydrophobic amino acid). This recognition sequence is present in 10 of 13 members of the P450II family (numbers 1-14 of Fig. 1). An eight-amino acid insertion appears to have interrupted this site in the P450I family (numbers 15-23 in Fig. 1). This recognition site includes Ser<sup>128</sup>. The established fact that microsomes form with their cytoplasmic surface facing out (21) and they are impermeable to proteins and small charged molecules (18) indicates that  $Ser^{128}$  in P-450<sub>LM2</sub> is a cytoplasmic residue.

Evidence has been presented that the NH<sub>2</sub>-terminal Met, Ser<sup>128</sup>, and Lys<sup>384</sup> of P-450<sub>LM2</sub> are cytoplasmic. Furthermore, the first hydrophobic segment (S1 in Fig. 1) is the most hydrophobic region in the P-450 sequence (see Table II). This region in P-450<sub>LM2</sub> is more hydrophobic than any of the seven transmembrane segments of bacteriorhodopsin, or the 11 transmembrane segments of the light reaction center of *Rhodopseudomonas capsulata*, or the transmembrane segment of glycophorin (4). Since P-450<sub>LM2</sub> is a membrane protein, it is

 $<sup>^{2}\,\</sup>mathrm{The}\,$  abbreviations used are: FITC, fluorescein isothiocyanate; ER, endoplasmic reticulum.

		· · · · ·		_		10	20		40	5	io <b>52</b>	60	70	80	
	2 P450	) PBC2	rappit	215 196				-LSCLL	LLSLWK	QSYC	GGKLPFGF	TEFF PILCONT	-LQIGBKDIS	KSFTKLSE	49
	3 P450	) 1	rabbit	PB	MDP			CLCCLL	LLOLDER	QSH0	GGGGFPPGP	TPPPILGHY	-LOLDFKDLS	KSLTNLSK	48
	4 P450	) f	rat	con.	M DL + + + +	••••	VTFLVL	TLSSLI	LLSLWR	055			- DO TOVENTS	SASLTKESE	59
	5 P450	PB1	rat	œn.	M D		VMLGVL	TLTCLI	LLSIWR	QSSG	RGKLPPOP	IPLPIIGHT	- ZOLNVKNI	OSLTSFSK	50
	6 P450	0.36	rabbit	con.	M DK		LIILGI	CLSCVV++	1155 <b>4</b> K	KT HG	KGKLPPGP	TPLPVVGNL	-LQLETKDIN	KSLSMLAK	59
	7 P430 8 P450	) 3a. ) 1	rappic	EtCH	- AV 5+G	*******	TVALLG	WHVILL	FISVNK	QIHS	SSWNLPPGP	<b>PPLPIIGNL</b>	-LQUDLKDIF	KSFGRLAE	61
1	9 P450	1	human	EtOH	MFAL-GI			NAATILL	VISING	KIYN	SWNLPPOP	PLPILGNI	-FQLDLKDIF	KSFTKLAK	62
v	0 P450	<b>`</b>	chicker	PB	MDFL-GI	P	TILLLY	CISCLL	IA-ANR	STRONG	BCKEPBCP	PEPILUNG	- FOLLELKNIP	KSFTRLAQ	62
1	1 P450	)e	rat	FB	MEPS)		LLLLAL	LVGFLL	LL-VRG	HPKS	RGNPPPOP	PLPLIGNL		NSFMOLDE	60
1	2 P450	Ъ	rat	PB	MEPS)	[	LLLLAL	LVGFLL	LL-VRG	HP KS	RGNPPPGP	PLPLLONL	-LQLDRGGLL	NSFMOLRE	60
1	3 P450		rabbit	PB TR	M <b>EF</b> S + + 1	<u>,</u>	LLLLAP	LAGLLL	LL-FRG	HP KA	HG RLPPCP	SPLPVLONL	-LQMDRKGLL	RSFLRLRE	60
1	5 P450	, ,	rat	MC	MPSVVG	D	*********		****						0
10	6 P450	P1	mouse	MC	MPSMYGI	P4	ATELLAV	TYPCLG	FWVVRV	-TKTWVPKG	-LKSPPGP	CLPFICHY	-LTL-GKNPH	LSLTKLSQ	72
1	7 P450	P1	human	MC	MLF	PI \$HS	ATEPLLAS	VIFCLV	WVIRA	-SRPOVPKG	- T. KNPPGP	IGUPLIGUE.	-LTL-GKNPH	LALSPMEN	12 68
10	B P450	96	rabbit	MC				••••				N	-LTL-GKNPH	VALAALSR	17
21	P450	4	numen. mabbit	MC	MALSQSV	P <b>P</b>	BATELLLAS	AIPCLV	FMATKC	-LRPRVPKG	- L X 6 7 7 2 7 9	GWPLLOWV	-LTL-GKNPH	LALSRMSQ	70
2	1 P450	LMA	rabbit	MC	-AMSPAA	P		WECT V.					*****		0
2	2 P450	d	rat	MC	MAFSQY	\$L	APELLLAT	ITCLV	EWVLRG	-SKPRVPRG	-LKOLFGP	GMPLLGML	-LIL-GKNPH	VALARLSQ	69
23	B P450	P3	11121398	MC	MAFSQY	\$L	APELLLAT	AIFCLV	FWMYRA	-SRTOVPKG	-LKNPPGP	GLPFIGHM	-LTV+GKNPH	LSLIRLSO	69
24	P450	17a	bovine				-MULLLAVI	LLTLAYL	FWPKTK	HSG	- AKYPRSLE	SLPLVGSL	FLFRRGQQH	KNFFKLQE	58
20	5 P450	(2)1	in testing		- METOTOR		-MALVAL	LLTCAYL	HPKRR	CPG	-AKYPESLI	SLPLVGSL	PERRHGHMH	NNFFKLQK	58
27	P450	C21	bovine		-MVLA			FLLAGARL		LRS	-LHLPPLA-	PGFLHL	-LQPDLP	IYLLGLTQ	53
28	P450	C21	mouse		-MCLP		GLLLLLI	LLAGTEN	WOOWK			POPLAL	TOPHLP	TYLLSLIQ	54
25	P450	нцр	human	glu.	MALI	PDL-AM	ETWLLLAVS	LV-LLYL	10	- THS HGLFK	KEGI-PGPT	PLPTLGN1-	LSY-HKGFC	MFDMECHK	66
30	P450	p La	rat	FON	MDLL	SAL-TL	THVLLAV	LV-LLYG	G	- TRTHGLFK	KOGT-POPE	PLPFF0 <u>T</u> V-	LNY-YHOLN	KFDVECHK	66
32	P450	900	bovine		-MLADER	BY BEAT WE	CRETCOVAS	EGECHUS	KAVOF	YLORONLLE	AFOOFPSPE	THWTTOHK	FQGD-KELQ	QIMTCVEN	80
33	P450	SCC	human		-MLAKBL	PPRSVLVE	YOTPLEAP	REGLOPT.PT	VPTGEGAGI	STRSPODE	#1#8-PG#1	AND NEY ME	REKGSORIH	FRHIENFQ	83
34	P450	cam	P. puti	da		T	ETIQSHANI	AP		-LPPNYPEH	-LVEDEDMY	N-PSNT		NAVIOFSN	49
	\$3	90		100	h	110	120 64	120							•••
1	VY G	PVP	TVYEG		VINGYDA	VKEALVDLG	FEFSGRUVE		140	150 131 - NG KI	DWKETDD.	0	170	180	
2	VYO	PVF	TVYEG	NKPTY	VYHGYEA	VKEALVDLG	HELSGREAT	LVTAKLN	GFG	VIFSNGK	RWTETRR	FSI	MTLENFOMG	-KRSTEEP	133
3	CYG	PVF	TYYLG	MKPT	<b>TVLH</b> GY <b>E</b> A	VKEALVDLG	EEFAGTOSV	FILEKVS	(GLG	IAPSNAK	TWKEMRR	FSL	MTLRNFGMG	-KRSIEDR	144
1	TYG	PVT	TLYLG	SOPT	TINGYEA	IKEALIDNG	EKFSGROSY	PHIENVT	(GFG	I V # S N G N	RWKEMRR	FT1	MNFRNLGIG	-KRNIEDR	144
6		818	TIVES		TUTNOVEC	VKEALIDHG	EEFAERGSE	PVAERINE	+++0LG	IVFSHGN	RWKEIRR	FTL	TTLRNLGMG	-KRNIEDR	144
7	REE	PVT	TVYLG		VLHGYKA	VREMLLNHK	NFFSGRGET	PAPER-PE		1VEDSGE	KWKETRR TWKDTPP	FSL	TVLRNLGMG	KOCHEER	144
8	REG	PVF	TLHLG		VISHGYKA	VKEVLLNHK	NEFSGREDI	PVFQE-Y	NKG	IIPNNGP	TWKDVRR	FSL	SILRDIGMG	-KOGNEDR	145
9	REG	PVF	TLYVG.	SQRMI	VNHGYKA	VKEALLDYK	DEFSGRODL	PAFNA-HA	DRG	IITHNGP	TWKDIRR	FSL	TTLRNYGMG	-KQGNESR	146
10	<b>UX</b> G		TINLG		VLYGYDI	VKEALIDNG	EAFSGREETL	PLIEKLEK	GTG	IVTSNGE	TWRQLRR	FAL	TTLRDFGMG	KKGIEER	147
12	KYG		TVMLG		MECOTOT	TREALVGUA	EDFSGRUTI	AVIEPIFE	EYG	VIXA NGE	RWKALRR	FSL	ATMRDFGMG	KRSVEER	145
13	KYG	DVT	LAAPG	SRPVI	VLCGTDA	IREALVDOA	EAFSGREET	AVVEPIFO	GYG	UTRA - NGE	RWRALKK	FSL	ATMROFGMG	-KRSVEER	145
14		-													0
15	QYG	DVL		STPY	VISGUNT	IKQALVKQG	DOFKGRPOK	YSPTLIAN	0QSI	MTFNFDSGP	LWAARRRLA	QNALKSFSI	ASDPTLAS-	-SCYLEEN	166
17	OYG	DV L		SIFVI STPVI	TTL SOUNT	I ROALVROG	DDFKGRPDE	YSFTLITN YTFTLICN	GKS	TENPOSOP	VWAARRRLA	QNALKSFSI	ASDPTSAS-	-SCYLEEN	166
18	PYG	DVF	IRLG	STPV	VLSGLDT	IKOALVROG	DDFKGRPD	YSTSTUT		TTASDSGP	VWAARRRLA UWAA <b>RRRL</b> A	QNGLKSFSI ONAPNSFSU	ASDPASST-	-SCYLEEN	162
19	RYG	DVL	<b>11816</b>	STPVI	VLSRLDT	IRQALVRQG	DOFKGRPDE	YTSTLITD	605	TESTOSGP	VWAARRRLA	ONALNTESI	ASDPASSS-	-SCYLEEN	164
æ		- <u>h-</u> -		• • • • •	H	IKQALVRQG	DDFKGRPDE	YSSSFIT	GQ5	TTSPDSGP	VWAARRELA	QDSLKSFSI	ASNPASSS-	-SCYLEEN	72
21	RYG	<b>DV</b> F	IRLG	STPV	VLSGLNT	IKQALVRQG	DDFKGRPDE	YSSSFITE	6051	TFSPDSGP	VWAARREA	QDSLKSFSI	ASNPASSS-	SCYLEEN	163
23	OYG	DVL		STOVI	VLSCINT	TROALVROG	DDFKGRPDE	YSFTLITN	GKS	TTTPPDSGP	VWAARRRLA	QDALKSFSI	ASDPTSVS-	-SCYLEEH	163
24	KIY6	FIYS	FRLG	KTTV	MIGHHOL	REVLLKKG	KEFSGRPKN	ATLDILSD	N0KG	LAFA-DHGAI	HWOLHRKLA	LNAFAL	FKDGNIK	-SCILEEN	145
25	KY G	PIYS	VEMG	<b>KTT</b> V	TVEHHQL	KEVLIKKG	KOFSGRPON	ATLOIASN	HRKG	ATA-DSGA	HWQLHRRLA	MATFAL	FKDGDQK	LEKI	145
26	GF G	PIYI	LMLG	QOV	VLNSKRT	EEAMVKKW.	ADFAGRPEP	LTYKLVSK	NYPD	LSEC-DYSLI	LWKAHKKLT		RSALLLGI-	RDSMEPV	138
24	in a	P 7 9 1	101 1000	0.000	TUINSNOT	LEEAMIRKW	V DFAGRPOD	PSYKLVSQ	RCQD	ISLO-DYSLI	LWKAHKKLT		RSALLLGT -	RSSMEPW	139
29	NY G	KVW	TTOG	OPVL	AITOPDM	IKTVLVK	ECYSVETNE	RECEVER	MKSA	STAEDFI	FWK RI. RSI.I.		SPTRTSGI	KUSMEPL Kikemudi	133
30	NdA C	KING	LTDG	MPLF	AITOTEM	KNVLVK	ECFSVFTNR	RDF GPVGI	MGKA	78 7 AKD E	EWKRYRALL		SPTFTSG	RLKEMFPI	148
31	EPS.	AFPI	WENGS	KAYL	TANDADA	KVIL	GRSDP	KANGVYEL	LAPWIGYG	LLL -NGQI	PWFQHRRML		TPAF HY D	ILKPYVKN :	160
32					YIINPED	/AM~LFKFE	GSYPERYDI Condernation	PPWLAYMR	YY-QKPIG	LF-KKSG-1	TWKKDRVVL	NTE	VMAPEAIKN	FIPLLNP	173
зĩ	VPO	200	RCNG		CAN SERVER	DREAVEDVRI	GENEER <u>EL</u> I H-FSSECPHE		VO-TTPTS	L DP	AWK KDRVAL Forofraia	NQE	VMAPEATKN	-FLPLLDA .	173
										<b>y</b> - <b>v</b> <sup>2</sup> - <b>v</b> <sup>2</sup>	EQROPANDA		VGMP	VVURLENR	130
	1	190		200	21	0 <u>\$5</u> 2	20	230	240	250	260	56 270	280		
1	VQE	EAR	LVEEL	RKTN	GSPCN	PIFIL	GAAPCNVI-	65.Y49	QNRFDYT-I	QDFLSLMGN	LNENFK	TENSPHYON	CONTRACTORS I	DYL-PGSH 2	220
2	IOF	EAH(	CLVEEL	RETN	ASPCO ASPC	ProFIL	GRAPCHVI-	CSVIF	UNRFOYT-I	VOFLSLMGK	FNENFK	IL SEPHYQI	-CRCFPILV	DYF-PGSN 2	19
4	voe	EAO	LVEET	RKTE	GSPCB	PBLIL	NCAPCHV1-	CSITF	QNHFDYK-	CEFLALMES DEEMLTPMPS	(VNENLK	INSSPREQU	-CHSPDel.	DYF-PGTH 2	:30 230
5	VQE	EAR	LVEEL	RKTN	GSPCD	PTFIL	GCAPCHVI-	CSIIF	QNRFDYK-I	QDFLNLMEK	LNENMK	ILSSPWTOR	-CSTFPVLI	YC-PGSH 2	230
6	IQE	EALC	LIQAL	RKTN	ASPCD	TILL	FCVPCBVI-	CSVIP	QNRFDYD-I	EKFKTLIKY	FHENFE	LLGTPWIQL	-YNIPPILS	NYL-PGSH 2	:30
1	TOP	EANE		RKTQ	GQPFD	PT VI	GCIFFRVI-	ARILE	NDRFDYK-	KQALRLMSL	FNENFY	LLSTPWLQV	-THATSHTL	QYM-PGSH 2	:31
9	IQR	EAHE	LLEAI	RKTO	GOPFO	PTFLI	GCAPCNVI-	ADILT	RKMFDYN-L	DEKFLRLMYL	FNENFH	LISTPWLOL	-YNNPPSPU	IYL-PGSH 2	232
10	IQE	EAHE	LVERI	RKTH	EEPFN	PGK#L	INAVANII-	CSIVF	GDRFDYE-I	KKFLDLIEM	LEENNK	YONRIGTLL	-YNFFFTIU	SL-PGPH 2	233
11	IQE	EAQC	LVEEL	RKSQ	GAPLD	PTFLF	QCITANII-	CSIVF	GERFDYT-L	RQFLRLLEL	FYRT <b>FS</b>	LLSSFSSQV	-FEFTSGFL)	(YF-PGAH 2	31
12	TOP	EAQC		BKSQ	GAPLD GALLD	T	QCITANII-	CSIVF	GERFDYT-C	ROFLRLLEL	FYRTFS	LLSSISSOV	-PEFFEGFL	(YF-PGAH 2	:31
14				RL	RANID	HTCFL	INTESNVI-	SSIVE	GORFDYK-	RELLSLEMT	HLVIVP	VHVNSTGOL	-YEMTSSYM	QL-PGPO	72
15	VSK	EAEY	LISKE	QKLM	AEVG-HFD	P#	VVSVANVI-	CAICF++-	GRRYDHD-D	QELLSIVNL	SNETGE	VTOSGYP	-ADFIPI-U	YL-PNSS 2	:51
16	VSK	EANY	LVSKL	QKVM	AEVG-HFD	TY KYL	VVSVANVI-	CAICF	GORYDHD-L	QELLSIVNL	SNE GE	VTGSGYP	-ADFIPV-L	YL-PNSS 2	51
18	VSO	EAEN	LIGRE	OELM	ABFG-MFN AAVG-MFN	PY	VMSVANVI-	CANCE	GRRYDHD-	OELLSLVNL	NDEFG	VAASGRP	ADTEL	YL-PNPS 2	.96
19	VSK	EAKA	LISRL	QELM	AGPG-HED	PY NOV	VVSVANVI-	GANCE	QHFPES-S	DEMLSLVKN	THE VE	TASSGNP	-LOFFPI-L	YL-PNPA 2	49
æ	VSQ	EAEN	LIGRE	QELM	AAVG-RED	TT SQL	VVSAARVI-	GANCY	GRHFPQG-S	EEMLOVVRN	SSKTVE	TASSGSP	-VOFTPI-G	RYL-PNRP 1	57
2	VSQ	EAEN	LIGRE	QELM	AAVG-RFD	PLSQL	VISAARVI-	GANCF	GIR-FPQGMS	EEMLOVVRN	SSNEVE-	TASSGSP	-VOFFPI-L	YL-POPN 2	48
23	VSK	EANH	LVSKL	Q KAM	AEVG-HFE	PV SOV	VESVANVI-	GAMCT	GKNFPRK-S	EEMLNIVNN	SKOTVE	NVTSGNA	-VOTPV-I	YL-PNPA 2	48
24	INQ	EANV	LCOFL	ATQH	GEAIDLSE	Pt	SLAVTNII-	SFICE	NESEKNE-C	PAL-KAIQN	VNDGIL	EVLSKEV	LLDIPPY-Q	IF-PSKA 2	26
25 T	ICQ	EIST	LCDML	ATHN	GQSIDISF	PU	FVAVTNVI-	SLICF	NTSYKNG-C	PEL-NVIQN	YN DOIL	ONLSKOS	LVOLVDW-L	LIF-PNKT 2	28
27	VDO	LTOP	FCERM	R	AQPGT VOAGA	PVAI-EEEE	SLATCSII-	CYLTF	GOK1-KD-C	NLMPAYYKC TLVHAPMDA	VODENE	TNOH-NGIO	IL DAVEPT-L	FF-PNPG 2	22
28	IEO	LTO	FCERM	R	AQAGT	PVAI-HK	SPLTCSII-	SCLTT	GDLN-S	TLVQTLNDC	VODELO	AWNN-WSTO	ILTIIPL-U	FL-PNPG 2	17
29	IAQ	YGDV	LVRNL	RRE-	A ETG K	PVTL-KOVE	GAYSMDVI-	T\$T\$F	VNIDSL-N	INPQ DPFVEN	TKKLLR	FOFLOPFFL	SITV <b>TPT</b> -L-	-I-PILE 2	34
30	TEO	YGDI	LVKYL	KQE-	AETGK	PVTM-KKVF	GAYSMOVI-	TSTS7	GVNVDSL-N	INP KOPFVEK	TKKLLR	FOFFOFLE	SVVLFPF-L-	T-PIXE 2	.34
32	VSO	DFVS	LLHKS	EVLA IKOO	GSGKFVAN	IKEDETAT	PESITNUM-		GERLGMT	EETVNPEAA	KOT I DAV	YENPHTEUR	LLNVPPer V	LF-RTET 2	262
39	VSR	DEVS	VLHRR	IKKA	GSGNYSGD	ISOOLFREA	FESITHVI-	<b>y</b>	GERQGML	EEVVNPEAQ	RTIDAI	YONFHISVP	NUNLPPOLVI	LF-RTKT 2	62
34	IOE	LACS	LISI	12-0	GO-++-CN				TIEDYA-E	PFPI I	FM	LLABLP	- EEDIPH-th	YLTDOMT 1	85

FIG. 1. Alignment of 34 cytochrome P-450 sequences. Shaded regions (S1-S11) represent potential transmembrane segments. Charged amino acids are shown in *bold type*. The column following the organism indicates the class of inducer. Numbers on the far right are the number of amino acids up to that position. The abbreviations used are: PB, phenobarbital; CON., constitutive; MC, 3-methylcholanthrene; GLU., glucocorticoids; PCN, pregnenolone-16 $\alpha$ -carbonitrile.

1	290 300	310 3	20 330	340	350	360	370 <b>57 380</b>	390
2	N-KILRN-NIVIR-NVVI	FETERNOFTLDI	NNPRDFI	DCFLI-KMEOEK	DN005E	-FTIENLMTT	T D. 4. 202 800 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	KH 306
	R-KAVKN-TEVVK-NVT	FOIKFHOKSLDI	NNPRDFI	DCFLI-KMEOEK	CN005 E	-FTIENLLTT	SOVEMAGTE TTSTTLEYGLLLL	KH 305
3	K-TILKN-ADVIK-NETN	FKVKFHOKLLDV		DCFLI-KMEOEN	NLE	-FTLESLVIA	S DEFGAGTE TTSTTERYSLLLL	KH 313
Ă	H-KTAKN-TNYMK-SVI.	KKTEEHOESLOV	TNPRDFV	DYYLI-KOKOAN	NIEOSE	-YSHENLTCS	MOLIGAGTE THETTLEYALLLM	KY 316
5	T-TLAKN-VYHID-NYLI	KKTKFHOFSLOV	TNPRDFI	DYYLI-KWKOEN	HNPHSE	-FTLENLSIT	T DEFGAGTE TTSTTLRYALLLL	KC 316
š	P-OLEKN-IDGOI-KEII	EXVOENCESLOS	NNPRDFV	DHFLI-KMEKEK	HKKOSE	-FTMDNLITT	WOVFSAGTO TTSHTLEFALLLL	KH 316
7	P-KUTKN-USETK-EVTI	APVEEHHESLOP	SCPRDFI	DSLLI-EMEKDK	HSTEPL	-YTLENIAVT	A DEFFAGTE TTSTTLEYGLLIL	KH 317
. 8	R-KINKN-VSEIK-OVTI	EXAKENLOSLDI	NCARDVT	DCLLI-EMEKEK	HSOEPM	-YTMENVSVT	ADLFFAGTETTSTTLRYGLLILI	KY 318
9	R-KVIKN-VAEVK-EYVS	ERVKENHOSLOP	NCFRDLT	DCLLV-EMEKEK	HSAERL	-YTMDGITVT	A DEFTACTE TTSTTLAYOLLILI	KY 318
10	K-TLIKN-TETVD-DFI	EIVIANCESEDA	SCPRDFI	DAFIN-KMEOEK	EN SY	-FTVESLTRT	LDEFLAGTE TYSTTLRYGLLIL	KH 317
ū	R-GISKN-LOEIL-DYIC	HIVEKHRATLDP	SAPRDFI	DTYLL - RMEKEK	SNHHTE	-FHHENLMIS	LISLFFAGTETOSTTLRYGFLLM	KY 317
12	R-OISKN-LOEIL-DYIC	HIVEKHRATLDP	SAPRDFI	DTYLL-RMEKEK		-FHHENLMIS	LLSLFFAGTETSSTTLEYGFLLM	<b>K</b> Y 317
13	R-OIYRN-LOEIN-TFIC	SOSVEKHRATLDP	SNP RD FI	DVYLL-RMEKDK	SDPSSE	-FHHQNLILT	LSLFFAGTETTSTTLRYGFGLM	<b>X</b> Y 317
14	0-0AFOL-LOGLE-DFI	KKVE-HNTPLDP	NSPRDFI	DSFLI-RMQEEE		-FYLEKLVMT	SLNLFIGGTE TVSTTLEYGFLLL	KH 157
15	L-DAFKD-LNKKFYSFM	KKLIKEHYRTFEK	GHIRDIT	DS-LIEHCODRR	LDENANVQ	-LSDDKVITI	/FDLFGAGFD TITTAISWSLMYL	TN 340
16	L-DAFKD-LNDKFYSFM	KLIKENYRTFEK	GHIRDIT	DS-LIEHCODRK	LDENANVQ	-LSDDKVITI	/LDEFGAGPD TVTTAISHSLMY61	TN 340
17	L-NAFKD-LNEKFYSFMC	KMVKENYKTFEK	GHIRDIT	DS-LIEHCQEKQ	LDENANVQ	-LSDEKIINI	/LOLFGAGTO TVTTAISHSCHYDI	<b>N</b> 336
18	L - DTFKD-LNERFYSFT	ERVKENCRSFEK	GHIRDIT	DS-LIKHYRVDR	LDENANVQ	VSDEKTVGI	LDLFGAGFO TVTTAISWSLMYL	TK 285
19	L-ORFKA-FNORFLWFL	KTVQEHYODFDK	NSV R D I T	GA-LFKHSKKGP	-RASGNL	-IPQEKIVNL	VN DIFGAGFD TVTTAISHSLMYL	тк 336
æ	L-ORFKD-FNORFLRFL	KTVREHYEDFDR	NSIQDIT	GA-LFKHSEKNS	-KANGGL	-IPQEKIVNL	NDIFGAGEDTITTALSWSLMYL	TN 244
21	L-RRFKD-FNQRFLRFL	KTVREHYEDFDR	NSIQDIT	GA-LFKHSEKN-	-KANGGL	- IPQEKIVNL	NDIFGAGED TITTALSWSLNYL	TN 334
22	L-KRFKN-FNDNFVLFL	KTVQEHYQDFNK	NSIQDIT	GA-LFKHSENY-	-KDNGGL	IPQEKIVNI	VNDIFGAGFETVTTAIPHSIGLG	TE 334
23	L-KRFKT-FNDNFVLFL	QKTVQEHYQDFNK	NSIQDIT	SA-LFKHSENY-	-KDNGGL	IPEEKIVNI	VN DI FGAGFD TVTTAITHSILLL'	TW 334
34	M-EKMKG-CVQTRNELLI	NEILEKCQENFSS	DSITNLL	HI-LIQAKVNAD	NNNAGPDQDSI	(LLSNRHMLAT	IG <b>DIFGAGVETTISVIKWIVAYL</b>	HH 321
25	L-EKLKS-HVKIRNDLL	NKILENYKEKFRS	DSITNML	DT-LMQAKMNSD	NGNAGPDQDS	LLSDNHILTT	IGDIFGAGVETTTSVVKHTLAFL	MN 321
26	L-RRLKQ-AIEKROHIV	EMQLRQHKESLVA	GQWRDMM	DY-MLQGVAQPS	MEE-GSGQ	- LLEGHVHMA	AV DELIGETETTANTESWAVVFC	HH 310
27	L-WRLKQ-AIENRDHMV	EKQLTRHKESMVA	GQWRDMT	DY-MLQGVGRQR	VEE-GPGQ	LLEGHVHMS	VVDLFIGGTETTASTLSWAVAPL	HH 309
28	L-QKLKQ-IQESRDHIV	KQQL KQHK <b>E</b> SLVA	GQW <b>KD</b> MI	DY-MLQGVEKQR	DGK-DEEQ	- L HEGHVHMS	<u>vvd</u> lfiggtettattlshava <u>fl</u>	HH 305
29	V-LNICV-FPREVTNFL	RKSVKRMKESRLE	DTQKHRV	D-FLQLMIDSQK	NSKETESHKA-	LSDLELVAQ	SIIVIPAGYETTSSVLSTINYEL.	TH 325
30	M-LNICM-FPKDSIEFF	KKFVYRMKETRLD	SVQ KH RV	D-FLQLMMNAHN	DSKOKESHTA-	LS DMEITAQ	ELIFIFAGYEPTSSTLSFVL <u>HSL</u>	TH 325
31	LANDHTDGVIKLRKDQL	QNAGELEKVKK	K R R L D F L	DILLLARME	DS-	LSDKDLRAE	DT FREEGRO TTASOVERIETAL	TH 339
32	W-RDHVA-AWDTIFNKA	EKYTEIFYQDLRR	K-TEFRNYPGIL	YCLLKSEK		MLLEDVKAN	IT ENLAGEVNITSMILEN	RS 344
33	W-KDHVA-AWDVIFSKA	DIYTQNFYWELRQ	KGSVHHDYRGML	YRLLGDSK		MSFEDIKAN	VTENLACOVOTTSNTLQWHLYEM	<b>RN 345</b>
- 34	RPDGSMT-FAEAK-EAL	Y <b>d</b> ylipii <b>e</b> q <b>rr</b> q	KPGTDAI	SIVANGQV	NGRPI	- TSDEAKR	GIALINGGIADIT VVR FLSISS EFL	KS 267
	400	410 420	430	<b>58</b> 440	450	460 S9	470 480 49	0
1	PEVIA-KVQEEIERVIG-	RHRSPCMQDR	SRM PYT D	TVH TO YTAND	PNNVPRATTCH	VKFRSYLIPK	GTAVITSLISHLY - NOKEFPNPD	FD 398
2	PEVIA-KVQEEIERVIG-	RHRSPCMQDR	SRMPYTD	TVHEIQRYINLI	PNNYPHITICH	LKFRNYLIPK	GTOVLTSLSSVLH-DOKEFPNPDI	FD 397
3	PEVAA-RVQEEIERVIG-	RHRSPCMQDR	SRMPYTD	VINEIQRFIDLL	PTNLPHAVTRO	VRFRNYFIPK	GTØIITSLTSVUN-DEKAFPNPKV	FD 405
4	PHVTA-KVQEEIDRVIG-	RHRSPCMQDR	KHMPYTD	MINEVORFINFU	PINLPHAVIC	DIKFRNYLIPK	GTKVLTSLTSVLH-DSKEFPNPEN	FD 408
5	PEVTA-KVQEEIDRVVG-	KHRSPCMQDR	SRM PYTD	HDHEVQRFIDLI	PTNLPHAVTC	DIKFRNYLIPK	GTT11TSLSSV1H-DSKEFPDPE1	FD 408
6	PEITA-KVQEEIEHVIG-	RHRSPCMQDR	SRMPYTD	VMHEIQRYVDLV	PTSLPHAVTQ	DIEFNGYLIPK	GTDIIPSLTSVLY-DDKEFPNPE	FD 408
7	PEIEE-KLHEEIDRVIG-	PSRMPSVRDR	VQMPYMD	VVHEIQEFIDLV	PSNLPHEATRI	<b>TTFQGYVIPK</b>	GTVVIPTLOSLLY-DKQEFPDPE	FK 409
8	PEIEE-KLNEEIDRVIG-	PSRVPAVRDR	LDMPYMD	VVHEIQRFINLV	PSNLPHEATRI	<b>DTVFQGYVIPK</b>	GTVVIPTL <b>D</b> SLLY-DSHEFPDPE	FK 410
9	PEIEE-KLHEEIDRVIG-	PSRIPAIKDR	QEMPYMD	VVHEIQRFITLV	PSNLPHEATRI	DTIFREYLIPK	GTVVVPTLDAVLY-DNQEFPDPEI	FK 410
: Ot	PEIEE-KMNKEIDRVVG	RDRSPCMADR	SQLPYT D	VIHEIQEFIOFI	PLNVPHAVIK	DTKLR <b>DYFIPK</b>	DTMIPPLLSPILQ-DCKEFPNPE	F <b>D</b> 409
11	PHVTV-KVQKEIDQVIG-	SHRPPSLDDR	TKMPYTD	VINEIQRFADLA	PIGLPHRVTK	DTMF RGYLLPK	NTEVYPILSSACH-DPQYFDHPD7	FN 409
12	PHVAE-KVQKEIDQVIG-	SHRLPTLDDR	SKM PYTDU	vineigrfsølv	PIGVPHRVTK	DTMF ROYLEPK	NTEVYPILSSACH-DPQYFDHPDS	FN 409
13	PHVTE-RVQKEIEQVIG-	SHRPPALDDR	AKM PYTD	VIHEIQRLGOLI	PFGVPHTVTK	TOFREYVIPK	NTEVPPULSSALH-DPRYFETPN1	FN 409
14	PGVEA-KVHEEIDRVIG-	KNRQPKFEDR	AKMPYME	HINELORFGDVI	PHINPGRVKK	DT KF R DE F G P K	GTEVYPMLGSVLR-DPIFLSKPQ	FN 249
15	PRIQR-KIQEELDTVIG-	RDRQPRLSDR	PQLPYL	FILETFRMSSFU	PFTIPHSTIR	DISLNGFYIPE	GHCYFYRQWQVMH-DQELWGDPN	FR 432
16	PRVQR-KIQEELDTVIG-	RDRQPRLSDR	PQLPYL	FILETFRMSSFY	PTTIPHSTTR	DTSLNGTYIPK	GCCVFVNQWQVNH-DRELWGDPN	FR 432
17	PRVQR-KIQEELDTVIG-	RSRRPRLSDR	SHLPYME	FILETERHSSFU	PFTIPHSTTR	DTSLKGFYIPE	GRCVFVNQWQINH-DQKLWVNPS	FL 428
18	RQHTREKIQEELDAVVG	RARRPRESOR	PQLPYL	VINETPENTSFL	PTTIPHSTTR	TSLGEFTIPE	GRCVFVNQWQHMH-DRELWGVPR	FR 378
19 1	PEIQR-KIQKELDTVIG-	RERRPRLSDR	PQLPYL	FILETFRNSSFL	PFTIPHSTTR	DITLNGFYLPK	CCVFVNQWQVNH-DPELWEDPSI	FR 428
20	PRRUK-KIUEELDAVVG-	RARQPLLSDR	PQLPYL	FILELERHISEV	PFTIPHSTTR	TTLNGFALPE	CCIFINGWQINH-DPQLWGDPE	FR 330
2	PRROR-KIQEELDAVVG-	RARQPRLSDR	PQLPYL	FILELFENTSFU	PETIPHSTIR	TTLNGFHIPK	ECCIFINGWQINH-DPQLWGDPE	FR 420
~	PRVQR-KIMEELDTVIG-	RDRQPRLSDR	PQLPYLE	FILEIYEYTSEV	PFTIPHSTIR	DISLNGFMIPE	CGIFINGWQVNH-DEKQWKDPF	FR 420
23	PNVQR-KIMEELDTVVG-	RDRQPRLSDR	PQLPYL	VILEIXEXTSEV	PETIPHSTIR	TSLNGFHIPK	RECITINGMOANH-DEROWEDPP	FR 425
	PSLAR-RIQUDIDQIIG-	FRRIFIISUR	NRLVLLE	<b>2356 2 5 675 56 6 5.8 0</b>	F 141 PHRAVIS		a Luff v f h Lin - A Lin A S E A E WU A F V i	EM 413
26	DETOO - BLOEEL OVELOD				COMPANY TOTAL MANAGER 17		THE FULL AND A THUN FREMHODDO	FM 413
25		CACCCOUD_VVDD		TIREVLALAPVA	PMLIPHKANVE	SSIGEFAVOR	STEVIINLW-ALMHNEKEWHOPDO	FM 413
25 25 26 27	PEIQQ-RLQEELDHELGP	GASSSRVP-YKDR	ARLPLLNA	TINEVLALAPVA TIAEVLALAPVV	PHLIPHKANVE PLALPHRTTRE	SSIGEFAVDK SSISGYDIPE	STEVIINLW-ALMHNEKEWHOPDO Stviipnl-Qgahldetvwerph Stviipnl-Qgahldetvwerph	FM 413 FM 413 FW 405 FP 404
25 25 27 28	PEIQR-RLQEELDHELGP PEIQR-RLQEELDRELGP PEIQK-RLQEELDRELGP	GASSSRVP-YKDR GASCSRVT-YKDR	NRLPLLNA ARLPLLNA ARLPLLNA MOLPLLNA	TIREVLELEPVA TIAEVLELEPVV TIAEVLELEPVV	PHLIPHKANVE PLALPHRTTRE PLALPHRTTRE	SSIGEFAVDE SSISGYDIPE SSIFGYDIPE	STEVIINLW-AL HHNEKEWHQPDO Stviipnl-Qgahldetvwerph Shvvipnl-Qgahldetvweqph Shvvipnl-Qgahldetvweqph	FM 413 FM 413 FW 405 FR 404 FW 397
25 26 27 28 29	PEIQQ-REQEELDHELGP PEIQR-REQEELDRELGP PEIQK-REQEELDLKLGP PDV00-KLOEEIDAVLP-	GASSSRVP-YKDR GASCSRVT-YKDR GSQLLYRNR NKAPPTYDTV	NRLLLL ARLPLLN ARLPLLN MQLPLLN LOMFXLD	TINEVLALAPVA TIAEVLALAPVV TIAEVLALAPVV TIAEVLALAPVV TIAEVLALAPVV	PHLIPHKANVE PLALPHRTTRE PLALPHRTTRE PLALPHRATRA	SSIGEFAVDA SSISGYDIPE SSIFGYDIPE SSIFGYDIPE SSISGYDIPE	STEVIINLW-ALHHNEKEWHQPDC 3TVIIPNL-QGAHLDETVWERPH GMVVIPNL-QGAHLDETVWEQPH DMVIIPNI-QGAHLDETVWEQPH DMVIIPNI-QGANLDEMVWELPSI GWVVMI-DSYATHBDPKYWEPSI	FM 413 FM 413 FW 405 FR 404 FW 397 FL 416
25 26 27 28 29 30	PEIQQ-RLQEELDHELGP( PEIQK-RLQEELDLKLGP( PDVQQ-KLQEEIDAVLP- PDVQK-KLQEEIDAVLP-	GASSSRVP-YKDR GASCSRVT-YKDR GSQLLYRNR NKAPPTYDTV NKAPPTYDTV	NRLLLLEA ARLPLLNA MQLPLLNA LQM <b>PLLNA</b> MEM <b>FVLD</b>	TINEVLALAPVA TIAEVLALAPVV TIAEVLALAPVV TIAEVLALAPVV TIAEVLALAPVV VVNETLALYPIA	PHLIPHKANVE PLALPHRTTRE PLALPHRTTRE PLALPHRATRA HRLERVC-KKE MRLERVC-KKE	SSIGEFAVOR SSISGYDIPE SSIFGYDIPE SSIFGYDIPE SSISGYDIPE VEINGMFIPE	STEVIINLW-ALWHNEKEWHQPDC IIVIIPNL-QCAHLDEIVWERPH INVVIPNL-QCAHLDEIVWERPH DHVIIPNI-QCANLDENVWELPS INVVNI-PSIALWRDPKWEEPS INVVNI-PSIALWRDPKWEEPS	FM 413 FM 413 FW 405 FR 404 FW 397 FL 416 FR 416
25 25 26 27 28 30 31	FEIQQ-RLQEELDRELGP PEIQR-RLQEELDRELGP PEIQK-RLQEELDLKLGP PDVQQ-KLQEEIDRALP- PDTQK-KLQEEIDRALP- PKN00-RCREEVOSVLG-	GASSSRVP-YKDR GASCSRVT-YKDR GSQLLYRNR NKAPPTYDTV NKAPPTYDTV DGSSITWDH	NRLLLLEA ARLPLLN MQLPLLN LQM <b>PLLN</b> MEM <b>EVLD</b> MEM <b>EVLD</b>	TINEVENERPVA TIAEVENERPVV TIAEVENERPVV TIAEVENERPVV VVNETEREPVA VENETEREPVA CIKEALNEVPPV	PHLIPHKANVO PLALPHRTTRE PLALPHRTTRE PLALPHRATRA PRLERVC-KKO MRLERVC-KKO POIVRELSTSV	SSISEFAVOR SSISGYDIPE SSIFGYDIPE SSIFGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSIGFFAVOR SSIGFFAVOR SSIGFFAVOR SSIGFFAVOR SSIGFFAVOR SSIGFFAVOR SSIGFFAVOR SSIGFFAVOR SSIGFFAVOR SSIGFFAVOR SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSISGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG SSIFG S	STEVIINLM-ALMHNEKEWHQPD STVIIPNL-QGAHLDETVWERPH SHVVIPNI-QGAHLDETVWEQPH BHVIIPNI-QGAHLDETVWEQPH SHVVMI-PSYALHRDPKYWTEPE SSVVMI-PSYALHRDPKYWTEPE SSVVMI-PSYALHRDPGHWPEPE	FM 413 FM 413 FW 405 FR 404 FW 397 FL 416 FR 416 FR 416 FD 431
25 26 27 28 29 30 31 32	PEIQE-RLQEELDRELGE PEIQK-RLQEELDRELGP PDVQQ-KLQEELDLKLGP PDVQQ-KLQEEIDAVLP- PDTQK-KLQEEIDALP- PKHQQ-RCREEVQSVLG- LNVQE-MLREE-VLN-	GASSSRVF-YKDR GASSSRVT-YKDR GSQLLYRNR NKAPPTYDTV NKAPPTYDTV DGSSITWDH ARROAEGDI	NRLPLLL ARLPLLN MQLPLLN LQMPLL LQMEVLO MEMEVLO LDQI-PYTT SKMLOMVPLC	TIREVIRIAPVA TIREVIRIAPVU TIREVIRIAPVU TIREVIRIAPVU VUNETLRIPVI VUNETLRIPPI GIRERIRIAPIS	PHLIPHKANVO PLALPHRTTRE PLALPHRTTRE PLALPHRATRA PLALPHRATRA PLALPHRATRA PLERVC-KKO POIVRELSTSV VTLORVP-ES	DSSIGEFAVOR PSSIFGYDIPE SSIFGYDIPE ASSISGYDIPE OVEINGMFIPE OVEINGMFIPE JTFPDGRSLPE	STEVIINLW-ALWHNEKEWHQPD 11VIIPNL-QGAHLDETVWERPM SHVVIPNL-QGAHLDETVWERPM SHVVIPNI-QGANLDETVWELPS SHVVHI-PSYALWRDPKYWTEPE SIVMI-PSYALWRDPQHWPEPI IIQV-TLSIYGLHMNPKVWPNPE STQV-TLSIYGLHMNPKVWPNPE	FM 413 FM 413 FW 405 FW 405 FW 397 FL 416 FF 416 FF 416 FD 431 FD 431
25 25 27 28 29 30 31 32 33	PEIQR-RLQEELDHELGY PEIQR-RLQEELDLKLGY PDVQ-KLQEELDLKLGY PDVQ-KLQEELDALP- PKNQQ-RCREEVQSVLG- LNVQE-MLREEVLN- LNVQE-MLREVLN-	5385829-34808 GASCSRVT-4KDR GASCSRVT-4KDR G8QLLYRNR NKAPPTYDTV DGSSITWDH ARRQAEGDI ARRQAOGDM	N RLPLLM A RLPLLM MQLPLLM LQMETLM MEMETLM LDQI-PYTT S KMLQM VPLL A TMLOLVPLLM	TIN VLALAPVA TIA VLALAPVA TIA VLALAPVA TIA VLALAPVA TIA VLALAPVA VLNTLALYPIG CIKEALALYPY SIKTLALAPIS SIKTLALAPIS	PHLIPHKANV PLALPHRTTRE PLALPHRTTRE PLALPHRATRA MRLERVC-KKI MRLERVC-KKI POIGRELSTSV VTLORYP-ESI VTLORYL-VNL	SSICEFAVOR SSISCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYDIPE SSIFCYD SSIFCYD SSIFC SSIFCYD SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC SSIFC	STEVIINLW-AL HHNEKEWHQPD STUIPNL-QGAHLDETVWERPH SHVIPNL-QGAHLDETVWERPH SHVIIPNI-QGANLDETVWELPS SHVVIIPNI-QGANLDEMVWELPS SHVVII-PSYALHADFAYWTEPEL SIQV-TLSIYGLHHNPKVWPNEV KTLVQV-AIYANGRDFAFFSSPD	FM 413 FM 413 FW 405 FR 404 FW 397 FL 416 FR 416 FD 431 FD 435 FD 436
25 26 27 28 29 30 31 32 33 34	PEIQR-RLQEELDNELGP PEIQR-RLQEELDLKLGP PDVQQ-KLQEEIDAVLP- PDVQQ-KLQEEIDRALP- PKNQQ-RCREEVQSVLG- LNVQE-MLREEVLN- LKVQD-MLRAEVLN- LKVQD-MLRAEVLN-	GASSSRVP-YKDR GASCSRVT-YKDR GSQLLYRNR NKAPPTYDTV DGSSITWDH ARRQAEGDI PENTPACE*	NRLPLLM ARLPLLM AQLPLLM LQMEVLM MQLEVLM LQMEVLM LDQI-PYTT SKMLQMVPLLK ATMLQLVPLLK	TIAUVIRIAPVA TIAUVIRIAPVV TIAUVIRIAPVV VUNETLEIPVV VUNETLEIPIA SIKETLEIMPIS SIKETLEIMPIS	PHLIPHKANV PLALPHRTTR PLALPHRTTR PLALPHRTR HRLERVC-KK MRLERVC-KK VTLQRYL-ES VTLQRYL-VN ADD-RL-TN	SSIGEFAVOR SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYDIPE SSIFGYSIFE SSIFGYSIFE SSIFGYSIFE SSIFGYSIFE	STEVIINLM-ALMHNEKENHOPO ITVIIPNL-QGAHLDETVWERPH HNVIIPNL-QGAHLDETVWERPH HNVIIPNL-QGANLDENVWELPS HNVNI-PSYALHOPKYWELPS GSVVMI-PSYALHOPKYWPPE GIQV-TLSIGCHMNPKWPNE KILVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGREPTFFDE HTLVQV-AIYALGRE	FM 413 FM 413 FW 405 FR 404 FW 397 FL 416 FR 416 FD 431 FD 435 FD 436
25 25 27 28 29 30 31 32 33 34	PEIQR-RLQEELDRELGP PEIQR-RLQEELDLKLGP PDVQQ-KLQEELDLKLGP PDTQK-KLQEELDRALP- PKNQQ-RCREEVQSVLG- LNVQE-MLREEVLA- PEHRQELIER	GASSSRVP-YKDR GASCSRVT-YKDR GSQLLYRNR NKAPPTYDTV NKAPPTYDTV DGSSITWDH ARMQAQGDM PERTPACE	N RLPLLM A RLPLLM A RLPLLM LQMEVLM MEMEYLM LDQI-PYTT S KMLQMVPLKA A TMLQLVPLKA	TIAUURIPU TIAUURIPU TIAUURIPU TIAUURIPU TIAUURIPU SIAUTALPI SIAUTALPI SIAUTALPI SIAUTALPI SIAUTALPI SIAUTALPI SIAUTALPI SIAUTALPI	PHLIPHKANV PLALPHRTTRI PLALPHRTTRI PLALPHRTRA MRLERVC-KKI MRLERVC-KKI VTLQRYL-VNI VTLQRYL-VNI ADG-RIL-TSI	SSIGEFAVER PSSIFGYDIPE SSIFGYDIPE SSIFGYDIPE VEINGMFIPE VEINGMFIPE VEINGMFIPE VEINGMFIPE VEINGMFIPE VEINGMFIPE VEINGYFIPE VEINGYFIPE VEINGYFIPE	STEVIINLW-ALMHNEKEWHQPD IIVIIPNL-QGAHLDETVWERPH HNVIPNI-QGANLDETVWERPH HNVIPNI-QGANLDETVWELPS SIVVII-PSYALHRDPCHWELPSI SIVVI-PSYALHRDPCHWPEPEI IIQV-TLSIVGLMHNPKVWPNPE KILVQV-AIVALGREPTFFFDE BDQILLPQMLSG-DDERENACPM	FM 413 FM 413 FW 405 FR 404 FW 397 FL 416 FF 416 FF 416 FF 431 FF 435 FF 435 FF 435
25 25 27 29 30 31 32 33 34	PEIQR-RLQEELDRELGP PEIQR-RLQEELDLKLGP PDVQQ-KLQEELDALP- PDTQK-KLQEELDALP- PKNQQ-RCREEVQSVLG- LNVQE-MLREVLN- LKVQD-MLRAEVLA- PEHRQELIER	GASSSRVP-YKDR GASSSRVT-YKDR GASCSRVT-YKDR GASCSRVT-YKDR 	N RLPLLN A RLPLLN MQLPLLN LQMEVLN MEMEVLN LDQI-PYTT S KMLQMVPLCK A ATMLQLVPLKA	TIATULALAPU TIATULALAPU TIATULALAPU TIATULALAPU VIVELLAPI CINEALALYPI SINETLAPI SINETLAPI SINETLAPI SINETLAPI SINETLAPI SI	PHLIPHKANVU PLALPHRTTRE PLALPHRTTRE PLALPHRATRE PRLERVC-KKI MALERVC-KKI POTURELSTS VTLQRYP-ESI VTLQRYP-ESI VTLQRYP-ESI ADG-RIL-TSI	SSIGEFAVOR SSIGEFAVOR SSIGEOIPE SSIGEOIPE SSIGEOIPE SSIGEOIPE VELOVENTE TPPDGRSLPK DIVLOPINE DIVLOPINE SSO S11	STEVIINLW-AL HHNEKEWHQPD STEVIINLW-AL HHNEKEWHQPD STVIIPNL-QGAHLDETVWERPH BHVIIPNI-QGANLDETVWEQPH BHVIIPNI-QGANLDENVWELPS STVMI-PSTALHRDPCWPEPEI STQV-TLSIVGLHHNPKVWPNPE KTLVQV-AIXANGRDPAFFSPD BDQILLPOHLSG-DERENACPH 570580	FM 413 FM 413 FW 405 FR 404 FW 397 FL 416 FR 416 FD 431 FD 435 FD 436 FD 436
28 25 26 27 28 29 30 31 32 33 1	PEIQR-RLQEELDNELGR' PEIQR-RLQEELDLKLGP PDVQQ-KLQEEIDAVLP- PDVQQ-KLQEEIDRALP- NVQE-MLREEVLN- LVVQE-MLREEVLN- ENVQE-MLREEVLN- 500 SI PGMFLDASGK-FRK-SD	GASSSRVP-YKDR GASSSRVT-YKDR GASCSRVT-YKDR GSQLLYRNR NKAPPTYDTV NKAPPTYDTV ARRQAEGDI ARRQAEGDI PER <u>FAACE</u> 0 520 51	NRLPLIM ARLPLIM MQLPLIM MQLEYLD MEMEYLD MEM	TIRULLAPUA TIATUALAPUA TIATUALAPUA TIATUALAPUA TIATUALAPIA VUNETLALAPIA VINETLALAPIA SIATIALAPIA SIATIALAPIA SIATIALAPIA SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATIAN SIATI	PHLIPHKANVU PLALPHRTTRE PLALPHRTTRE PLALPHRTTRE PLALPHRATRA MRLERVC-KKI MRLERVC-KKI MRLERVC-KKI MRLERVC-KKI MRLERVC-KKI VTLQRYL-VKI VTLQRYL-VKI S50 PKPLVDPKDI	SSIGEFAVE SSIGEFAVE SSIGYDIPE SSIGYDIPE SSIGYDIPE SSIGYDIPE SSIGYDIPE SSIGYDIPE SSIGYDIPE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGEFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE SSIGFAVE	STEVIINLM-ALMHNEKEWHOPO ITVIIPNL-QGAHLDETVWERPHI HVVIPNL-QGAHLDETVWERPHI HVVIPNL-QGANLDETVWERPHI HVVIPNI-QGANLDENVWELPSI GSVVMI-PSXALHRDPKWPPEI GSVVMI-PSXALHRDPKWPPEI JIQV-TLSIVGLHNPKVWPNE KTLVQV-AIYALGREPTFFFDE BOILLPGHLSG-DERENACPHI 570 590 VPPLVQLSFI-PA	FM 413 FM 413 FW 405 FW 405 FW 405 FR 404 FFW 397 FL 416 FP 431 FD 435 FD 436 FD 436
24 25 26 27 28 29 30 31 32 33 1 2 29 30 1 2 29 30 31 2 33 1	PEIQR-RLQEELDRELGP PEIQR-RLQEELDRLGP PDVQQ-KLQEELDRLGP PDVQC-KLQEELDRLP PKNQQ-RCREVQSVLG- LNVQE-MLREEVLA- DVQE-MLRAEVLA- PENRQELIER 500 50 PGHFLDASGK-FRKSD PGHFLDASGN-FRK-SD	GASSSRVP-YKDR GASSSRVT-YKDR GASCSRVT-YKDR NKAPPTYDTV NKAPPTYDTV DGSSITWDH ARNQAQGDM 	NRLPLLM ARLPLLM ARLPLLM MQLPLLM LQMEYLDM MEMEYLDM MEM	TIRUCHLAPVA TIRUCHLAPVA TIRUCHLAPVA TIRUCHLAPVA VUNTILLYPIO CIREALLYPIO SIRTICHPIS SIRTICHPIS 	PHLIPHKANVU PLALPHRITR PLALPHRITR PLALPHRITR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRAT PLALPHRAT PLALPHRAT PLALPHRAT PLALPHRAT SO SO PKPLVDPKDI PKPLVDPKDI	SSIGEFAVER SSIFEVENTE ASSISEVENTE ASSISEVENTE ASSISEVENTE VELNEWIPE TIPEORSLER DUVLOVINE VITEORIA SSO SII DELIFSSIVE	STEVIINLW-ALWHNEKEWHQPD IVIIPNL-QGAHLDETVWERPH HVVIPNL-QGAHLDETVWERPH HVVIPNI-QGANLDETVWEQPH HVVIPNI-QSANLDEMVWELPSI SVVMI-PSYALWRDPQHWELPSI SVVMI-PSYALWRDPQHWELPSI IIQV-ILSIVGLHNPKVWPNEL IIQV-ILSIVGLHNPKVWPNEL SVDJLLPQHLSG-DDERENACPM 570 590 VFFLYQLSFI-PA VFFLYQLSFI-PA VFFLYQLSFI-PA	FM 413 FM 413 FW 405 FW 405 FR 404 FW 397 FL 416 FR 416 FD 431 FD 435 FD 435 FD 436 FD 436 480 480
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DTQK - KLQEEIDRALP - 500 PGHFLDASGK - FRK - SD PGHFLDASGN - FRK - SD PGHFLDESGN - FKK - SD PGHFLDASGK - FKK - SD PEHFLNEGK - FKY - SD PEHFLDADGT - LKK - SE PEHFLDADGT - LKK - SE PEHFLTPSGT - LDKRLSE	GASSSRVP-YKDR GASSSRVP-YKDR GASCSRVT-YKDR GASCSRVT-YKDR NKAPPTYDTV NKAPPTYDTV ARRQAEGDI ARRQAEGDI 		TIRULERPUT TIRULERPUT TIRULERPUT TIRULERPUT UNTIRULERPUT UNTIRULERPUT UNTIRULERPUT UNTIRUM TIRULERPIT UNTIRUM SIGTIRUM TATION	RHLIRHKANU PLALPHRTTR PLALPHRTTR PLALPHRTTR PLALPHRTTR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPHRATR PLALPH	SSIGGYAVAR SSIGGYAVAR SSIGGYAVAR SSIGGYAVAR SSIGGYAVAR SSIGGYAVAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR SSIGGYAPAR	STEVIINLW-ALMHNEKEMHQPO ITVIIPNI-QGAHLDETVWERPH HVVIPNI-QGAHLDETVWERPH HVVIPNI-QGANLDETVWERPH HVVIPNI-QGANLDETVWERPH SVVMI-PSYALHRDPKWEPE GSVVMI-PSYALHRDPKWEPE GSVVMI-PSYALHRDPKWEPE GSVVMI-PSYALHRDPKWEPE GSVVMI-PSYALHRDPKWEPE GSVVMI-PSYALHRDPKWEPE GSVVMI-PSYALHRDPKWEPE GSVVMI-PSYALHRDPKWEPE GSVVMI-PSYALHRDPKWEPE GSVVMI-PSYALH HVPSYALGT-PA VPFLYQLGTI-PS LPPYYLGTI-PS LPPYYLGTI-PS LPPYYLGTI-PS IPFIFYLGVI-PK SSGVV VFFLYQLGTI-PS IPFIFYLGVI-PK SSGVV VFFLYQLGTI-PS IPFIFYLGVI-PK SSGVV VFFLYQLGTI-RS IPFIFYLGVI-FR MPRYTMSTI-FR KNACCHNRQVQMRSSGPCHLQA	FM 413 FW 413 FW 405 FW 405 FR 404 FF 416 FF 416 FF 416 FF 416 FF 416 FF 416 FF 416 FF 436 FF 446 FF
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PDTQQ - MLQEIDRALP         PKMQQ - RCREEVQSVLG         LNVQE-MLREE VLN         SOO         PGHFLDASGK-FRKSD         PGHFLDASGN-FKKSD         PGHFLDSGN-FKKSD         PGHFLDGNGK-FKKSD         PGHFLDGNGK-FKKSD         PGHFLDBSGN-FKKSD         PGHFLDBSGN-FKKSD         PGHFLDBSGN-FKK-SD         PGHFLDASGK-FKY-SD         PGHFLDASGN-FKK-SD         PGHFLDASGN-FKK-SD         PGHFLDASGN-FKK-SD         PGHFLDASGN-FKK-SD         PGHFLDASGN-FKK-SD         PGHFLDASGN-FKK-SD         PGHFLDASGN-FKK-SD         PGHFLDASGN-FKK-SD         PGHFLDASGN-FKK-SD         PEHFLDASGN-FKK-SD         PEHFLDASGN-FKK-SD         PEHFLDASGN-FKK-SD         PEHFLDASGN-FKK-SD         PEHFLDASGN-FKK-SD         PEHFLDASGN-FKK-SD         PEHFLDASGN-FKK-SD         PEHFLDASGN-FKK-SD         PEHFLDASGN-FKK-SD         PEFLDASGN-FKK-SD         PEFLTADGAAINKPLSE         PERFLTADGAAINKPLSE         PERFLDASGN-SKLSSNS<td>GASSSRVP-YKOR GASCSRVT-YKOR GASCSRVT-YKOR GASCSRVT-YKOR GASCSRVT-YKOR NKAPPTYDTV NKAPPTYDTV ARRQAEGDI PERTFACCE 0 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FIG. 1-continued



FIG. 2. Hydropathy plots of cytochrome P-450 sequences computed as described under "Materials and Methods." The dark boxes numbered 1-11 above and below each column of plots represent the approximate location of the 11 potential transmembrane segments shown in Fig. 1.

# Membrane Topology of Cytochrome P-450

## TABLE II

# Possible transmembrane segments and their hydropathic indices

The position of the first amino acid is given under pos. The number of amino acids in each segment is given in parentheses under win (for window width). The values of the hydropathic indices were calculated as described under "Materials and Methods," using either the Goldman, Engelman, and Steitz (GES) scale or the Kyte and Doolittle (KD) scale. (See Table I for the two scales.)

		Segment 1				Segment 2			Segment 3		
		pos (win)	GES	KD	pos (win)	GES	KD	pos (win)	GES	KD	
1	PBc1		_		54 (19)	-18.8	-15.3	86 (18)	-19.8	-22.1	
2	PBc2				54 (17)	-13.9	-10.2	86 (18)	-19.3	-21.8	
3	1	3 (18)	-40.4	-49.2	54 (17)	-15.0	-11.9	86 (18)	-18.9	-19.7	
4	f	3 (18)	-40.5	-41.4	54 (17)	-14.7	-11.2	86 (18)	-20.7	-14.1	
5	<b>PB</b> 1	3 (18)	-44.1	-49.1	54 (17)	-16.6	-16.4	86 (18)	-18.9	-17.7	
6	3b	3 (18)	-42.2	-50.6	54 (17)	-12.5	-10.9	87 (17)	-19.7	-19.4	
7	3 <b>a</b>	3 (21)	-50.0	-51.7	54 (17)	-16.0	-15.0	87 (17)	-4.3	-20.0	
8	j rat	3 (21)	-47.8	-53.0	54 (17)	-16.9	-14.0	87 (17)	-2.7	-18.0	
9	j human	3 (21)	-47.3	-47.8	54 (17)	-16.9	-14.0	87 (17)	-13.9	-16.8	
10	Chicken	3 (21)	-46.9	-51.3	55 (17)	-6.9	-4.3	87 (20)	-4.9	-12.4	
11	е	3 (18)	-43.0	-52.7	54 (17)	-0.3	-5.3	90 (17)	-13.8	-18.5	
12	b	3 (18)	-43.0	-52.7	54 (17)	-0.3	-5.3	90 (17)	-13.8	-18.5	
13	LM2	3 (18)	-46.7	-52.6	54 (17)	-12.7	-8.5	90 (17)	-16.1	-23.5	
14	Human										
15	с	9 (22)	-37.0	-35.7	54 (18)	-21.7	-9.3	90 (17)	-12.8	-24.5	
16	P1 mouse	9 (22)	-39.8	-45.5	54 (18)	-22.9	-7.5	90 (17)	-12.8	-24.5	
17	P1 human	9 (22)	-41.9	-46.4	54 (18)	-15.3	-0.6	90 (17)	-12.8	-24.5	
18	6							90 (17)	-13.4	-22.8	
19	4 human	9 (20)	-36,3	-41.5	54 (18)	-14.5	-3.6	90 (17)	-12.6	-23.7	
20	4 rabbit										
21	LM4	9 (20)	-35.7	-45.0	55 (17)	-22.2	-10.7	90 (17)	-13.4	-22.8	
22	d	7 (21)	-37.7	-46.2	54 (18)	-22.5	-7.0	90 (17)	-12.8	-24.5	
23	<b>P</b> 3	7 (21)	-38.3	-44.3	54 (18)	-16.9	-4.7	90 (17)	-12.8	-24.5	
24	17ab	19 (17)	-36.9	-34.6	54 (18)	-9.1	-9.4	87 (18)	-2.6	-4.9	
25	17ah	19 (17)	-25.0	-28.3	54 (18)	-15.6	-15.4	87 (18)	-1.9	-6.8	
26	C21h	3 (18)	-25.4	-37.6	54 (21)	-13.8	-19.6	87 (17)	1.7	-16.7	
27	C21b	3 (20)	-38.5	-41.6	54 (21)	-16.9	-20.1	87 (17)	11.4	-16.1	
28	C21m	3 (20)	-27.9	-33.8	54 (21)	7.0	-15.7	87 (17)	1.7	-16.5	
29	HLp	13 (20)	-29.3	-35.4	52 (18)	-19.6	-13.1	87 (18)	5.3	0.1	
30	р	13 (20)	-32.7	-40.1	53 (22)	-16.2	-8.0	87 (18)	-7.3	-9.3	
31	LAw	12 (22)	-41.4	-43.3	47 (19)	-10.5	-1.5	86 (19)	-5.9	-6.5	
32	sccb	6 (20)	-7.4	-17.9	49 (19)	6.8	8.5	87 (18)	24.5	0.7	
33	scch	6 (19)	3.2	-3.3	49 (19)	7.8	7.5	87 (18)	25.2	0.6	
34	cam	16 (18)	6.7	4.3	58 (18)	-0.3	-3.5	89 (19)	9.3	-1.5	

		Segment 4				Segment 5			Segment 6		
		pos (win)	GES	KD	pos (win)	GES	KD	pos (win)	GES	KD	
1	PBc1	124 (18)	-6.8	-16.6	212 (17)	-29.7	-32.9	264 (17)	-10.2	-13.6	-
2	PBc2	124 (18)	3.7	-11.8	212 (17)	-29.7	-32.9	264 (17)	-17.9	-18.8	
3	1	124 (18)	-9.6	-16.8	212 (17)	-30.1	-33.6	264 (17)	-10.5	-11.0	
4	f	124 (18)	-13.4	-11.3	212 (17)	-21.4	-26.5	264 (17)	-19.1	-11.8	
5	PB1	124 (18)	-3.9	-13.7	212 (17)	-30.6	-33.9	264 (17)	-27.9	-21.0	
6	3b	124 (18)	-11.2	-21.3	212 (17)	-33.5	-38.5	264 (17)	-22.0	-20.8	
7	3a	124 (17)	17.3	-2.7	212 (17)	-21.6	-27.6	259 (19)	-4.7	-2.3	
8	j rat	124 (17)	19.8	2.0	212 (17)	-20.1	-29.8	259 (16)	-8.9	-6.2	
9	j human	124 (17)	26.3	3.0	212 (17)	-24.7	-31.5	264 (17)	-10.9	-6.4	
10	Chicken	124 (18)	-12.5	-19.3	212 (18)	-19.0	-29.7	264 (17)	7.3	-1.9	
11	e	124 (18)	-13.8	-24.0	212 (18)	-29.6	-31.6	259 (19)	-25.5	-20.2	
12	b	124 (18)	-13.8	-24.0	212 (18)	-29.6	-31.6	259 (19)	-25.5	-20.2	
13	LM2	124 (18)	-7.7	-20.3	212 (18)	-27.4	-27.0	259 (19)	-24.1	-21.1	
14	Human				212 (18)	-19.3	-25.7	254 (24)	-21.7	-26.0	
15	с	126 (17)	-11.1	-4.6	212 (18)	-25.7	-35.9	258 (17)	-6.9	-10.2	
16	P1 mouse	126 (17)	-6.0	-1.7	212 (18)	-21.3	-31.7	258 (17)	-6.4	-9.9	
17	P1 human	126 (17)	-15.5	-4.7	212 (18)	-12.8	-27.1	258 (17)	-4.2	-12.9	
18	6	126 (17)	-15.0	-9.4	212 (18)	-20.4	-26.9	258 (17)	-16.6	-20.7	
19	4 human	126 (17)	-10.0	-4.1	212 (18)	-16.6	-22.9	258 (17)	-8.9	-11.8	
20	4 rabbit	126 (17)	-9.9	-0.1	212 (18)	-13.7	-21.8	258 (17)	-14.1	-15.0	
21	LM4	126 (17)	-9.9	-0.1	212 (18)	-13.7	-21.8	258 (17)	-14.1	-15.0	
22	d	126 (17)	-6.0	-1.7	212 (18)	-9.1	-20.7	258 (17)	-5.6	-15.1	
23	P3	126 (17)	-6.0	-1.7	212 (18)	-14.5	-23.4	258 (17)	-5.6	-15.1	
24	17ab	126 (17)	1.4	-12.9	212 (18)	-29.3	-30.7	258 (18)	-7.2	-29.9	
25	17ah	126 (17)	14.6	-3.9	212 (18)	-23.7	-28.2	258 (18)	5.7	-13.9	
26	C21h	126 (17)	7.2	0.2	219 (15)	-29.9	-26.3	258 (19)	-11.7	-18.7	
27	C21b	126 (17)	9.5	-2.7	219 (15)	-29.9	-26.3	258 (19)	-7.8	-12.5	
28	C21m	126 (13)	2.4	-6.7	219 (15)	-28.2	-21.4	258 (19)	-17.4	-20.2	
29	HLp	128 (15)	-16.8	-14.8	218 (17)	-19.6	-17.0	266 (19)	-33.6	-37.1	
30	р	128 (15)	-6.6	-14.4	218 (17)	-19.6	-17.0	266 (19)	-29.3	-31.0	

				Т	ABLE II—conti	nued					
			Segment 4	_		Segment 5			Segment 6		
		pos (win)	GES	KD	pos (win)	GES	KD	pos (win)	GES	KD	
31	LAw	130 (17)	-15.1	-22.5	218 (15)	-20.0	-20.5	266 (18)	4.8	3.3	
32	sccb	126 (19)	8.3	-0.3	215 (15)	-20.7	-18.7	256 (23)	-10.6	-12.6	
33	scch	124 (21)	-1.8	-8.7	215 (15)	-15.8	-20.6	256 (23)	-16.1	-17.3	
34	cam	126 (17)	5.7	-2.7	190 (18)	-0.7	-6.7	249 (18)	0.9	-18.5	
			Segment 7			Segment 8			Segment 9		
		pos (win)	GES	KD	pos (win)	GES	KD	pos (win)	GES	KD	
1	PBc1	368 (21)	-13.7	-14.9	433 (18)	11.3	-2.7	461 (18)	-18.9	-16.6	
2	PBc2	368 (21)	-16.1	-17.2	433 (18)	11.3	-2.7	461 (18)	-10.0	-13.8	
3	1	368 (21)	-12.9	-16.0	433 (18)	-1.2	-15.8	461 (18)	-12.3	-13.9	
4	f	368 (21)	-16.1	-21.0	433 (18)	-1.9	-10.5	461 (18)	-2.0	-9.8	
5	PB1	368 (21)	-13.9	-18.7	433 (18)	15.5	-2.1	461 (18)	-12.2	-13.9	
6	3b	368 (21)	-14.2	-20.5	433 (18)	-1.8	-11.6	461 (18)	-15.8	-17.1	
7	3a	368 (21)	-16.9	-18.4	433 (18)	0.2	-15.5	461 (18)	-8.3	-18.1	
8	j rat	368 (21)	-16.9	-18.4	433 (18)	0.4	-13.7	461 (18)	-8.3	-18.1	
9	j human	368 (21)	-16.9	-18.4	433 (18)	-5.6	-16.5	461 (18)	-7.8	-17.8	
10	Chicken	368 (21)	-24.6	-24.4	433 (18)	-3.5	-19.4	462 (17)	-11.0	-17.4	
11	e	368 (21)	-17.3	-17.0	433 (18)	-6.2	-19.1	461 (18)	-6.8	-10.0	
12	b	368 (21)	-16.9	-16.6	433 (18)	-6.0	-19.3	461 (18)	-6.8	-10.0	
13	LM2	368 (21)	-17.5	-16.7	433 (18)	-6.6	-19.3	461 (18)	-10.8	-14.9	
14	Human	368 (21)	-17.4	-23.7	433 (18)	-9.2	-15.3	462 (17)	-18.6	-16.8	
15	c	368 (21)	-30.0	-25.5	433 (18)	-19.4	-18.3	461 (18)	6.3	0.5	
16	P1 mouse	368(21)	-29.5	-25.2	433 (18)	-19.5	-18.3	461 (18)	1.3	-5.2	
17	P1 human	368 (22)	-32.9	-27.1	433 (18)	-19.5	-18.3	461 (18)	15.1	1.5	
18	6	368 (21)	-29.5	-25.2	433 (18)	-19.8	-17.5	461 (18)	23.0	9.5	
19	4 human	368 (21)	-29.8	-25.9	433 (18)	-19.6	-17.9	461 (18)	11.1	-1.7	
20	4 rabbit	368 (21)	-30.0	-25.5	433 (18)	-21.7	-22.9	461 (18)	5.7	-4.5	
21	LM4	368 (21)	-30.0	-25.5	433 (18)	-21.7	-22.9	461 (18)	5.7	-4.5	
22	d	368 (21)	-37.1	-37.2	433 (18)	-18.4	-19.7	461 (18)	6.2	-4.2	
23	P3	368 (21)	-33.6	-33.7	433 (18)	-18.4	-19.7	461 (18)	24.9	7.0	
24	17ah	368 (21)	-20.0	-26.8	433 (18)	3.6	-16.2	459 (19)	1.9	-17.5	
25	17ah	368 (21)	-22.2	-25.0	433 (18)	1.7	-18.1	459 (19)	-1.4	-19.3	
26	C21h	368(21)	-25.5	-26.0	433 (18)	-4.9	-23.7	459 (19)	3.2	-6.6	
27	C21h	368(21)	-30.8	-25.3	433 (18)	-4.9	-23.7	459 (19)	-1.6	-12.5	
28	C21m	368(21)	-31.4	-25.4	432 (19)	8.3	-25.6	459 (19)	2.5	-10.1	
29	HLD	365(21)	-30.1	-27.0	430 (17)	-4.9	-18.1	459 (19)	-19.2	-19.7	
30	n	365 (20)	-26.9	-24.1	430 (17)	8.2	-6.0	459 (19)	-17.4	-19.5	
31	ĹAw	367 (22)	-15.4	-11.3	433 (17)	-4.6	-16.8	463 (15)	-7.8	-11.2	
32	sech	368 (21)	-17.3	-8.7	430 (19)	3.1	-14.4	462 (17)	-12.9	-19.6	
33	sech	368 (21)	-12.9	-8.7	430 (19)	3.1	-14.4	462 (17)	-12.9	-19.6	
	00011		T 20.0	<b>v.</b> .				/			

			Segment 10		Segment 11			
		pos (win)	GES	KD	pos (win)	GES	KD	
1	PBc1	521 (20)	-24.7	-41.1	559 (20)	-11.1	-13.0	
2	PBc2	521 (20)	-23.7	-38.7	560 (19)	0.7	-15.0	
3	1	521 (20)	-22.9	-31.6	559 (20)	-23.8	-25.3	
4	f	521 (20)	-25.7	-31.6	559 (20)	-22.3	-16.2	
5	PB1	521 (20)	-22.4	-29.3	559 (20)	-19.4	-16.1	
6	3b	521 (20)	-20.8	-32.6	559 (20)	-3.3	-7.8	
7	3a	521 (20)	-21.6	-37.4	559 (20)	17.0	-9.8	
8	i rat	521 (20)	-21.6	-37.4	559 (20)	-19.9	-22.0	
9	i human	521 (20)	-21.9	-38.3	559 (20)	-5.5	-18.3	
10	Chicken	521 (20)	-21.8	-32.5	559 (20)	-13.2	-15.8	
11	e	521 (20)	-16.3	-28.2	559 (21)	-6.6	-7.7	
12	b	521 (20)	-16.3	-28.2	559 (21)	1.8	-1.6	
13	LM2	521 (20)	-22.3	-31.0	559 (21)	13.2	1.4	
14	Human	522 (19)	-22.2	-25.2	559 (20)	12.2	4.0	
15	c	522 (19)	-21.7	-37.7	559 (17)	9.3	1.3	
16	P1 mouse	522 (19)	-19.5	-33.1	559 (17)	9.7	3.8	
17	P1 human	522 (19)	-20.9	-34.8	559 (17)	-7.1	-6.6	
18	6	522 (19)	-20.4	-34.7	559 (17)	7.2	0.5	
19	4 human	522 (19)	-24.7	-39.9	559 (17)	8.9	-2.8	
20	4 rabbit	522 (19)	-23.0	-39.7	559 (17)	10.7	0.6	
21	LM4	522 (19)	-21.1	-34.4	559 (17)	12.6	5.8	
22	d	522 (19)	-21.7	-34.5	559 (17)	4.3	2.7	
23	P3	522 (19)	-21.7	-34.5	559 (17)	6.7	5.3	
24	17ab	521 (20)	-1.8	-19.4	556 (17)	0.1	-9.2	
25	17ah	521 (20)	-16.6	-30.2	556 (17)	-15.9	-23.8	
26	C21h	521 (20)	-6.0	-31.6	555 (20)	-8.0	-10.8	
27	C21b	521 (20)	-8.4	-36.9	553 (22)	6.4	-3.9	

· · -			Segment 10		Segment 11						
		pos (win)	GES	KD	pos (win)	GES	KD				
28	C21m	521 (20)	-6.4	-34.1	554 (21)	8.8	-1.3				
29	HLp	521 (20)	2.9	-22.7	556 (19)	2.8	-14.5				
30	r D	521 (20)	1.3	-18.1	556 (19)	12.6	-6.5				
31	ĹAw	521 (21)	-3.6	-21.3	557 (20)	9.7	-12.0				
32	sccb	521 (20)	-5.8	-26.0	560 (17)	-10.6	-22.0				
33	sech	521 (20)	-3.3	-21.8	557 (20)	-13.8	-12.8				
34	cam	521 (16)	14.1	-12.4	558 (20)	-3.6	-10.3				

TABLE II—continued

highly probable that this first segment is a transmembrane segment.

Experimental evidence has recently appeared to support this contention. A fusion protein composed of the first 29 amino acids of rabbit P-450 6 (P450IA1) and interleukin 2 minus its signal peptide is correctly targeted to the ER membrane. The targeting is dependent on the presence of signal recognition particle. When only 20 amino acids of P450 6 are used the fusion protein is not targeted to the membrane (14). These results suggest that the first 29 amino acids of P450 6 act as a signal sequence. The transmembrane nature of signal sequences is an essential feature of the signal sequence hypothesis.

The consequence of a cytoplasmic NH<sub>2</sub>-terminal, a cytoplasmic residue at alignment position 168, and a transmembrane orientation for S1 in Fig. 1 is the need for a second transmembrane segment between S1 and position 168. Evidence for a second transmembrane segment in this region is lacking, but the geometric argument that requires the existence of such a segment follows naturally from the experimental evidence described above. Referring to Fig. 1, there are three transmembrane candidates for this second transmembrane segment. Two of these can be eliminated with certainty by reference to a study (13) in which site-specific antibodies were used to identify the sideness of regions in rat P450IIB1 (P-450b). In this study 15 synthetic peptides were used to raise polyclonal antibodies, then the antibody binding to microsomes was assessed. Four peptides were clearly cytoplasmic by two different methods <sup>125</sup>I-IgG binding and immunocytochemistry with colloidal gold antibody. These four peptides correspond to alignment position 86-97, 133-146, 154-171, and 481-491 in sequence 12. The first two of these segments occur in the third and fourth shaded region of Fig. 1. Therefore, S2 is the only candidate remaining. Based on experimental evidence and geometric arguments, we conclude that a transmembrane segment is very probably in the region between S1 and position 168 and that S2 is the most likely candidate for this transmembrane segment.

Before continuing, it is necessary to establish that the heme groups of all membrane-bound P-450s are parallel to the membrane and outside the lipid bilayer on the cytoplasmic side. Then, by making an analogy to the crystal structure of cytochrome P-450<sub>cam</sub>, regions S7 and S10 in Fig. 1 will be eliminated as potential transmembrane segments. The orientation of the heme relative to the membrane surface has been studied by EPR spectroscopy. Membrane preparations (submitochondrial particles) containing P450XIA1 (P-450<sub>scc</sub>) and P450XIB1 (P-450<sub>11 $\beta$ </sub>) were sedimented against a mylar sheet and partially dehydrated under controlled humidity conditions. The result was an oriented multilayer with the plane of the membranes being parallel to the plane of the mylar sheet. The angle dependence of the P-450 EPR signals indicated that the heme plane was within 10 ° of being parallel to the mylar sheet (22, 23). When similar experiments were done with purified reconstituted  $P-450_{scc}$  or  $P-450_{11\beta}$  or with

adrenal microsomes similar results were obtained (23, 24). In contrast, the heme of cytochrome c oxidase was perpendicular to the membrane (25) and cytochrome  $b_5$ , which is only tethered to the membrane and is free to sway, showed no angle dependence (24). These counter examples argue for the validity of the results. Important for our discussion, the microsomal P-450s appear to have the same heme orientation as the mitochondrial ones, parallel to the membrane.

The most highly conserved region in the P-450 molecules is the heme-binding site. In bacterial P450CIA1 (P-450<sub>cam</sub>) the heme is sandwiched between two nearly parallel  $\alpha$ -helices I and L (2). The sequences in Fig. 1 show a high degree of conservation at alignment positions 371, 372, 374, and 375, indicating a conserved structure. In P-450<sub>cam</sub> this regions lies in the middle of helix I (positions 356-390) at the site of oxygen binding to heme. Oxygen actually contacts Thr<sup>252</sup> in P-450<sub>cam</sub> (alignment position 375), requiring a distortion in the I-helix. Poulos et al. (3) give a detailed description of the similarity in this region between P-450<sub>cam</sub> and all other known P-450 sequences. These authors conclude that a very similar structure (a distal helix with a local helical distortion) is a feature common to all P-450 species (3). Furthermore, modification of rat P-450 in vivo with suicide substrates (26) has shown the heme pyrrole ring B is sterically blocked from reaction and a lipophilic pocket (suitable for substrates) exists over pyrrole ring C. In P-450<sub>cam</sub> ring B is sandwiched between helices I and L, and the substrate camphor sits above ring C. The heme orientation and topology appears to be the same in rat liver P-450 and P-450 $_{\rm cam}$  (the two papers use different nomenclature for the rings).

The L-helix also appears to be conserved based on sequence similarity and secondary structure prediction. The region between alignment positions 515 and 546 brackets the L-helix (P-450<sub>cam</sub> positions 524-543). This region contains four of the ten 100% conserved amino acids and is the most conserved region in the whole alignment (Fig. 3F). Secondary structure prediction of all P-450 sequences in the alignment between positions 524 and 543 (method of Garnier et al. (27)) predicts over 90% of the residues will adopt a helical conformation.<sup>3</sup> A similar prediction in the helix I region (alignment positions 356-390) predicts helical structure at the start and finish of this region. Since the I-helix is known to contain a distortion in the middle, the failure to predict helix in the middle of this region is not unexpected. In the L-helix region, Gly at position 524 is conserved in 33 of 34 sequences, with Ala in the one remaining sequence. This glycine is at the end of the L-helix in P-450<sub>cam</sub>, and it makes a very close approach to the heme (2). The extreme conservation of this glycine suggests a similar function in all P-450s. This and other conserved features described in detail by Poulos et al. (2 and 3) argue strongly for a conserved helix-heme-helix sandwich structure in all P-450s. Because EPR spectral evidence supports mitochondrial and microsomal P-450 hemes being parallel to the membrane surface, the helices that are predicted to sandwich the heme

<sup>&</sup>lt;sup>3</sup> D. R. Nelson and H. W. Strobel, submitted.



AMINO ACID POSITION

FIG. 3. The maximum number of identical amino acids as a function of alignment position for six sets of P-450 sequences. A, nine members of the P450I family (numbers 15-23 of Fig. 1); B, 14 members of the P450II family (numbers 1-14 of Fig. 1); C, numbers 1-23 of Fig. 1 taken together; D, all microsomal P-450s (numbers 1-31 in Fig. 1); E, all vertebrate P-450s (numbers 1-33 in Fig. 1), F, all P-450s (numbers 1-34 in Fig. 1). Asterisks indicate residues 100% conserved in all P-450 sequences. Letters in A-E indicate 100% conserved residues not 100% conserved in the set just below. There are 193, 101, 51, 14, 13, and 10 100% conserved residues in A-F, respectively. Space does not permit showing these residues in panel A.

also should be parallel to the membrane. Such helices cannot be transmembrane segments as these must be nearly perpendicular to the membrane. Arguments for transmembrane helices being nearly perpendicular are very well presented by Engelman *et al.* (4). This implies that the heme is not buried in the membrane but lies outside of it.

Evidence to support this view is available from other EPR experiments. By introducing paramagnetic ions near a heme in a protein, a line broadening of the heme EPR signal occurs due to magnetic dipole interactions (for a discussion of this effect see Case and Leigh (28)). When dysprosium complexed with EDTA was added to a solution containing P-450<sub>scc</sub>, line broadening of the EPR signal for the heme was observed (23). The extent of line broadening was similar whether the P-450 was in native membranes, reconstituted phospholipid vesicles, or in pure form with detergent. The line broadening effect and hence the access of the dysprosium-EDTA complex to the heme was not affected by the environment of the membrane portion of the molecule. Furthermore, adrenodoxin, the soluble electron donor protein for P-450<sub>scc</sub>, partially relieved the line broadening effect by displacing some of the dysprosium. The extent of line broadening was comparable to that seen with metalloproteins four to five times smaller than P-450<sub>scc</sub>, implying that the heme must have been as close to the surface in P-450<sub>ecc</sub> as it was in these smaller proteins. Together these results strongly suggest that dysprosium-EDTA interacts with the P-450 heme through a hydrophilic domain and the heme is fairly close to the aqueous surface of this domain. Further studies using dysprosium have restricted the distance between the heme and the paramagnetic ions to less than 20 Å (24). For adrenodoxin to approach within 20 Å of the heme, the heme would have to be on the same side of the membrane as the adrenodoxin. In microsomal P-450s this would correspond to the cytoplasmic side.

An additional argument that favors a cytoplasmic location of the proposed helices S7 and S10 involves Lys<sup>384</sup> (position 466) of P450<sub>LM2</sub>. Since evidence presented above suggested Lys<sup>384</sup> was cytoplasmic, the shaded region S9 (positions 461– 478 in Fig. 1) is unlikely to be a transmembrane segment. Because S7 and S10 are postulated to be on the same side of the membrane, sandwiching the heme, S8 is also unlikely to cross the membrane. If S8 were to cross, S7 and S10 would be on opposite sides. Therefore, it seems very probable that S7–S10 are all on the same side of the membrane. Because Lys<sup>384</sup> is strongly suggested to be cytoplasmic, all four of these segments S7–S10 are also very probably on the cytoplasmic side of the membrane.

The status of the last shaded region (S11 in Fig. 1) will determine the sideness of the COOH-terminal amino acid. Assuming the previous arguments hold, and S7-S10 are cytoplasmic, then if S11 crosses the membrane, the COOHterminal will be on the lumen side of the ER. A recent study suggests that this is not the case. A fusion protein was made containing at the  $NH_2$ -terminal the rat P450IA1 (P-450c) protein except the last five amino acids and at the COOHterminal, the NADPH-cytochrome P-450 reductase minus the first 56 amino acids. This hybrid protein expressed in yeast, functioned four times better than the separate proteins (29). Trypsin treatment showed the reductase portion of the molecule was on the cytoplasmic side of microsomal membranes. Since the reductase minus its first 56 amino acids does not contain any transmembrane segments, the COOH terminus of the P-450 was concluded to have been on the cytoplasmic side of the membrane. Presumably this is true in the unfused P-450 protein. Additional experimental support comes from Sakaguchi et al. (14) who found that only the  $NH_2$ -terminal 29 amino acids were required to target rabbit P-450 6 to rough microsomes. These authors concluded that only this short amino terminal segment is inserted in the membrane with the remainder of the molecule, including the COOH-terminal, being cytoplasmic. However, they did not determine the sideness of the  $NH_{2}$ - or COOH-terminals.

Evidence and arguments have been presented above that regions S5 and S6 in Fig. 1 are surrounded on both sides by cytoplasmic portions of the P-450 molecule. Position 168 contains a phosphorylatable serine which must be accessible to ATP and cAMP-dependent protein kinase on the outer cytoplasmic surface of microsomes (19, 20). This region (positions 154-171) is also bound by antibodies from the cytoplasmic surface (13). Positions 368-388 contain invariant Gly and Thr residues as well as other conserved residues which are highly suggestive of an identical role in P-450 function, namely, the role played by the distal helix I of  $P-450_{cam}$  in oxygen binding to the heme. Oxygen binding is a function shared by all P-450s even though these proteins use many different substrates and produce different products. The distal helix is most probably cytoplasmic for reasons already given. To allow both of these regions (positions 168 and S7) to be on the cytoplasmic surface, geometry requires that both S5 and S6 cross or neither may do so. There are four reasons why these two segments are unlikely to cross the membrane. First, the structural model we have developed so far has only 8-12 residues on the ER lumen side of the membrane (positions 38–53). If S5 and S6 cross, this would add another 19– 23 residues (positions 237-260). Clearly, the functional part of the molecule is on the cytoplasmic side, a fact also demonstrated by monoclonal antibody inhibition of P-450 activity (30). If the two segments S5 and S6 cross, then Phe<sup>233</sup> will be at the lumen surface. This Phe is 100% conserved in the 34 sequences, only 1 of 10 residues so highly conserved (see Fig. 3F). It is improbable that this highly conserved residue would appear on the lumen side of the ER membrane when the functional part of the molecule is most probably cytoplasmic. Second, the site-directed antibody study mentioned earlier (13) also found that antibodies against alignment position 238-246 of sequence 12 (P-450b) bound on the cytoplasmic surface. The result was not as clear as with the four other peptide-directed antibodies discussed previously, but the authors were convinced of its correctness. This area is between regions S5 and S6. A cytoplasmic location for this region would preclude S5 and S6 from being transmembrane segments. The third argument against S5 and S6 crossing is the shortness of possible transmembrane segments in the C21 hydroxylase sequences (26-28 in Fig. 1), the scc sequences (32 and 33 in Fig. 1), and the  $LA_{\omega}$  sequence (31 in Fig. 1). These proteins only have potential transmembrane segments of 15 amino acids. This is too short to cross a lipid bilayer. Finally, secondary structure prediction of 44 P-450 sequences has revealed that 10 of 13 helical regions in P-450<sub>cam</sub> are detected in the membrane-bound P-450s and 6 of 7  $\beta$ -sheet segments are also detected. This makes it very likely that the overall three-dimensional structure of membrane bound P-450s is quite similar to P-450<sub>cam</sub>.<sup>3</sup> One of the helices detected in this manner was helix E of P-450<sub>cam</sub>. This helical region spans alignment positions 245-260 which lie just between S5 and S6. Again, we would argue that the functional part of the molecule is cytoplasmic, including the helical region corresponding to helix E in  $P-450_{cam}$ . Although none of these arguments is compelling, overall they are very suggestive that S5 and S6 are cytoplasmic segments and do not serve as transmembrane segments in membrane bound P-450s.

The final conclusion is that cytochrome P-450 is held in

the ER membrane by an  $NH_2$ -terminal hairpin loop. Only two transmembrane segments are present in the molecule. Production of a deletion mutant missing the first 44–66 residues, depending on the sequence, should result in a soluble protein or an extrinsic membrane protein that can be removed from the membrane without detergent. The second possibility is more likely because the EPR data shows a molecule with a restricted orientation, not freely swaying with respect to the membrane (24).

There are three problems which seem to conflict with this model. First, the peptide-directed antibody study (13) found, in addition to the five segments already mentioned, that antibodies against alignment position 48-62 in P-450b were bound to the cytoplasmic side of microsomes. This would preclude region two of Fig. 1 from being a transmembrane segment. Further, it would require that the first region's orientation be reversed so the NH2-terminal was in the lumen. This seemed improbable, and upon examining the sequence of rat P450b a string of five amino acids was found that could explain this result. GPRPL occurs in the peptide used to make the antibodies in question (alignment position 57-61). GPRPV occurs at position 96-100. Region 86-97 was clearly shown to be cytoplasmic by antibody labeling (13). Therefore, the cytoplasmic location of segment 96-100 is highly probable. Polyclonal antibodies to peptide 48-62 of P-450b (containing GPRPL) are very likely to cross-react with the GPRPV epitope at the cytoplasmic surface, causing the misinterpretation that the original peptide used to make the antibodies (48-62) is cytoplasmic. The possibility of an antibody to a five-amino-acid segment cross-reacting with a second fiveamino-acid sequence with one amino acid difference is illustrated by the following example. Antibodies to Met-enkephalin (YGGFM) cross-react with Leu-enkephalin (YGGFL). The reverse is also true and both antibodies cross-react with dynorphin, an opioid peptide that contains the Leu-enkephalin sequence at its NH<sub>2</sub>-terminal (31).

The second problem is that only the first 29 amino acids of P-450 6 are required to target interleukin 2 to microsomes (14). A second transmembrane segment does not appear to be required. What was not shown in this paper was the sideness of the NH<sub>2</sub>-terminal. The NH<sub>2</sub>-terminal was assumed to be on the lumen side. We feel this is unlikely. The data are compatible with a model where the NH<sub>2</sub>-terminal is on the cytoplasmic side, and a second transmembrane segment is donated by the interleukin 2 sequence. The sequence of interleukin 2 which immediately follows the P-450 leader sequence has a 31-amino-acid stretch with only one charged amino acid (32). This could serve as a substitute for the proposed second transmembrane segment of P-450.

The third problem is with the mitochondrial side chain cleavage P-450 sequences (sequences 32 and 33). The hydropathy plots of these sequences show no hydrophobic sequence in either the first or second potential transmembrane regions (Fig. 2, sccb and scch in the third column of graphs). This suggests that the mitochondrial P-450s may be held to the membrane in a different manner. Since these sequences have a processed leader sequence and they must undergo a different targeting procedure, a different membrane topology is possible. These mitochondrial sequences may have no permanent transmembrane segments.

Conservation of Amino Acids and Interaction with P-450 Reductase—Fig. 3 shows the maximum number of identical amino acids as a function of sequence alignment position for six different sets of P-450s. These "skyline plots" show alignment positions with amino acid conservation as tall spikes. Gaps in the alignment appear as valleys. The sets of P-450s shown represent, from bottom to top, more and more closely related P-450s. By progressing from bottom to top, the amino acids that are important in the smaller subsets emerge. Initially, in all 34 sequences, there are 10 amino acids that are 100% conserved (marked with an *asterisk* in Fig. 3F). Only two of these are charged residues. In addition, positions 157 and 495 have 100% conserved positive charges. Position 520 has 33 positive charges and one proline.

Fig. 3E shows the plot when P-450<sub>cam</sub> has been deleted. Three additional residues emerge as 100% conserved in these 33 vertebrate sequences. Presumably, similar functions were accomplished in P-450<sub>cam</sub> by alternative amino acids. The tryptophan at position 153 is of interest because tryptophan is the least common of the amino acids. The high conservation of this residue suggests an important function. Four residues away, position 157 has a 100% conserved positive charge. In P-450<sub>cam</sub> this Arg is known to interact with a heme propionate group (2). Therefore, the tryptophan at position 153 is relatively close to the heme if the eukaryotic P-450s have a similar structure. The aromatic nature of the tryptophan and its nearness to the heme suggest it may act in electron transfer between NADPH-cytochrome P-450 reductase and the P-450 heme. Phe<sup>515</sup> is also highly conserved (100%), and it actually contacts the heme proximal surface in the bacterial enzyme (2). This Phe may also be important in electron transfer.

In Fig. 3D only 1 additional 100% conserved residue appears as the set of proteins now excludes the mitochondrial sequences. All the P-450s in Fig. 3D use the flavoprotein NADPH-cytochrome P-450 reductase as a source of electrons. The mitochondrial and bacterial P-450s used an iron sulfur protein instead. Since all the microsomal P-450s use the same reductase, and the mitochondrial and bacterial P-450s do not, one would anticipate the emergence of at least a few 100% conserved residues in Fig. 3D. These would attest to different interactions occurring between mitochondrial/bacterial P-450s and their iron sulfur redox proteins and the microsomal P-450s and their flavoprotein reductase. The absence of these residues suggests that the interaction between the two types of electron donor proteins and their P-450s is not very different. It is known in bacteria that ferredoxins (iron sulfur proteins) may substitute for flavodoxins (flavoproteins) in some electron transfer reactions (33). This ability indicates a high degree of similarity in their interactions. The suggestion has been made that bacterial iron sulfur proteins and flavodoxins share a common evolutionary ancestor (34). More recently, the cytochrome P-450 reductase has been sequenced, and it appears to have a common ancestry with bacterial flavodoxins (35). These observations, coupled with the absence of any new 100% conserved charged residues in Fig. 3D, imply that all P-450s, bacterial, mitochondrial, and microsomal, interact with their electron donor proteins via similar charged residues on their surfaces.

Fig. 3C is limited to P-450s in the drug-metabolizing families P450I and P450II. This is a much more homogeneous group than Fig. 3D. An additional 37 residues emerge that are 100% conserved. Thirteen are charged amino acids. Charged amino acids are thought to play a significant role in the interaction between the P-450s and the reductase (16, 36). This is also suggested for other pairs of electron transfer donors and recipients such as bacterial flavodoxin and cytochrome c (37, 38), cytochrome c and cytochrome c peroxidase (39), cytochrome c and cytochrome  $b_5$  (40), and cytochrome  $b_5$  and hemoglobin (41). Studying the location of conserved charged amino acids in the aligned P-450<sub>cam</sub> sequence and the corresponding three-dimensional structure may suggest how P-450s interact with the reductase. The three-dimensional structure of  $P-450_{cam}$  is approximately triangular with the heme lying in the plane of the triangle. Since EPR spectroscopy has indicated that membrane-bound P-450s have their heme parallel to the membrane, one may envision a membrane P-450 molecule as a thick triangle lying flat on the membrane surface. The lipidsoluble substrates enter the P-450 active site from the membrane (42) and, therefore, the active site and the putative access channel should be below the heme and facing the membrane. The thiolate anion from cysteine (position 522) should be above the heme plane, away from the membrane.

Most charged residues that are labeled in Fig. 3C are clustered in two regions (alignments positions 157–199 and 400–466). The region 184–199 is highly conserved between P- $450_{cam}$  and P450IIB1 and 2 (rat b and e). There are 10 identities in 16 amino acids suggesting a conserved structure at this location in these proteins. Five of the 10 identical amino acids are charged. This region corresponds to the Dhelix of P- $450_{cam}$  (2). The two arginines at 157–158 are located in the alignment at a position that corresponds to the C-helix of P- $450_{cam}$  (2). As mentioned above,  $Arg^{157}$  ( $Arg^{108}$  in P- $450_{cam}$ ) interacts with a heme propionate. The second Arg, although it is not present in P- $450_{cam}$ , may be available to interact with P-450 reductase. Arg or Lys is present at position 158 in 29 of 31 microsomal P-450s.

The second region (400-466) contains nine conserved charges (400, 403, 404, 414, 420, 437, 440, 456, and 466). The sequence from 400 to 417 has eight identities and one conservative replacement in 14 amino acids between human P450IIE1 (P-450<sub>j</sub>) and the bacterial sequence. Again, this suggests a conserved structure. Seven charges, including the two 100% conserved charged amino acids in Fig. 3F, are present in a segment corresponding to the J- and K-helices of P-450<sub>cam</sub>. The two remaining conserved charges (456 and 466) are found at positions equivalent to the two connecting strands between  $\beta 3$  and  $\beta 4$  (2) in P-450<sub>cam</sub>. One of these charges (Lys<sup>466</sup>) is the Lys labeled by FITC and is shown to be involved in the interaction between rabbit P450IIB1 (LM2) and its reductase (15, 16).

Two other areas may also be involved in charge pairing between the reductase and P-450. These areas contain six charges. Segment 481-484 has four charges in P-450<sub>cam</sub>, and these charges are exactly matched in P450IIC2 and 3 (P-450s PBc2 and 3b). All other sequences show at least some conservation of these charges. In P-450<sub>cam</sub> these amino acids are behind helix A as depicted in Fig. 2 of Ref. 2. The other region (109-112) is identical between P450IIB1 (LM2) and P-450<sub>cam</sub>, and it is partially conserved in many other P-450s. This region in P-450<sub>cam</sub> corresponds to the middle of helix B.

All of the charged residues so far discussed are accessible from the edges or back surface of P-450<sub>cam</sub> (the surface hidden from view in Fig. 2 of Ref. 2). Conservation of sequence implies a conserved structure for the D-, J-, and K-helices. The structure around the heme has been postulated to be very similar to all P-450s (2). This would include the F-, I-, and Lhelices. If membrane-bound P-450s are anchored by an NH<sub>2</sub>terminal hairpin loop as we propose, then the cytoplasmic portion of these molecules would be approximately the same size as the bacterial P-450. Since much of the helical structure of P-450<sub>cam</sub> appears to be conserved in microsomal P-450s, it is not difficult to imagine that the membrane-bound P-450s are very similar in their three dimensional structure to the bacterial enzyme. One may anticipate that the conserved charged residues will be located in very similar positions in the bacterial- and membrane-bound P-450s.

The interaction between the reductase and the P-450 mol-



FIG. 4. A model of microsomal cytochrome P-450 structure.

ecules is probably dependent on multiple complementary charge pairs between the proteins (16, 36). More than half of the charges discussed are found in the D-, J-, and K-helix regions. This is certainly an attractive site to consider for interaction with the reductase. However,  $Lys^{466}$  has been implicated in this interaction, and it is at the opposite end of the molecule. For both regions to be involved would require that much of the exposed surface of the P-450 be in contact with the reductase. It is too soon to offer any more detailed speculation on the nature of this interaction.

A model that is consonant with existing evidence and the inferences made here is shown in Fig. 4. The P-450 is anchored to the membrane by two  $NH_2$ -terminal transmembrane helices. The heme is parallel to the membrane surface with the back side (proximal surface) of the molecule exposed.

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