Compilation

AMINO ACID:tRNA LIGASES (EC 6.1.1.-)

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Received 24 May 1980

1. Introduction

Aminoacyl-tRNA synthetases (AARS) are family of ligases (EC 6.1.1.-) which catalyse charging of transfer ribonucleic acids (tRNA) during protein biosynthesis with their specific amino acids according to the reaction:

$$AA + ATP + tRNA \overset{AARS}{\rightleftharpoons} AA\text{-}tRNA + AMP + PP_i$$

Since the discovery of these enzymes in the late fifties [1], many experimental data on the isolation, properties and mechanism of action of the synthetases have been accumulated. The highly specific interaction between tRNA and aminoacyl-tRNA synthetase is a very good model for studies on recognition mechanisms between nucleic acids and proteins [2,3]. During the past few years the amount of research on AARS has rapidly increased. This area has attracted investigators with widely different interests [4]. New interesting results have appeared and therefore many people look for new enzymes and compare their properties [5].

In the literature there are many reviews dealing with aminoacyl-tRNA synthetases but they are restricted only to the ligases of known relative molecular mass (M_r) and subunit structure [4].

The aim of this compilation is a short presentation of known aminoacyl-tRNA synthetases to give a general view on data presently available. We have included here information on any enzyme isolated whether totally or partly characterized. The papers cited here were published in the last twenty years and represent different levels of exactness. In cases where there are no data on relative molecular mass and subunit structure only literature citations are given. One can easily compare how many enzymes have been purified and how many detected and partially characterized for particular amino acids. This is shown in part 1 of the compilation.

The second part of this work is a table of aminoacyl-tRNA synthetase mutants. Here we have mentioned only the type of mutation and literature references.

The last part is a presentation of the number of known aminoacyl-tRNA synthetases from different organisms for each amino acid. Here we counted all sources of AARS without any classification. Only in the case of the bacteria *Escherichia coli* and *Bacillus stearothermophilus* have all synthetases been isolated.

The authors would welcome any information from readers regarding missing material or erroneous presentation. We hope that this material will be very useful to many people working in this field.

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Table 1
Amino acid:tRNA ligases

Amino acid–tRNA ligase	Organism	M_r ($\times 10^{-3}$)	Subunit structure ($M_r \times 10^{-3}$)	[Ref.]
Alanine (EC 6.1.1.7)	*Escherichia coli*	160	α_2 ($\alpha = 80$)	[6]
	E. coli	380	α_4 ($\alpha = 95$)	[6a]
	Bacillus stearothermophilus	173		[7]
	Saccharomyces cerevisiae	130	α	[8]
	Rat liver			[9]
Arginine (EC 6.1.1.19)	*E. coli*	72	α	[10,11]
	E. coli K-12	63	α	[12]
	E. coli	74	α	[13]
	B. stearothermophilus	78	α	[14]
	Neurospora crassa	85	α	[15]
	Baker's yeast			[16]
	S. cerevisiae	73	α	[16,105]
	Wheat germ	73	α	[18]
	Lupinus luteus	140	α_2 ($\alpha = 70$)	[5,19]
	Rat liver	89		[20,84]
	Rat liver neoplastic			[20a]
	Halobacterium cutirubrum			[235]
Aspartic acid (EC 6.1.1.12)	*E. coli*	119	α_2 ($\alpha = 61$)	[6]
	B. stearothermophilus	129		[7]
	N. crassa			[22]
	N. crassa mitochondria		α_2	[22]
	S. cerevisiae	120	($\alpha = 60$)	[23,232]
	S. cerevisiae	114	($\alpha = 57$)	[23,232]
	Phaseolus aureus			[24]
	Lactobacillus arabinosa			[25]
	Tobacco leaf			[26]
	Baker's yeast	113		[30]
Asparagine (EC 6.1.1.13)	*E. coli*	100		[4,27]
	B. stearothermophilus	127	α_2 ($\alpha = 51$)	[7,21]
	B. stearothermophilus	120	α_2 ($\alpha = 60$)	[7]
	Chick embryo			[51]
	Staphyloccocus aureus			[52]
Histidine (EC 6.1.1.14)	*E. coli*	85	α_2 ($\alpha = 42.5$)	[53]
	B. stearothermophilus	102		[7]
	Salmonella typhimurium	80	α_2	[54,58]
	S. cerevisiae			[55]
	Yeast			[56]
	Tobacco leaf			[26]
	Rabbit reticulocytes	122	α_2 ($\alpha = 64$)	[54,57]
	Rat liver			[9]
Isoleucine (EC 6.1.1.5)	*E. coli* B	112	α	[59,230]
	E. coli MRE 600	102	α	[60]
	B. stearothermophilus	110	α	[61]
		115		[159]
	S. cerevisiae	125	α	[8]
	Baker's yeast			[62]
	Tobacco leaf			[26]
	Rat liver			[63]
	H. cutirubrum			[235]
Leucine (EC 6.1.1.4)	*E. coli*	104	α	[6,64]
	E. coli MRE 600	99		[65,230]
	B. stearothermophilus	110	α	[7,66]
	S. cerevisiae	120	α_2 ($\alpha = 60$)	[67]
	Candida utilis	128		[68]
	Baker's yeast			[69]
	N. crassa	110	α	[70]
	N. crassa mitochondria	90	α	[70]
	Euglena gracilis	110	α	[71]
	E. gracilis chloroplasts	105	α	[71]

	L. arabinosa			[28]
	N. crassa			[29]
	Gardner lymphoma			[47]
	P. aureus			[24]
Cysteine (EC 6.1.1.16)	*E. coli* K-12	55		[31,32]
	B. stearothermophilus	61		[7]
	Baker's yeast	160		[33]
	P. aureus			[34]
	Astragalus crotariae			[35]
	A. bisulcatus			[35]
	A. racemosus			[35]
	A. lentigenosus			[35]
	Tobacco leaf			[26]
	Rat liver	240	α_2	[36]
	Human placenta			[37]
Glutamic acid (EC 6.1.1.17)	*E. coli*	50		[38]
	E. coli	59	α	[39]
	E. coli	62	α	[40]
	E. coli	56	α	[41,41a]
	E. coli	102	$\alpha\beta$	[42]
	B. stearothermophilus	42	α	[7]
	Yeast			[43]
	Tobacco leaf			[26]
	Rat liver	180		[44]
	Beef brain			[45]
	Calf brain			[46]
Glutamine (EC 6.1.1.18)	*E. coli*	69	α	[48]
	B. stearothermophilus	126		[7]
	N. crassa			[22]
	P. aureus			[24]
	Albizzia julibrissizn			[24]
	Beef brain			[45]
	Pork liver			[49]
	B. subtilis			[224]
Glycine (EC 6.1.1.8)	*E. coli*	227	$\alpha_2\ \beta_2$ ($\alpha = 33$) ($\beta = 80$)	[50]
	E. coli CH754 (pLC 1-3)	205	$\alpha_2\ \beta_2$ ($\alpha = 40$) ($\beta = 65$)	[50a]
	B. brevis	226	$\alpha_2\ \beta_2$ ($\alpha = 30\,000$) ($\beta = 81\,000$)	[233]
	T. pyriformis	120	α	[72]
	mitochondria	100	α	[72]
	Lupinus luteus seeds	170		[73]
	Wheat germ	110	α_2 ($\alpha = 63$)	[18]
	Soybean			[74]
	Aesculus hippocastanum			[75]
	Tobacco leaf			[26]
	P. aeruginosa			[76]
	Rat liver	108		[20]
	Drosophila melanogaster	75		[4,77]
	Tenebrio molitor	99	α	[78]
	Cow mammary gland	182	α_2 ($\alpha = 83$)	[79]
	B. subtilis			[225]
	H. cutirubrum			[235]
Lysine (EC 6.1.1.6)	*E. coli* MRE 600	104	α_2 ($\alpha = 52$)	[6,80]
	B. stearothermophilus	112	α_2 ($\alpha = 58$)	[7,21]
	B. subtilis	130		[81]
	S. cerevisiae	138	α_2 ($\alpha = 69$)	[80,82]
	Baker's yeast	150		[16]
	Yeast	113		[83]
	Rat liver	129		[20,84]
	Rabbit reticulocytes	122	α_2	[54,57]
Methionine (EC 6.1.1.10)	*E. coli*	170	α_2 ($\alpha = 85$)	[85,86]
	S. faecalis			[87]
	Mycobacterium smegmatis A	65	α_2	[88]
	M. smegmatis B	85	$\alpha_2\ \beta_2$ ($\alpha = 31$) ($\beta = 10$)	[88]
	B. brevis			[89]
	Yeast			[90]
	Yeast mitochondria	110	α_2	[90a]
	S. cerevisiae			[91]
	B. stearothermophilus	153	α_2 ($\alpha = 82$)	[66,92]

continued

Table 1 (continued)
Amino acid:tRNA ligases

Amino acid–tRNA ligase	Organism	M_r ($\times 10^{-3}$)	Subunit structure ($M_r \times 10^{-3}$)	[Ref.]
	Sarcina lutea			[93]
	Wheat germ	165	α_2 ($\alpha = 74$)	[94]
	Wheat germ A	105	α	[95]
	Wheat germ B	70	α	[95]
	L. luteus seeds	170	α_2 ($\alpha = 85$)	[96]
	Sheep mammary gland	78	α	[97]
	Sheep liver	78	α	[226]
	Rabbit reticulocytes			[98]
	Rat liver	90		[20]
Phenylalanine (EC 6.1.1.20)	*E. coli* B	180	α_4 ($\alpha = 45$)	[99,100]
	E. coli K-10, K-12	270	$\alpha_2\ \beta_2$ ($\alpha = 38$) ($\beta = 96$)	[6,101]
	B. subtilis			[102]
	B. stearothermophilus	221		[7]
	S. cerevisiae	230	$\alpha_2\ \beta_2$ ($\alpha = 56$) ($\beta = 63$)	[107]
	S. cerevisiae	270	$\alpha_2\ \beta_2$ ($\alpha = 63$) ($\beta = 75$)	[103] [104]
	Baker's yeast	180		[105]
	Baker's yeast	276	$\alpha_2\ \beta_2$ ($\alpha = 63$) ($\beta = 75$)	[106]
	Yeast mitochondria	266	$\alpha_2\ \beta_2$ ($\alpha = 57$) ($\beta = 72$)	[106a]
	Soybean cotyledons			[231]
	L. luteus seeds	260	$\alpha_2\ \beta_2$ ($\alpha = 59$) ($\beta = 75$)	[5,19]
	Wheat germ	250	$\alpha_2\ \beta_2$ ($\alpha = 50$) ($\beta = 80$)	[108]
		260	$\alpha_2\ \beta_2$ ($\alpha = 61$) ($\beta = 69$)	[108a]
	Rat liver	90		[130,131]
	Hen liver	122	α_2 ($\alpha = 63$)	[132]
Threonine (EC 6.1.1.3)	*E. coli*	117		[133]
	E. coli	152	α_2 ($\alpha = 76$)	[134]
	B. stearothermophilus	120		[7]
	S. carlsbergensis	150	α_2 ($\alpha = 82$)	[135]
	Baker's yeast	170	α_2	[16,136]
	A. hippocastanum			[75]
	Rat liver	170	α_2	[137,137a]
Tryptophan (EC 6.1.1.2)	*E. coli*	74	α_2 ($\alpha = 37$)	[138,139]
	B. stearothermophilus	70	α_2 ($\alpha = 35$)	[7,66]
	B. subtilis	87		[140]
	S. cerevisiae	110	α_2 ($\alpha = 55$)	[141]
	L. luteus seeds	200	($\alpha = 37$)	[129]
	P. aureus			[142]
	Polygonatum multiflorum			[142]
	Beef pancreas	108	α_2 ($\alpha = 54$)	[143,144]
	Beef pancreas	120	α_2	[145,146]
	Buffalo brain	150	α_3	[147]
	Human placenta	116	α_2 ($\alpha = 58$)	[148]
	Human skin	116	α_2 ($\alpha = 58$)	[149]
	Human fibroblasts			[236]
	Chinese hamster cells			[236]
Tyrosine (EC 6.1.1.1)	*E. coli*	97	α_2	[150,151]
	B. stearothermophilus	88	α_2	[66,152]
	B. subtilis	88		[150]
	S. cerevisiae	116	α_4	[8,153]
	S. cerevisiae	46.5	α	[154]
	Baker's yeast	80	α_2 ($\alpha = 40$)	[155]

	Aesculus californica			[109]
	A. glabra			[109]
	A. hippocastanum			[109]
	A. parviflora			[109]
	N. crassa			[110]
	E. gracilis	65		[111,112]
	D. melanogaster	180		[113,114]
	Rat liver	287	$\alpha_2\ \beta_2$ ($\alpha = 69$) ($\beta = 74.5$)	[115,116]
	Rat liver C_1			[117]
	Rat liver C_2			[117]
	Rat liver mitochondria			[117]
	Human placenta	130	$\alpha\ \beta$ ($\alpha = 55$) ($\beta = 72$)	[118]
	H. cutirubrum			[235]
Proline (EC 6.1.1.15)	*E. coli*	94	α_2 ($\alpha = 47$)	[119,120]
	B. stearothermophilus	125		[7]
	P. aureus			[121]
	Delonix regia			[121]
	Rat liver			[51]
Serine (EC 6.1.1.11)	*E. coli* B	103	α_2 ($\alpha = 53$)	[122,123]
	E. coli K-12	95	α_2 ($\alpha = 50$)	[124,125]
	B. stearothermophilus	88	α_2 ($\alpha = 49$)	[7,21]
	Saccharomyces carlsbergensis	95	α_2 ($\alpha = 47.5$)	[126,127] [229]
	S. cerevisiae	120	α_2 ($\alpha = 60$)	[128]
	S. cerevisiae	89		[105]
	L. luteus seeds	110	α_2 ($\alpha = 55$)	[129]
	Soybean	122	α_2	[156]
	Soybean chlorop.	86	α_2	[156]
	P. aeruginosa			[76]
	Calf liver	65		[157]
	Rat liver	150	α_2 ($\alpha = 68$)	[158]
	Rat liver	124	$\alpha\ \beta$ ($\alpha = 61$) ($\beta = 62$)	[159]
	Hog pancreas	118	α_2 ($\alpha = 58.7$)	[160] [161]
	Pig pancreas			[161]
Valine (EC 6.1.1.9)	*E. coli* K-12	110	α	[7,162]
	E. coli	100		[163]
	E. coli (T4 phage modified)	170		[164]
	B. stearothermophilus	110	α	[21,66] [165]
	B. subtilis			[166]
	S. cerevisiae	140	α	[8]
	S. cerevisiae	122	α	[80,167]
	Baker's yeast	130	α	[168] [169]
	M. smegmatis	120	α_4	[170]
	N. crassa			[171]
	E. gracilis chloroplasts	126	α	[172]
	E. gracilis	125	α	[172a]
	T. pyriformis			[173]
	T. pyriformis mitochondria			[173]
	Tobacco leaf			[26]
	A. californica			[75]
	L. luteus seeds	125	α	[129,174]
	S. typhimurium			[175]
	Chick embryo brain	110		[176]
—	Beef liver			[9,177]
	Rat liver			[175]

Table 2
Amino acid:tRNA ligase mutants

Amino acid–tRNA ligase	Organism	Type of mutant	[Ref.]
Alanine	*Escherichia coli*	Temp.-sensitive	[178]
(EC 6.1.1.7)	Chinese hamster	Auxotrophic	[179]
	Mouse cells	Temp.-sensitive	[180]
Arginine	*E. coli*	Analogue-resistant	[181,182]
(EC 6.1.1.19)	Chinese hamster	Temp.-sensitive	[183]
Asparagine	*E. coli*	Temp.-sensitive	[184]
(EC 6.1.1.13)	Chinese hamster	Temp.-sensitive	[183,185]
	Hamster	Temp.-sensitive	[186]
Glutamic acid	*E. coli*	Temp.-sensitive	[187]
		Streptomycin-dependent	[188]
(EC 6.1.1.17)	*M. cryophilis*	Temp.-resistant	[227]
Glutamine	*E. coli*	Temp.-sensitive	[189]
(EC 6.1.1.18)	Chinese hamster	Temp.-sensitive	[183]
Glycine	*E. coli*	Auxotrophic	[190]
(EC 6.1.1.8)		Temp.-sensitive	[191]
Histidine	*E. coli*	Bradytrophic	[192]
(EC 6.1.1.14)	*S. typhimurium*	Analogue-resistant	[193]
	Chinese hamster	Temp.-sensitive	[183]
Isoleucine	*E. coli*	Auxotrophic	[194,195]
(EC 6.1.1.5)		Analogue resistant	[196]
		Temp.-sensitive	[197]
	S. typhimurium	Auxotrophic	[198]
	S. cerevisiae	Temp.-sensitive	[199,200]
Leucine	*E. coli*	Temp.-sensitive	[201]
(EC 6.1.1.4)	*S. typhimurium*	Analogue-resistant	[202]
	N. crassa	Temp.-sensitive	[70]
		Auxotrophic	[70]
	Chinese hamster	Temp.-sensitive	[204,204a] [205]
Lysine	*B. subtilis*	Temp.-sensitive	[206]
(EC 6.1.1.6)	*E. coli*	Analogue-resistant	[207]
Methionine	*E. coli*	Auxotrophic	[203]
(EC 6.1.1.10)		Analogue-resistant	[208]
	S. typhimurium	Auxotrophic	[209]
	S. cerevisiae	Temp.-sensitive	[200]
	Chinese hamster	Temp.-sensitive	[183]
Phenylalanine	*E. coli*	Analogue-resistant	[210]
(EC 6.1.1.20)		Temp.-sensitive	[187]
Serine	*E. coli*	Temp.-sensitive	[201,201a]
(EC 6.1.1.11)		Serine hydroxamate-resistant	[212]
	E. coli	Auxotrophic	[228]
Threonine	*E. coli*	Borrelidin-resistant	[134]
(EC 6.1.1.3)			[213]
		Auxotrpphic	[214]
Tryptophan	*E. coli*	Auxotrophic	[215]
(EC 6.1.1.2)		Temp.-sensitive	[216]
	B. subtilis	Temp.-sensitive	[187]
		Analogue-resistant	[217]
	N. crassa	Auxotrophic	[218]
Proline	*M. cryophilis*	Temp.-resistant	[227]
(EC 6.1.1.15)	*E. coli*	Temp.-sensitive	[234]
Tyrosine	*E. coli*	Analogue-resistant	[187]
(EC 6.1.1.1)	*S. typhimurium*	Auxotrophic	[219]
			[220]
Valine	*E. coli*	Temp.-sensitive	[221]
(EC 6.1.1.9)			[222]
			[223]
	S. typhimurium	Temp.-sensitive	[4]

Table 3
Amino acid:tRNA ligases from different sources

Source	Ala	Arg	Asp	Asn	Cys	Glu	Gln	Gly	His	Ile	Leu	Lys	Met	Phe	Pro	Ser	Thr	Trp	Tyr	Val
E. coli	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. stearoth.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. subtilis							+				+	+		+				+	+	+
S. cerevisiae	+	+	+	+	+	+			+	+	+	+	+	+		+		+	+	+
S. carlsberg.																+	+			
N. crassa		+	+	+			+				+			+				+		+
N. crassa mit.			+								+									
P. aureus			+	+	+		+								+			+		
L. arabinosa			+	+																
G. lymphoma				+																
B. brevis								+					+							

continued

Table 3 (continued)
Amino acid:tRNA ligases from different sources

Source	Ala	Arg	Asp	Asn	Cys	Glu	Gln	Gly	His	Ile	Leu	Lys	Met	Phe	Pro	Ser	Thr	Trp	Tyr	Val
A. crotoriae					+															
A. bisculcatus					+															
A. racemosus					+															
A. lentigenos.					+															
A. julibrissin							+													
S. faecalis													+							
S. aureus								+												
P. multiflor.																		+		
S. typhimurium										+	+	+	+						+	+
M. smegmatis													+							+
D. melanogaster											+			+						
C. utilis											+									
S. lutea													+							
P. aeruginosa											+								+	
E. gracilis											+			+						+
E. gracilis chl.											+									+
T. pyriformis											+									+
T. pyriformis mit.											+									+
T. molitor											+									
A. hyppocast.											+			+			+			
A. californica														+						+
A. gabra														+						
A. parvifl.														+						
D. regia															+					
L. luteus		+									+		+	+		+				+
M. cryophilis						+									+					
H. cutirubrum		+								+	+			+						
Wheat germ		+									+		+	+						
Soybean											+								+	
Soybean chl.																			+	
Tobacco leaf			+		+	+			+	+	+									+
Sheep mam. gland													+							
Sheep liver													+							
Pork liver							+													
Rat liver	+	+			+	+			+	+	+	+	+	+	+	+	+		+	+
Rat liver mit.														+						
Beef liver																				+
Beef brain						+	+													
Beef pancreas																		+		
Cal brain						+														
Calf liver																			+	
Rabbit reticul.									+			+	+							
Cow mam. gland											+									
Human placenta					+									+				+		
Human skin																		+		
Human fibrobl.														+						
Buffalo brain																		+		
Hog pancreas																			+	
Hen liver																+				
Chick embryo								+												+
Chinese hamster	+	+		+		+			+		+		+					+		
Mouse cells	+																			