

Proposed Changes to the Enzyme List

The entries below are proposed additions and amendments to the [Enzyme Nomenclature list](#). The entries below are proposed additions and amendments to the Enzyme Nomenclature list. They were prepared for the NC-IUBMB by Kristian Axelsen, Richard Cammack, Ron Caspi, Masaaki Kotera, Andrew McDonald, Gerry Moss, Dietmar Schomburg, Ida Schomburg and Keith Tipton. Comments and suggestions on these draft entries should be sent to [Dr Andrew McDonald](#) (Department of Biochemistry, Trinity College Dublin, Dublin 2, Ireland). The entries were added on the date indicated and fully approved after four weeks.

An asterisk before 'EC' indicates that this is an amendment to an existing enzyme rather than a new enzyme entry.

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*EC 1.1.1.47

Accepted name: glucose 1-dehydrogenase [NAD(P)⁺]

Reaction: D-glucose + NAD(P)⁺ = D-glucono-1,5-lactone + NAD(P)H + H⁺

Other name(s): D-glucose dehydrogenase (NAD(P)⁺); hexose phosphate dehydrogenase; β -D-glucose:NAD(P)⁺ 1-oxidoreductase; glucose 1-dehydrogenase

Systematic name: D-glucose:NAD(P)⁺ 1-oxidoreductase

Comments: This enzyme has similar activity with either NAD⁺ or NADP⁺. *cf.* [EC 1.1.1.118](#), glucose 1-dehydrogenase (NAD⁺) and [EC 1.1.1.119](#), glucose 1-dehydrogenase (NADP⁺).

Links to other databases: [BRENDA](#), [EXPASY](#), [GTD](#), [KEGG](#), [Metacyc](#), [PDB](#), CAS registry number: 9028-53-9

References:

1. Banauch, D., Brummer, W., Ebeling, W., Metz, H., Rindfrey, H., Lang, H., Leybold, K. and Rick, W. A glucose dehydrogenase for the determination of glucose concentrations in body fluids. *Z. Klin. Chem. Klin. Biochem.* 13 (1975) 101-107. [PMID: [810982](#)]
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3. Pauly, H.E. and Pfeleiderer, G. D-Glucose dehydrogenase from *Bacillus megaterium* M 1286: purification, properties and structure. *Hoppe-Seylers Z. Physiol. Chem.* 356 (1975) 1613-1623. [PMID: [2530](#)]
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[EC 1.1.1.47 created 1961, modified 2013]

*EC 1.1.1.49

Accepted name: glucose-6-phosphate dehydrogenase (NADP⁺)

Reaction: D-glucose 6-phosphate + NADP⁺ = 6-phospho-D-glucono-1,5-lactone + NADPH + H⁺

For diagram of reaction [click here](#).

Other name(s): NADP-glucose-6-phosphate dehydrogenase; Zwischenferment; D-glucose 6-phosphate dehydrogenase; glucose 6-phosphate dehydrogenase (NADP); NADP-dependent glucose 6-phosphate dehydrogenase; 6-phosphoglucose dehydrogenase; Entner-Doudoroff enzyme; glucose-6-phosphate 1-dehydrogenase; G6PDH; GPD; glucose-6-phosphate dehydrogenase

Systematic name: D-glucose-6-phosphate:NADP⁺ 1-oxidoreductase

Comments: The enzyme catalyses a step of the pentose phosphate pathway. The enzyme is specific for NADP⁺. *cf.* [EC 1.1.1.363](#), glucose-6-phosphate dehydrogenase [NAD(P)⁺].

Links to other databases: [BRENDA](#), [EXPASY](#), [GTD](#), [KEGG](#), [Metacyc](#), [PDB](#), CAS registry number: 9001-40-5

References:

1. Engel, H.J., Domschke, W., Alberti, M. and Domagk, G.F. Protein structure and enzymatic activity. II. Purification and properties of a crystalline glucose-6-phosphate dehydrogenase from *Candida utilis*. *Biochim. Biophys. Acta* 191 (1969) 509-516. [PMID: [5363983](#)]
2. Glaser, L. and Brown, D.H. Purification and properties of D-glucose-6-phosphate dehydrogenase. *J. Biol. Chem.* 216 (1955) 67-79. [PMID: [13252007](#)]
3. Julian, G.R., Wolfe, R.G. and Reithel, F.J. The enzymes of mammary gland. II. The preparation of glucose 6-phosphate dehydrogenase. *J. Biol. Chem.* 236 (1961) 754-758. [PMID: [13790996](#)]
4. Noltmann, E.A., Gubler, C.J. and Kuby, S.A. Glucose 6-phosphate dehydrogenase (Zwischenferment). I. Isolation of the crystalline enzyme from yeast. *J. Biol. Chem.* 236 (1961) 1225-1230. [PMID: [13729473](#)]
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[EC 1.1.1.49 created 1961, modified 2013]

*EC 1.1.1.78

Accepted name: methylglyoxal reductase (NADH)

Reaction: (R)-lactaldehyde + NAD⁺ = methylglyoxal + NADH + H⁺

Glossary: methylglyoxal = 2-oxopropanal

Other name(s): methylglyoxal reductase; D-lactaldehyde dehydrogenase; methylglyoxal reductase (NADH-dependent)

Systematic name: (R)-lactaldehyde:NAD⁺ oxidoreductase

Comments: This mammalian enzyme differs from the yeast enzyme, [EC 1.1.1.283](#), methylglyoxal reductase (NADPH-dependent), in preferring NADH over NADPH as reductant.

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 37250-16-1

References:

1. Ting, S.-M., Miller, O.N. and Sellinger, O.Z. The metabolism of lactaldehyde. VII. The oxidation of D-lactaldehyde in rat liver. *Biochim. Biophys. Acta* 97 (1965) 407-415. [PMID: [14323585](#)]

2. Ray, M. and Ray, S. Purification and partial characterization of a methylglyoxal reductase from goat liver. *Biochim. Biophys. Acta* 802 (1984) 119-127. [PMID: [6386056](#)]

[EC 1.1.1.78 created 1972, modified 2005, modified 2013]

*EC 1.1.1.283

Accepted name: methylglyoxal reductase (NADPH)

Reaction: (S)-lactaldehyde + NADP⁺ = methylglyoxal + NADPH + H⁺

Glossary: methylglyoxal = 2-oxopropanal

Other name(s): lactaldehyde dehydrogenase (NADP⁺); GRE2 (gene name); methylglyoxal reductase (NADPH-dependent); lactaldehyde:NADP⁺ oxidoreductase

Systematic name: (S)-lactaldehyde:NADP⁺ oxidoreductase

Comments: The enzyme from the yeast *Saccharomyces cerevisiae* catalyses the reduction of a keto group in a number of compounds, forming enantioisomeric products. Among the substrates are methylglyoxal (which is reduced to (S)-lactaldehyde) [1,2], 3-methylbutanal [3], hexane-2,5-dione [4] and 3-chloro-1-phenylpropan-1-one [5]. It differs in coenzyme requirement from [EC 1.1.1.78](#), methylglyoxal reductase (NADH), which is found in mammals.

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 78310-66-4

References:

1. Murata, K., Fukuda, Y., Simosaka, M., Watanabe, K., Saikusa, T. and Kimura, A. Metabolism of 2-oxoaldehyde in yeasts. Purification and characterization of NADPH-dependent methylglyoxal-reducing enzyme from *Saccharomyces cerevisiae*. *Eur. J. Biochem.* 151 (1985) 631-636. [PMID: [3896793](#)]

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4. Muller, M., Katzberg, M., Bertau, M. and Hummel, W. Highly efficient and stereoselective biosynthesis of (2S,5S)-hexanediol with a dehydrogenase from *Saccharomyces cerevisiae*. *Org. Biomol. Chem.* 8 (2010) 1540-1550. [PMID: [20237665](#)]

5. Choi, Y.H., Choi, H.J., Kim, D., Uhm, K.N. and Kim, H.K. Asymmetric synthesis of (S)-3-chloro-1-phenyl-1-propanol using *Saccharomyces cerevisiae* reductase with high enantioselectivity. *Appl. Microbiol. Biotechnol.* 87 (2010) 185-193. [PMID: [20111861](#)]

6. Breicha, K., Muller, M., Hummel, W. and Niefind, K. Crystallization and preliminary crystallographic analysis of Gre2p, an NADP(+)-dependent alcohol dehydrogenase from *Saccharomyces cerevisiae*. *Acta Crystallogr. Sect. F Struct. Biol. Cryst. Commun.* 66 (2010) 838-841. [PMID: [20606287](#)]

[EC 1.1.1.283 created 2005, modified 2013]

EC 1.1.1.361

Accepted name: glucose-6-phosphate 3-dehydrogenase

Reaction: D-glucose 6-phosphate + NAD⁺ = 3-dehydro-D-glucose 6-phosphate + NADH + H⁺

For diagram of reaction [click here](#).

Glossary: kanosamine = 3-amino-3-deoxy-D-glucose

Other name(s): *ntdC* (gene name)

Systematic name: D-glucose-6-phosphate:NAD⁺ oxidoreductase

Comments: The enzyme, found in the bacterium *Bacillus subtilis*, is involved in a kanosamine biosynthesis pathway.

References:

1. Vetter, N.D., Langill, D.M., Anjum, S., Boisvert-Martel, J., Jagdhane, R.C., Omene, E., Zheng, H., van Straaten, K.E., Asiamah, I., Krol, E.S., Sanders, D.A. and Palmer, D.R. A previously unrecognized kanosamine biosynthesis pathway in *Bacillus subtilis*. *J. Am. Chem. Soc.* 135 (2013) 5970-5973. [PMID: [23586652](#)]

[EC 1.1.1.361 created 2013]

EC 1.1.1.362

Accepted name: aklaviketone reductase

Reaction: aklavinone + NADP⁺ = aklaviketone + NADPH + H⁺

For diagram of reaction [click here](#).

Glossary: aklavinone = methyl (1*R*,2*R*,4*S*)-2-ethyl-2,4,5,7-tetrahydroxy-6,11-dioxo-1,2,3,4,6,11-hexahydrotetracene-1-carboxylate
aklaviketone = methyl (1*R*,2*R*)-2-ethyl-2,5,7-trihydroxy-4,6,11-trioxo-1,2,3,4,6,11-hexahydrotetracene-1-carboxylate

Other name(s): *dauE* (gene name); *aknU* (gene name)

Systematic name: aklavinone:NADP⁺ oxidoreductase

Comments: The enzyme is involved in the synthesis of the aklavinone aglycone, a common precursor for several anthracycline antibiotics including aclacinomycins, daunorubicin and doxorubicin. The enzyme from the Gram-negative bacterium *Streptomyces* sp. C5 produces daunomycin.

References:

1. Dickens, M.L., Ye, J. and Strohl, W.R. Cloning, sequencing, and analysis of aklaviketone reductase from *Streptomyces* sp. strain C5. *J. Bacteriol.* 178 (1996) 3384-3388. [PMID: [8655529](#)]

[EC 1.1.1.362 created 2013]

EC 1.1.1.363

Accepted name: glucose-6-phosphate dehydrogenase [NAD(P)⁺]

Reaction: D-glucose 6-phosphate + NAD(P)⁺ = 6-phospho-D-glucono-1,5-lactone + NAD(P)H + H⁺

Other name(s): G6PDH; G6PD; Glc6PD

Systematic name: D-glucose-6-phosphate:NAD(P)⁺ 1-oxidoreductase

Comments: The enzyme catalyses a step of the pentose phosphate pathway. The enzyme from the Gram-positive bacterium *Leuconostoc mesenteroides* prefers NADP⁺ while the enzyme from the Gram-negative bacterium *Gluconacetobacter xylinus* prefers NAD⁺. cf. [EC 1.1.1.49](#), glucose-6-phosphate dehydrogenase (NADP⁺).

References:

1. Olive, C., Geroch, M.E. and Levy, H.R. Glucose 6-phosphate dehydrogenase from *Leuconostoc mesenteroides*. Kinetic studies. *J. Biol. Chem.* 246 (1971) 2047-2057. [PMID: [4396688](#)]

2. Lee, W.T. and Levy, H.R. Lysine-21 of *Leuconostoc mesenteroides* glucose 6-phosphate dehydrogenase participates in substrate binding through charge-charge interaction. *Protein Sci.* 1 (1992) 329-334. [PMID: [1304341](#)]

3. Cosgrove, M.S., Naylor, C., Paludan, S., Adams, M.J. and Levy, H.R. On the mechanism of the reaction catalyzed by glucose 6-phosphate dehydrogenase. *Biochemistry* 37 (1998) 2759-2767. [PMID: [9485426](#)]

4. Raganathan, S. and Levy, H.R. Purification and characterization of the NAD⁺-preferring glucose 6-phosphate dehydrogenase from *Acetobacter Hansenii* (*Acetobacter xylinum*). *Arch. Biochem. Biophys.* 310 (1994) 360-366. [PMID: [8179320](#)]

[EC 1.1.1.363 created 2013]

EC 1.1.3.45

Accepted name: aclacinomycin-N oxidase

Reaction: aclacinomycin N + O₂ = aclacinomycin A + H₂O₂

For diagram of reaction [click here](#).

Glossary: aclacinomycin N = 2-ethyl-2,5,7-trihydroxy-6,11-dioxo-4-[[2,3,6-trideoxy-4-O-[2,6-dideoxy-4-O-[(2*S*,5*S*,6*S*)-5-hydroxy-6-methyltetrahydro-2*H*-pyran-2-yl]-α-*L*-*lyxo*-hexopyranosyl]-3-(dimethylamino)-α-*L*-*lyxo*-hexopyranosyl]oxy]-1,2,3,4,6,11-hexahydronaphthacene-1-carboxylic acid methyl ester
aclacinomycin A = 2-ethyl-2,5,7-trihydroxy-6,11-dioxo-4-[[2,3,6-trideoxy-4-O-[2,6-dideoxy-4-O-[(2*R*,6*S*)-6-methyl-5-oxotetrahydro-2*H*-pyran-2-yl]-α-*L*-*lyxo*-hexopyranosyl]-3-(dimethylamino)-α-*L*-*lyxo*-hexopyranosyl]oxy]-1,2,3,4,6,11-hexahydronaphthacene-1-carboxylic acid methyl ester

Other name(s): AknOx (ambiguous); aclacinomycin oxidoreductase (ambiguous)

Systematic name: aclacinomycin-N:oxygen oxidoreductase

Comments: A flavoprotein (FAD). This bifunctional enzyme is a secreted flavin-dependent enzyme that is involved in the modification of the terminal sugar residues in the biosynthesis of aclacinomycins. The enzyme utilizes the same active site to catalyse the oxidation of the rhodnose moiety of aclacinomycin N to the cinerulose A moiety of aclacinomycin A and the oxidation of the latter to the L-aculose moiety of aclacinomycin Y (cf. [EC 1.3.3.14](#), aclacinomycin A oxidase).

References:

1. Alexeev, I., Sultana, A., Mantsala, P., Niemi, J. and Schneider, G. Aclacinomycin oxidoreductase (AknOx) from the biosynthetic pathway of the antibiotic aclacinomycin is an unusual flavoenzyme with a dual active site. *Proc. Natl. Acad. Sci. USA* 104 (2007) 6170-6175. [PMID: [17395717](#)]

2. Sultana, A., Alexeev, I., Kursula, I., Mantsala, P., Niemi, J. and Schneider, G. Structure determination by multiwavelength anomalous diffraction of aclacinomycin oxidoreductase: indications of multidomain pseudomeroheredral twinning. *Acta Crystallogr. D Biol. Crystallogr.* 63 (2007) 149-159. [PMID: [17242508](#)]

[EC 1.1.3.45 created 2013]

EC 1.2.7.11

Accepted name: 2-oxoacid oxidoreductase (ferredoxin)

Reaction: a 2-oxocarboxylate + CoA + 2 oxidized ferredoxin = an acyl-CoA + CO₂ + 2 reduced ferredoxin + 2 H⁺

Other name(s): OFOR

Systematic name: 2-oxocarboxylate:ferredoxin 2-oxidoreductase (decarboxylating, CoA-acylating)

Comments: Contains thiamine diphosphate and [4Fe-4S] clusters [2]. This enzyme is a member of the 2-oxoacid oxidoreductases, a family of enzymes that oxidatively decarboxylate different 2-oxoacids to form their CoA derivatives, and are differentiated based on their substrate specificity. For example, see [EC 1.2.7.3](#), 2-oxoglutarate synthase and [EC 1.2.7.7](#), 3-methyl-2-oxobutanoate dehydrogenase (ferredoxin).

References:

1. Kersch, L. and Oesterhelt, D. Purification and properties of two 2-oxoacid:ferredoxin oxidoreductases from *Halobacterium halobium*. *Eur. J. Biochem.* 116 (1981) 587-594. [PMID: [6266826](#)]
2. Zhang, Q., Iwasaki, T., Wakagi, T. and Oshima, T. 2-oxoacid:ferredoxin oxidoreductase from the thermoacidophilic archaeon, *Sulfolobus* sp. strain 7. *J. Biochem.* 120 (1996) 587-599. [PMID: [8902625](#)]
3. Fukuda, E., Kino, H., Matsuzawa, H. and Wakagi, T. Role of a highly conserved YPITP motif in 2-oxoacid:ferredoxin oxidoreductase: heterologous expression of the gene from *Sulfolobus* sp. strain 7, and characterization of the recombinant and variant enzymes. *Eur. J. Biochem.* 268 (2001) 5639-5646. [PMID: [11683888](#)]
4. Fukuda, E. and Wakagi, T. Substrate recognition by 2-oxoacid:ferredoxin oxidoreductase from *Sulfolobus* sp. strain 7. *Biochim. Biophys. Acta* 1597 (2002) 74-80. [PMID: [12009405](#)]
5. Nishizawa, Y., Yabuki, T., Fukuda, E. and Wakagi, T. Gene expression and characterization of two 2-oxoacid:ferredoxin oxidoreductases from *Aeropyrum pernix* K1. *FEBS Lett* 579 (2005) 2319-2322. [PMID: [15848165](#)]
6. Park, Y.J., Yoo, C.B., Choi, S.Y. and Lee, H.B. Purifications and characterizations of a ferredoxin and its related 2-oxoacid:ferredoxin oxidoreductase from the hyperthermophilic archaeon, *Sulfolobus solfataricus* P1. *J. Biochem. Mol. Biol.* 39 (2006) 46-54. [PMID: [16466637](#)]

[EC 1.2.7.11 created 2013]

*EC 1.3.1.9

Accepted name: enoyl-[acyl-carrier-protein] reductase (NADH)

Reaction: an acyl-[acyl-carrier protein] + NAD⁺ = a *trans*-2,3-dehydroacyl-[acyl-carrier protein] + NADH + H⁺

Other name(s): enoyl-[acyl carrier protein] reductase; enoyl-ACP reductase; NADH-enoyl acyl carrier protein reductase; NADH-specific enoyl-ACP reductase; acyl-[acyl-carrier-protein]:NAD⁺ oxidoreductase; *fabI* (gene name); *inhA* (gene name)

Systematic name: acyl-[acyl-carrier protein]:NAD⁺ oxidoreductase

Comments: The enzyme catalyses an essential step in fatty acid biosynthesis, the reduction of the 2,3-double bond in enoyl-acyl-[acyl-carrier-protein] derivatives of the elongating fatty acid moiety. The enzyme from the bacterium *Escherichia coli* accepts substrates with carbon chain length from 4 to 18 [3]. The enzyme from the bacterium *Mycobacterium tuberculosis* prefers substrates with carbon chain length from 12 to 24 carbons [4,5].

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), [PDB](#), CAS registry number: 37251-08-4

References:

1. Shimakata, T. and Stumpf, P.K. Purification and characterizations of β -ketoacyl-[acyl-carrier-protein] reductase, β -hydroxyacyl-[acyl-carrier-protein] dehydrase, and enoyl-[acyl-carrier-protein] reductase from *Spinacia oleracea* leaves. *Arch. Biochem. Biophys.* 218 (1982) 77-91. [PMID: [6756317](#)]
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5. Rozwarski, D.A., Vilcheze, C., Sugantino, M., Bittman, R. and Sacchettini, J.C. Crystal structure of the *Mycobacterium tuberculosis* enoyl-ACP reductase, InhA, in complex with NAD⁺ and a C₁₆ fatty acyl substrate. *J. Biol. Chem.* 274 (1999) 15582-15589. [PMID: [10336454](#)]

[EC 1.3.1.9 created 1972, modified 2013]

*EC 1.3.1.21

Accepted name: 7-dehydrocholesterol reductase

Reaction: cholesterol + NADP⁺ = cholesta-5,7-dien-3 β -ol + NADPH + H⁺

For diagram of reaction [click here](#).

Other name(s): DAF-36 (gene name); DHCR7 (gene name); 7-DHC reductase; 7-dehydrocholesterol dehydrogenase/cholesterol oxidase; Δ^7 -sterol reductase

Systematic name: cholesterol:NADP⁺ Δ^7 -oxidoreductase

Comments: In mammals the enzyme is part of the cholesterol biosynthesis pathway [2] and catalyses the reduction reaction. In the nematode *Caenorhabditis elegans* the enzyme catalyses the oxidation reaction as part of the biosynthesis of daifachronic acids that are important for control of developmental timing and longevity [3,4].

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 9080-21-1

References:

1. Dempsey, M.E., Seaton, J.D., Schroeffer, G.J. and Trockman, R.W. The intermediary role of $\Delta^{5,7}$ -cholestadien-3 β -ol in cholesterol biosynthesis. *J. Biol. Chem.* 239 (1964) 1381-1387. [PMID: [14189869](#)]
2. Moebius, F.F., Fitzky, B.U., Lee, J.N., Paik, Y.K. and Glossmann, H. Molecular cloning and expression of the human Δ^7 -sterol reductase. *Proc. Natl. Acad. Sci. USA* 95 (1998) 1899-1902. [PMID: [2465114](#)]
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4. Wollam, J., Magomedova, L., Magner, D.B., Shen, Y., Rottiers, V., Motola, D.L., Mangelsdorf, D.J., Cummins, C.L. and Antebi, A. The Rieske oxygenase DAF-36 functions as a cholesterol 7-desaturase in steroidogenic pathways governing longevity. *Aging Cell* 10 (2011) 879-884. [PMID: [21749634](#)]
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[EC 1.3.1.21 created 1972, modified 2013]

*EC 1.3.1.39

Accepted name: enoyl-[acyl-carrier-protein] reductase (NADPH, *Re*-specific)

Reaction: an acyl-[acyl-carrier protein] + NADP⁺ = a *trans*-2,3-dehydroacyl-[acyl-carrier protein] + NADPH + H⁺

Other name(s): acyl-ACP dehydrogenase; enoyl-[acyl carrier protein] (reduced nicotinamide adenine dinucleotide phosphate) reductase; NADPH 2-enoyl Co A reductase; enoyl-ACP reductase; enoyl-[acyl-carrier-protein] reductase (NADPH₂, A-specific); acyl-[acyl-carrier-protein]:NADP⁺ oxidoreductase (A-specific); *fabL* (gene name); enoyl-[acyl-carrier-protein] reductase (NADPH, A-specific); acyl-[acyl-carrier protein]:NADP⁺ oxidoreductase (A-specific)

Systematic name: acyl-[acyl-carrier protein]:NADP⁺ oxidoreductase (*Re*-specific)

Comments: This enzyme completes each cycle of fatty acid elongation by catalysing the stereospecific reduction of the double bond at position 2 of a growing fatty acid chain, while linked to an acyl-carrier protein. It is also one of the activities of [EC 2.3.1.85](#), animal fatty-acid synthase. The mammalian enzyme is *Re*-specific with respect to NADP⁺. *cf.* [EC 1.3.1.9](#), enoyl-[acyl-carrier-protein] reductase (NADH) and [EC 1.3.1.10](#), enoyl-[acyl-carrier-protein] reductase (NADPH, *Si*-specific).

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number:

References:

1. Dugan, R.E., Slakey, L.L. and Porter, L.W. Stereospecificity of the transfer of hydrogen from reduced nicotinamide adenine dinucleotide phosphate to the acyl chain in the dehydrogenase-catalyzed reactions of fatty acid synthesis. *J. Biol. Chem.* 245 (1970) 6312-6316. [PMID: [4394955](#)]
2. Carlisle-Moore, L., Gordon, C.R., Machutta, C.A., Miller, W.T. and Tonge, P.J. Substrate recognition by the human fatty-acid synthase. *J. Biol. Chem.* 280 (2005) 42612-42618. [PMID: [16215233](#)]
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4. Kim, K.H., Ha, B.H., Kim, S.J., Hong, S.K., Hwang, K.Y. and Kim, E.E. Crystal structures of Enoyl-ACP reductases I (FabI) and III (FabL) from *B. subtilis*. *J. Mol. Biol.* 406 (2011) 403-415. [PMID: [21185310](#)]

[EC 1.3.1.39 created 1986, modified 2013]

EC 1.3.1.104

Accepted name: enoyl-[acyl-carrier-protein] reductase

Reaction: an acyl-[acyl-carrier protein] + NADP⁺ = a *trans*-2,3-dehydroacyl-[acyl-carrier protein] + NADPH + H⁺

Other name(s): acyl-ACP dehydrogenase (ambiguous); enoyl-[acyl carrier protein] (reduced nicotinamide adenine dinucleotide phosphate) reductase; NADPH 2-enoyl Co A reductase; enoyl-ACP reductase (ambiguous); *fabL* (gene name)

Systematic name: acyl-[acyl-carrier protein]:NADP⁺ oxidoreductase

Comments: The enzyme completes each cycle of fatty acid elongation by catalysing the stereospecific reduction of the double bond at position 2 of a growing fatty acid chain, while linked to the acyl-carrier protein, in an NADPH-dependent manner. This entry stands for enzymes whose stereo-specificity with respect to NADP⁺ is not known. [*cf.* [EC 1.3.1.39](#) enoyl-[acyl-carrier-protein] reductase (NADPH, *Re*-specific), [EC 1.3.1.10](#), enoyl-[acyl-carrier-protein] reductase (NADPH, *Si*-specific) and [EC 1.3.1.9](#), enoyl-[acyl-carrier-protein] reductase (NADH)].

References:

1. Heath, R.J., Su, N., Murphy, C.K. and Rock, C.O. The enoyl-[acyl-carrier-protein] reductases FabI and FabL from *Bacillus subtilis*. *J. Biol. Chem.* 275 (2000) 40128-40133. [PMID: [11007778](#)]
2. Kim, K.H., Park, J.K., Ha, B.H., Moon, J.H. and Kim, E.E. Crystallization and preliminary X-ray crystallographic analysis of enoyl-ACP reductase III (FabL) from *Bacillus subtilis*. *Acta Crystallogr. Sect. F Struct. Biol. Cryst. Commun.* 63 (2007) 246-248. [PMID: [17329825](#)]
3. Kim, K.H., Ha, B.H., Kim, S.J., Hong, S.K., Hwang, K.Y. and Kim, E.E. Crystal structures of Enoyl-ACP reductases I (FabI) and III (FabL) from *B. subtilis*. *J. Mol. Biol.* 406 (2011) 403-415. [PMID: [21185310](#)]

[EC 1.3.1.104 created 2013]

EC 1.3.3.14

Accepted name: aclacinomycin-A oxidase

Reaction: aclacinomycin A + O₂ = aclacinomycin Y + H₂O₂

For diagram of reaction [click here](#).

Glossary: aclacinomycin A = 2-ethyl-1,2,3,4,6,11-hexahydro-2,5,7-trihydroxy-6,11-dioxo-4-[[2,3,6-trideoxy-4-O-[2,6-dideoxy-4-O-[(2R,6S)-tetrahydro-6-methyl-5-oxo-2H-pyran-2-yl]-α-L-lyxo-hexopyranosyl]-3-(dimethylamino)-α-L-lyxo-hexopyranosyl]oxy]naphthacene-1-carboxylic acid methyl ester
aclacinomycin Y = 2-ethyl-1,2,3,4,6,11-hexahydro-2,5,7-trihydroxy-6,11-dioxo-4-[[2,3,6-trideoxy-4-O-[2,6-dideoxy-4-O-[(2R,6S)-5,6-dihydro-6-methyl-5-oxo-2H-pyran-2-yl]-α-L-lyxo-hexopyranosyl]-3-(dimethylamino)-α-L-lyxo-hexopyranosyl]oxy]naphthacene-1-carboxylic acid methyl ester

Other name(s): AknOx (ambiguous); aclacinomycin oxidoreductase (ambiguous)

Systematic name: aclacinomycin-A: oxygen oxidoreductase

Comments: A flavoprotein (FAD). This bifunctional enzyme is a secreted flavin-dependent enzyme that is involved in the modification of the terminal sugar residues in the biosynthesis of aclacinomycins. The enzyme utilizes the same active site to catalyse the oxidation of the rhodinose moiety of aclacinomycin N to the cinerulose A moiety of aclacinomycin A (cf. [EC 1.1.3.45](#)) and the oxidation of the latter to the L-aculose moiety of aclacinomycin Y.

References:

- Yoshimoto, A., Ogasawara, T., Kitamura, I., Oki, T., Inui, T., Takeuchi, T. and Umezawa, H. Enzymatic conversion of aclacinomycin A to Y by a specific oxidoreductase in *Streptomyces*. *J. Antibiot. (Tokyo)* 32 (1979) 472-481. [PMID: [528393](#)]
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- Sultana, A., Alexeev, I., Kursula, I., Mantsala, P., Niemi, J. and Schneider, G. Structure determination by multiwavelength anomalous diffraction of aclacinomycin oxidoreductase: indications of multidomain pseudomeroheredral twinning. *Acta Crystallogr. D Biol. Crystallogr.* 63 (2007) 149-159. [PMID: [17242508](#)]

[EC 1.3.3.14 created 2013]

*EC 1.3.8.6

Accepted name: glutaryl-CoA dehydrogenase (decarboxylating)

Reaction: glutaryl-CoA + electron-transfer flavoprotein = crotonyl-CoA + CO₂ + reduced electron-transfer flavoprotein (overall reaction)

(1a) glutaryl-CoA + electron-transfer flavoprotein = (E)-glutaconyl-CoA + reduced electron-transfer flavoprotein

(1b) (E)-glutaconyl-CoA = crotonyl-CoA + CO₂

Glossary: (E)-glutaconyl-CoA = (2E)-4-carboxybut-2-enoyl-CoA
crotonyl-CoA = (E)-but-2-enoyl-CoA

Other name(s): glutaryl coenzyme A dehydrogenase; glutaryl-CoA:(acceptor) 2,3-oxidoreductase (decarboxylating); glutaryl-CoA dehydrogenase

Systematic name: glutaryl-CoA:electron-transfer flavoprotein 2,3-oxidoreductase (decarboxylating)

Comments: Contains FAD. The enzyme catalyses the oxidation of glutaryl-CoA to glutaconyl-CoA (which remains bound to the enzyme), and the decarboxylation of the latter to crotonyl-CoA (cf. [EC 4.1.1.70](#), glutaconyl-CoA decarboxylase). FAD is the electron acceptor in the oxidation of the substrate, and its reoxidation by electron-transfer flavoprotein completes the catalytic cycle. The anaerobic, sulfate-reducing bacterium *Desulfococcus multivorans* contains two glutaryl-CoA dehydrogenases: a decarboxylating enzyme (this entry), and a non-decarboxylating enzyme that only catalyses the oxidation to glutaconyl-CoA ([EC 1.3.99.32](#)).

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), [PDB](#), [UM-BBD](#), CAS registry number: 37255-38-2

References:

- Besrat, A., Polan, C.E. and Henderson, L.M. Mammalian metabolism of glutaric acid. *J. Biol. Chem.* 244 (1969) 1461-1467. [PMID: [4304226](#)]
- Hartel, U., Eckel, E., Koch, J., Fuchs, G., Linder, D. and Buckel, W. Purification of glutaryl-CoA dehydrogenase from *Pseudomonas* sp., an enzyme involved in the anaerobic degradation of benzoate. *Arch. Microbiol.* 159 (1993) 174-181. [PMID: [8439237](#)]
- Dwyer, T.M., Zhang, L., Muller, M., Marrugo, F. and Frerman, F. The functions of the flavin contact residues, αArg²⁴⁹ and βTyr¹⁶, in human electron transfer flavoprotein. *Biochim. Biophys. Acta* 1433 (1999) 139-152. [PMID: [10446367](#)]
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[EC 1.3.8.6 created 1972 as EC 1.3.99.7, transferred 2012 to EC 1.3.8.6, modified 2013]

*EC 1.3.99.32

Accepted name: glutaryl-CoA dehydrogenase (non-decarboxylating)

Reaction: glutaryl-CoA + acceptor = (E)-glutaconyl-CoA + reduced acceptor

Glossary: (E)-glutaconyl-CoA = (2E)-4-carboxybut-2-enoyl-CoA

Other name(s): GDHDes; nondecarboxylating glutaryl-coenzyme A dehydrogenase; nondecarboxylating glutaconyl-coenzyme A-forming GDH

Systematic name: glutaryl-CoA:acceptor 2,3-oxidoreductase (non-decarboxylating)

Comments: The enzyme contains FAD. The anaerobic, sulfate-reducing bacterium *Desulfococcus multivorans* contains two glutaryl-CoA dehydrogenases: a decarboxylating enzyme ([EC 1.3.8.6](#)), and a nondecarboxylating enzyme (this entry). The two enzymes cause different structural changes around the glutaconyl carboxylate group, primarily due to the presence of either a tyrosine or a valine residue, respectively, at the active site.

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number:

References:

1. Wischgoll, S., Taubert, M., Peters, F., Jehmlich, N., von Bergen, M. and Boll, M. Decarboxylating and nondecarboxylating glutaryl-coenzyme A dehydrogenases in the aromatic metabolism of obligately anaerobic bacteria. *J. Bacteriol.* 191 (2009) 4401-4409. [PMID: [19395484](#)]
2. Wischgoll, S., Demmer, U., Warkentin, E., Gunther, R., Boll, M. and Ermler, U. Structural basis for promoting and preventing decarboxylation in glutaryl-coenzyme A dehydrogenases. *Biochemistry* 49 (2010) 5350-5357. [PMID: [20486657](#)]

[EC 1.3.99.32 created 2012, modified 2013]

EC 1.4.4.2*Accepted name:** glycine dehydrogenase (aminomethyl-transferring)**Reaction:** glycine + [glycine-cleavage complex H protein]-N⁶-lipoyl-L-lysine = [glycine-cleavage complex H protein]-S-aminomethyl-N⁶-dihydrolipoyl-L-lysine + CO₂For diagram of reaction [click here](#).**Glossary:** [dihydrolipoyl group](#)**Other name(s):** P-protein; glycine decarboxylase; glycine-cleavage complex; glycine:lipoylprotein oxidoreductase (decarboxylating and acceptor-aminomethylating); protein P1; glycine dehydrogenase (decarboxylating); glycine cleavage system P-protein; glycine-cleavage complex P-protein**Systematic name:** glycine:H-protein-lipoyllysine oxidoreductase (decarboxylating, acceptor-amino-methylating)**Comments:** A pyridoxal-phosphate protein. A component of the glycine cleavage system, which is composed of four components that only loosely associate: the P protein (EC 1.4.4.2), the T protein ([EC 2.1.2.10](#), aminomethyltransferase), the L protein ([EC 1.8.1.4](#), dihydrolipoyl dehydrogenase) and the lipoyl-bearing H protein [3]. Previously known as glycine synthase.**Links to other databases:** [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), [PDB](#), CAS registry number: 37259-67-9**References:**

1. Hiraga, K. and Kikuchi, G. The mitochondrial glycine cleavage system. Functional association of glycine decarboxylase and aminomethyl carrier protein. *J. Biol. Chem.* 255 (1980) 11671-11676. [PMID: [7440563](#)]
2. Perham, R.N. Swinging arms and swinging domains in multifunctional enzymes: catalytic machines for multistep reactions. *Annu. Rev. Biochem.* 69 (2000) 961-1004. [PMID: [10966480](#)]
3. Nesbitt, N.M., Baleanu-Gogonea, C., Cicchillo, R.M., Goodson, K., Iwig, D.F., Broadwater, J.A., Haas, J.A., Fox, B.G. and Booker, S.J. Expression, purification, and physical characterization of *Escherichia coli* lipoyl(octanoyl)transferase. *Protein Expr. Purif.* 39 (2005) 269-282. [PMID: [15642479](#)]

[EC 1.4.4.2 created 1984, modified 2003, modified 2006, modified 2013]

EC 1.5.5.2**Accepted name:** proline dehydrogenase**Reaction:** L-proline + a quinone = (S)-l-pyrroline-5-carboxylate + a quinol**Other name(s):** L-proline dehydrogenase; L-proline:(acceptor) oxidoreductase**Systematic name:** L-proline:quinone oxidoreductase**Comments:** A flavoprotein (FAD). The electrons from L-proline are transferred to the FAD cofactor, and from there to a quinone acceptor [3]. In many organisms, ranging from bacteria to mammals, proline is oxidized to glutamate in a two-step process involving this enzyme and [EC 1.2.1.88](#), L-glutamate γ -semialdehyde dehydrogenase. Both activities are carried out by the same enzyme in enterobacteria.**References:**

1. Scarpulla, R.C. and Sofer, R.L. Membrane-bound proline dehydrogenase from *Escherichia coli*. Solubilization, purification, and characterization. *J. Biol. Chem.* 253 (1978) 5997-6001. [PMID: [355248](#)]
2. Brown, E.D. and Wood, J.M. Redesigned purification yields a fully functional PutA protein dimer from *Escherichia coli*. *J. Biol. Chem.* 267 (1992) 13086-13092. [PMID: [1618807](#)]
3. Moxley, M.A., Tanner, J.J. and Becker, D.F. Steady-state kinetic mechanism of the proline:ubiquinone oxidoreductase activity of proline utilization A (PutA) from *Escherichia coli*. *Arch. Biochem. Biophys.* 516 (2011) 113-120. [PMID: [22040654](#)]

[EC 1.5.5.2 created 1980 as 1.5.99.8, transferred 2013 to 1.5.5.2.]

[**EC 1.5.99.8 Transferred entry:** proline dehydrogenase. Now [EC 1.5.5.2](#), proline dehydrogenase. (EC 1.5.99.8 created 1980, transferred 2013 to 1.5.5.2, deleted 2013)]***EC 1.6.3.1****Accepted name:** NAD(P)H oxidase (H₂O₂-forming)**Reaction:** NAD(P)H + H⁺ + O₂ = NAD(P)⁺ + H₂O₂**Other name(s):** THOX2; ThOX; dual oxidase; p138tox; thyroid NADPH oxidase; thyroid oxidase; thyroid oxidase 2; NADPH oxidase; NAD(P)H:oxygenn oxidoreductase; NAD(P)H oxidase**Systematic name:** NAD(P)H:oxygenn oxidoreductase (H₂O₂-forming)**Comments:** Requires FAD, heme and calcium. When calcium is present, this transmembrane glycoprotein generates H₂O₂ by transferring electrons from intracellular NAD(P)H to extracellular molecular oxygen. The electron bridge within the enzyme contains one molecule of FAD and probably two heme groups. This flavoprotein is expressed at the apical membrane of thyrocytes, and provides H₂O₂ for the thyroid peroxidase-catalysed biosynthesis of thyroid hormones.**Links to other databases:** [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 77106-92-4

References:

1. Moreno, J.C., Bikker, H., Kempers, M.J., van Trotsenburg, A.S., Baas, F., de Vijlder, J.J., Vulsma, T. and Ris-Stalpers, C. Inactivating mutations in the gene for thyroid oxidase 2 (THOX2) and congenital hypothyroidism. *N. Engl. J. Med.* 347 (2002) 95-102. [PMID: [12110737](#)]
2. De Deken, X., Wang, D., Dumont, J.E. and Miot, F. Characterization of ThOX proteins as components of the thyroid H₂O₂-generating system. *Exp. Cell* 273 (2002) 187-196. [PMID: [11822874](#)]
3. De Deken, X., Wang, D., Many, M.C., Costagliola, S., Libert, F., Vassart, G., Dumont, J.E. and Miot, F. Cloning of two human thyroid cDNAs encoding new members of the NADPH oxidase family. *J. Biol. Chem.* 275 (2000) 23227-23233. [PMID: [10806195](#)]
4. Dupuy, C., Ohayon, R., Valent, A., Noel-Hudson, M.S., Deme, D. and Virion, A. Purification of a novel flavoprotein involved in the thyroid NADPH oxidase. Cloning of the porcine and human cDNAs. *J. Biol. Chem.* 274 (1999) 37265-37269. [PMID: [10601291](#)]
5. Leseney, A.M., Deme, D., Legue, O., Ohayon, R., Chanson, P., Sales, J.P., Pires de Carvalho, D., Dupuy, C. and Virion, A. Biochemical characterization of a Ca²⁺/NAD(P)H-dependent H₂O₂ generator in human thyroid tissue. *Biochimie* 81 (1999) 373-380. [PMID: [10401672](#)]
6. Dupuy, C., Virion, A., Ohayon, R., Kaniewski, J., Deme, D. and Pommier, J. Mechanism of hydrogen peroxide formation catalyzed by NADPH oxidase in thyroid plasma membrane. *J. Biol. Chem.* 266 (1991) 3739-3743. [PMID: [1995628](#)]

[EC 1.6.3.1 created 2003, modified 2013]

EC 1.6.3.2**Accepted name:** NAD(P)H oxidase (H₂O-forming)**Reaction:** 2 NAD(P)H + 2 H⁺ + O₂ = 2 NAD(P)⁺ + 2 H₂O**Systematic name:** NAD(P)H: oxygen oxidoreductase (H₂O-forming)**Comments:** A flavoprotein (FAD). NADPH is a better substrate than NADH [1,3]. By removal of oxygen the enzyme is involved in aerobic tolerance in the thermophilic anaerobic archaeon *Thermococcus profundus* and in *Giardia intestinalis*, a microaerophilic single-celled parasite of the order Diplomonadida.**References:**

1. Brown, D.M., Upcroft, J.A. and Upcroft, P. A H₂O-producing NADH oxidase from the protozoan parasite *Giardia duodenalis*. *Eur. J. Biochem.* 241 (1996) 155-161. [PMID: [8898901](#)]
2. Li, L. and Wang, C.C. A likely molecular basis of the susceptibility of *Giardia lamblia* towards oxygen. *Mol. Microbiol.* 59 (2006) 202-211. [PMID: [16359329](#)]
3. Jia, B., Park, S.C., Lee, S., Pham, B.P., Yu, R., Le, T.L., Han, S.W., Yang, J.K., Choi, M.S., Baumeister, W. and Cheong, G.W. Hexameric ring structure of a thermophilic archaeon NADH oxidase that produces predominantly H₂O. *FEBS J.* 275 (2008) 5355-5366. [PMID: [18959761](#)]
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[EC 1.6.3.2 created 2013]

EC 1.6.3.3**Accepted name:** NADH oxidase (H₂O₂-forming)**Reaction:** NADH + H⁺ + O₂ = NAD⁺ + H₂O₂**Other name(s):** NOX-1; H₂O₂-forming NADH oxidase**Systematic name:** NADH: oxygen oxidoreductase (H₂O₂-forming)**Comments:** A flavoprotein (FAD). The bacterium *Streptococcus mutans* contains two distinct NADH oxidases, a H₂O₂-forming enzyme and a H₂O-forming enzyme (*cf.* [EC 1.6.3.4](#), NADH oxidase (H₂O-forming)) [1]. The enzymes from the anaerobic archaea *Methanocaldococcus jannaschii* [6] and *Pyrococcus furiosus* [3] also produce low amounts of H₂O. Unlike [EC 1.6.3.1](#) (NAD(P)H oxidase) it has no activity towards NADPH.**References:**

1. Higuchi, M., Shimada, M., Yamamoto, Y., Hayashi, T., Koga, T. and Kamio, Y. Identification of two distinct NADH oxidases corresponding to H₂O₂-forming oxidase and H₂O-forming oxidase induced in *Streptococcus mutans*. *J. Gen. Microbiol.* 139 (1993) 2343-2351. [PMID: [8254304](#)]
2. Ward, D.E., Donnelly, C.J., Mullendore, M.E., van der Oost, J., de Vos, W.M. and Crane, E.J., 3rd. The NADH oxidase from *Pyrococcus furiosus*. Implications for the protection of anaerobic hyperthermophiles against oxidative stress. *Eur. J. Biochem.* 268 (2001) 5816-5823. [PMID: [11722568](#)]
3. Kengen, S.W., van der Oost, J. and de Vos, W.M. Molecular characterization of H₂O₂-forming NADH oxidases from *Archaeoglobus fulgidus*. *Eur. J. Biochem.* 270 (2003) 2885-2894. [PMID: [12823559](#)]
4. Yang, X. and Ma, K. Characterization of an exceedingly active NADH oxidase from the anaerobic hyperthermophilic bacterium *Thermotoga maritima*. *J. Bacteriol.* 189 (2007) 3312-3317. [PMID: [17293421](#)]
5. Hirano, J., Miyamoto, K. and Ohta, H. Purification and characterization of thermostable H₂O₂-forming NADH oxidase from 2-phenylethanol-assimilating *Brevibacterium* sp. KU1309. *Appl. Microbiol. Biotechnol.* 80 (2008) 71-78. [PMID: [18521590](#)]
6. Case, C.L., Rodriguez, J.R. and Mukhopadhyay, B. Characterization of an NADH oxidase of the flavin-dependent disulfide reductase family from *Methanocaldococcus jannaschii*. *Microbiology* 155 (2009) 69-79. [PMID: [19118348](#)]

[EC 1.6.3.3 created 2013]

EC 1.6.3.4**Accepted name:** NADH oxidase (H₂O-forming)

Reaction: $2 \text{ NADH} + 2 \text{ H}^+ + \text{O}_2 = 2 \text{ NAD}^+ + 2 \text{ H}_2\text{O}$

Other name(s): H₂O-forming NADH oxidase; Nox-2

Systematic name: NADH:oxygen oxidoreductase (H₂O-forming)

Comments: A flavoprotein (FAD). The bacterium *Streptococcus mutans* contains two distinct NADH oxidases, a H₂O-forming enzyme and a H₂O₂-forming enzyme (*cf.* [EC 1.6.3.3](#), NADH oxidase (H₂O₂-forming)) [1].

References:

- Schmidt, H.L., Stocklein, W., Danzer, J., Kirch, P. and Limbach, B. Isolation and properties of an H₂O-forming NADH oxidase from *Streptococcus faecalis*. *Eur. J. Biochem.* 156 (1986) 149-155. [PMID: [3082630](#)]
- Higuchi, M., Shimada, M., Yamamoto, Y., Hayashi, T., Koga, T. and Kamio, Y. Identification of two distinct NADH oxidases corresponding to H₂O₂-forming oxidase and H₂O-forming oxidase induced in *Streptococcus mutans*. *J. Gen. Microbiol.* 139 (1993) 2343-2351. [PMID: [8254304](#)]
- Matsumoto, J., Higuchi, M., Shimada, M., Yamamoto, Y. and Kamio, Y. Molecular cloning and sequence analysis of the gene encoding the H₂O-forming NADH oxidase from *Streptococcus mutans*. *Biosci. Biotechnol. Biochem.* 60 (1996) 39-43. [PMID: [8824824](#)]
- Kawasaki, S., Ishikura, J., Chiba, D., Nishino, T. and Niimura, Y. Purification and characterization of an H₂O-forming NADH oxidase from *Clostridium aminovalericum*: existence of an oxygen-detoxifying enzyme in an obligate anaerobic bacteria. *Arch. Microbiol.* 181 (2004) 324-330. [PMID: [15014929](#)]
- Zhang, Y.W., Tiwari, M.K., Gao, H., Dhiman, S.S., Jeya, M. and Lee, J.K. Cloning and characterization of a thermostable H₂O-forming NADH oxidase from *Lactobacillus rhamnosus*. *Enzyme Microb. Technol.* 50 (2012) 255-262. [PMID: [22418266](#)]

[EC 1.6.3.4 created 2013]

*EC 1.8.1.14

Accepted name: CoA-disulfide reductase

Reaction: $2 \text{ CoA} + \text{NADP}^+ = \text{CoA-disulfide} + \text{NADPH} + \text{H}^+$

Other name(s): CoA-disulfide reductase (NADH₂); NADH₂:CoA-disulfide oxidoreductase; CoA:NAD⁺ oxidoreductase (misleading); CoADR; coenzyme A disulfide reductase

Systematic name: CoA:NADP⁺ oxidoreductase

Comments: A flavoprotein. Not identical with [EC 1.8.1.6](#) (cystine reductase), [EC 1.8.1.7](#) (glutathione-disulfide reductase) or [EC 1.8.1.13](#) (bis-γ-glutamylcystine reductase). The enzyme from the bacterium *Staphylococcus aureus* has a strong preference for NADPH [3], while the bacterium *Bacillus megaterium* contains both NADH and NADPH-dependent enzymes [1].

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [PDB](#), [Metacyc](#), CAS registry number: 206770-55-0

References:

- Setlow, B. and Setlow, P. Levels of acetyl coenzyme A, reduced and oxidized coenzyme A, and coenzyme A in disulfide linkage to protein in dormant and germinated spores and growing and sporulating cells of *Bacillus megaterium*. *J. Bacteriol.* 132 (1977) 444-452. [PMID: [410791](#)]
- delCardayré, S.B., Stock, K.P., Newton, G.L., Fahey, R.C. and Davies, J.E. Coenzyme A disulfide reductase, the primary low molecular weight disulfide reductase from *Staphylococcus aureus*. Purification and characterization of the native enzyme. *J. Biol. Chem.* 273 (1998) 5744-5751. [PMID: [9488707](#)]
- Luba, J., Charrier, V. and Claiborne, A. Coenzyme A-disulfide reductase from *Staphylococcus aureus*: evidence for asymmetric behavior on interaction with pyridine nucleotides. *Biochemistry* 38 (1999) 2725-2737. [PMID: [10052943](#)]

[EC 1.8.1.14 created 1992 as EC 1.6.4.10, transferred 2002 to EC 1.8.1.14, modified 2005, modified 2013]

EC 1.8.1.19

Accepted name: sulfide dehydrogenase

Reaction: $\text{hydrogen sulfide} + (\text{sulfide})_n + \text{NADP}^+ = (\text{sulfide})_{n-1} + \text{NADPH} + \text{H}^+$

Other name(s): SuDH

Systematic name: hydrogen sulfide:polysulfide:NADP⁺ oxidoreductase

Comments: A iron-sulfur flavoprotein. In the archaeon *Pyrococcus furiosus* the enzyme is involved in the oxidation of NADPH which is produced in peptide degradation. The enzyme also catalyses the reduction of sulfur with lower activity.

References:

- Ma, K. and Adams, M.W. Sulfide dehydrogenase from the hyperthermophilic archaeon *Pyrococcus furiosus*: a new multifunctional enzyme involved in the reduction of elemental sulfur. *J. Bacteriol.* 176 (1994) 6509-6517. [PMID: [7961401](#)]
- Hagen, W.R., Silva, P.J., Amorim, M.A., Hagedoorn, P.L., Wassink, H., Haaker, H. and Robb, F.T. Novel structure and redox chemistry of the prosthetic groups of the iron-sulfur flavoprotein sulfide dehydrogenase from *Pyrococcus furiosus*; evidence for a [2Fe-2S] cluster with Asp(Cys)₃ ligands. *J. Biol. Inorg. Chem.* 5 (2000) 527-534. [PMID: [10968624](#)]

[EC 1.8.1.19 created 2013]

EC 1.13.11.76

Accepted name: 2-amino-5-chlorophenol 1,6-dioxygenase

Reaction: $2\text{-amino-5-chlorophenol} + \text{O}_2 = 2\text{-amino-5-chloromuconate 6-semialdehyde}$

Other name(s): *cnbC* (gene name)

Systematic name: 2-amino-5-chlorophenol:oxygen 1,6-oxidoreductase (decyclizing)

Comments: The enzyme, a member of the nonheme-iron(II)-dependent dioxygenase family, is an extradiol-type dioxygenase that utilizes a non-heme ferrous iron to cleave the aromatic ring at the *meta* position (relative to the hydroxyl substituent). The enzyme from the bacterium *Comamonas testosteroni* CNB-1 also has the activity of [EC 1.3.1.74](#), 2-aminophenol 1,6-dioxygenase.

References:

1. Wu, J.F., Sun, C.W., Jiang, C.Y., Liu, Z.P. and Liu, S.J. A novel 2-aminophenol 1,6-dioxygenase involved in the degradation of *p*-chloronitrobenzene by *Comamonas* strain CNB-1: purification, properties, genetic cloning and expression in *Escherichia coli*. *Arch. Microbiol.* 183 (2005) 1-8. [PMID: [15580337](#)]

[EC 1.13.11.76 created 2013]

EC 1.13.12.21

Accepted name: tetracenomycin-F1 monooxygenase

Reaction: tetracenomycin F1 + O₂ = tetracenomycin D3 + H₂O

For diagram of reaction [click here](#).

Glossary: tetracenomycin D3 = 3,8,10,12-tetrahydroxy-1-methyl-6,11-dioxo-6,11-dihydro-2-tetracenecarboxylate = 6,11-dihydro-3,8,10,12-tetrahydroxy-1-methyl-6,11-dioxonaphthacene-2-carboxylic acid
tetracenomycin F1 = 3,8,10,12-tetrahydroxy-1-methyl-11-oxo-6,11-dihydro-2-tetracenecarboxylate = 6,11-dihydro-3,8,10,12-tetrahydroxy-1-methyl-11-oxonaphthacene-2-carboxylic acid

Other name(s): *tmH* (gene name)

Systematic name: tetracenomycin-F1:oxygen C5-monooxygenase

Comments: The enzyme is involved in biosynthesis of the anthracycline antibiotic tetracenomycin C by the bacterium *Streptomyces glaucescens*.

References:

1. Shen, B. and Hutchinson, C.R. Tetracenomycin F1 monooxygenase: oxidation of a naphthacene to a naphthacenequinone in the biosynthesis of tetracenomycin C in *Streptomyces glaucescens*. *Biochemistry* 32 (1993) 6656-6663. [PMID: [8329392](#)]

[EC 1.13.12.21 created 2013]

EC 1.14.11.42

Accepted name: tRNA^{Phe} (7-(3-amino-3-carboxypropyl)wyosine³⁷-C²)-hydroxylase

Reaction: 7-(3-amino-3-carboxypropyl)wyosine³⁷ in tRNA^{Phe} + 2-oxoglutarate + O₂ = 7-(2-hydroxy-3-amino-3-carboxypropyl)wyosine³⁷ in tRNA^{Phe} + succinate + CO₂

Glossary: 7-(3-amino-3-carboxypropyl)wyosine = 7-[(3S)-3-amino-3-carboxypropyl]-4,6-dimethyl-3-(D-ribofuranosyl)-3,4-dihydro-9H-imidazo[1,2-a]purin-9-one
7-(2-hydroxy-3-amino-3-carboxypropyl)wyosine = 4-[4,6-dimethyl-9-oxo-3-(D-ribofuranosyl)-4,9-dihydro-3H-imidazo[1,2-a]purin-7-yl]-L-threonine

Other name(s): TYW5; tRNA yW-synthesizing enzyme 5

Systematic name: tRNA^{Phe} 7-(3-amino-3-carboxypropyl)wyosine³⁷,2-oxoglutarate:oxygen oxidoreductase (2-hydroxylating)

Comments: Requires Fe²⁺. The enzyme is not active with wybutosine.

References:

1. Noma, A., Ishitani, R., Kato, M., Nagao, A., Nureki, O. and Suzuki, T. Expanding role of the jumonji C domain as an RNA hydroxylase. *J. Biol. Chem.* 285 (2010) 34503-34507. [PMID: [20739293](#)]

2. Kato, M., Arais, Y., Noma, A., Nagao, A., Suzuki, T., Ishitani, R. and Nureki, O. Crystal structure of a novel JmjC-domain-containing protein, TYW5, involved in tRNA modification. *Nucleic Acids Res.* 39 (2011) 1576-1585. [PMID: [20972222](#)]

[EC 1.14.11.42 created 2013]

EC 1.14.11.43

Accepted name: (S)-dichlorprop dioxygenase (2-oxoglutarate)

Reaction: (1) (S)-2-(4-chloro-2-methylphenoxy)propanoate + 2-oxoglutarate + O₂ = 4-chloro-2-methylphenol + pyruvate + succinate + CO₂
(2) (S)-(2,4-dichlorophenoxy)propanoate + 2-oxoglutarate + O₂ = 2,4-dichlorophenol + pyruvate + succinate + CO₂

Glossary: (S)-2-(4-chloro-2-methylphenoxy)propanoate = (S)-mecoprop
(S)-(2,4-dichlorophenoxy)propanoate = (S)-dichlorprop

Other name(s): SdpA; α-ketoglutarate-dependent (S)-dichlorprop dioxygenase; (S)-phenoxypropionate/α-ketoglutarate-dioxygenase; 2-oxoglutarate-dependent (S)-dichlorprop dioxygenase; (S)-mecoprop dioxygenase; 2-oxoglutarate-dependent (S)-mecoprop dioxygenase

Systematic name: (S)-2-(4-chloro-2-methylphenoxy)propanoate,2-oxoglutarate:oxygen oxidoreductase (pyruvate-forming)

Comments: Fe²⁺-dependent enzyme. The enzymes from the Gram-negative bacteria *Delftia acidovorans* MC1 and *Sphingomonas herbicidovorans* MH are involved in the degradation of the (S)-enantiomer of the phenoxyalkanoic acid herbicides mecoprop and dichlorprop [1,2].

References:

1. Westendorf, A., Benndorf, D., Muller, R.H. and Babel, W. The two enantiospecific dichlorprop/α-ketoglutarate-dioxygenases from *Delftia acidovorans* MC1 - protein and sequence data of RdpA and SdpA. *Microbiol. Res.* 157 (2002) 317-322. [PMID: [12501996](#)]

2. Muller, T.A., Fleischmann, T., van der Meer, J.R. and Kohler, H.P. Purification and characterization of two enantioselective α -ketoglutarate-dependent dioxygenases, RdpA and SdpA, from *Sphingomonas herbicidovorans* MH. *Appl. Environ. Microbiol.* 72 (2006) 4853-4861. [PMID: [16820480](#)]
3. Muller, T.A., Zavodszky, M.I., Feig, M., Kuhn, L.A. and Hausinger, R.P. Structural basis for the enantiospecificities of *R*- and *S*-specific phenoxypropionate/ α -ketoglutarate dioxygenases. *Protein Sci.* 15 (2006) 1356-1368. [PMID: [16731970](#)]

[EC 1.14.11.43 created 2013]

EC 1.14.11.44**Accepted name:** (*R*)-dichlorprop dioxygenase (2-oxoglutarate)

Reaction: (1) (*R*)-2-(4-chloro-2-methylphenoxy)propanoate + 2-oxoglutarate + O₂ = 4-chloro-2-methylphenol + pyruvate + succinate + CO₂
 (2) (*R*)-(2,4-dichlorophenoxy)propanoate + 2-oxoglutarate + O₂ = 2,4-dichlorophenol + pyruvate + succinate + CO₂

Glossary: (*R*)-2-(4-chloro-2-methylphenoxy)propanoate = (*R*)-mecoprop
 (*R*)-(2,4-dichlorophenoxy)propanoate = (*R*)-dichlorprop

Other name(s): RdpA; α -ketoglutarate-dependent (*R*)-dichlorprop dioxygenase; (*R*)-phenoxypropionate/ α -ketoglutarate-dioxygenase; 2-oxoglutarate-dependent (*R*)-dichlorprop dioxygenase; (*R*)-mecoprop dioxygenase; 2-oxoglutarate-dependent (*R*)-mecoprop dioxygenase

Systematic name: (*R*)-2-(4-chloro-2-methylphenoxy)propanoate,2-oxoglutarate:oxygen oxidoreductase (pyruvate-forming)

Comments: Fe²⁺-dependent enzyme. The enzymes from the Gram-negative bacteria *Delftia acidovorans* MC1 and *Sphingomonas herbicidovorans* MH are involved in the degradation of the (*R*)-enantiomer of the phenoxyalkanoic acid herbicides mecoprop and dichlorprop [1,2].

References:

- Westendorf, A., Benndorf, D., Muller, R.H. and Babel, W. The two enantiospecific dichlorprop/ α -ketoglutarate-dioxygenases from *Delftia acidovorans* MC1 - protein and sequence data of RdpA and SdpA. *Microbiol. Res.* 157 (2002) 317-322. [PMID: [12501996](#)]
- Muller, T.A., Fleischmann, T., van der Meer, J.R. and Kohler, H.P. Purification and characterization of two enantioselective α -ketoglutarate-dependent dioxygenases, RdpA and SdpA, from *Sphingomonas herbicidovorans* MH. *Appl. Environ. Microbiol.* 72 (2006) 4853-4861. [PMID: [16820480](#)]
- Muller, T.A., Zavodszky, M.I., Feig, M., Kuhn, L.A. and Hausinger, R.P. Structural basis for the enantiospecificities of *R*- and *S*-specific phenoxypropionate/ α -ketoglutarate dioxygenases. *Protein Sci.* 15 (2006) 1356-1368. [PMID: [16731970](#)]

[EC 1.14.11.44 created 2013]

EC 1.14.13.180**Accepted name:** aklavinone 12-hydroxylase**Reaction:** aklavinone + NADPH + H⁺ + O₂ = ϵ -rhodomycinone + NADP⁺ + H₂OFor diagram of reaction [click here](#).

Glossary: aklavinone = methyl (1*R*,2*R*,4*S*)-2-ethyl-2,4,5,7-tetrahydroxy-6,11-dioxo-1,2,3,4,6,11-hexahydrotetracene-1-carboxylate
 ϵ -rhodomycinone = methyl (1*R*,2*R*,4*S*)-2-ethyl-2,4,5,7,12-pentahydroxy-6,11-dioxo-1,2,3,4,6,11-hexahydrotetracene-1-carboxylate

Other name(s): DnrF; RdmE; aklavinone 11-hydroxylase (incorrect)**Systematic name:** aklavinone,NADPH:oxygen oxidoreductase (12-hydroxylating)

Comments: The enzymes from the Gram-positive bacteria *Streptomyces peucetius* and *Streptomyces purpurascens* participate in the biosynthesis of daunorubicin, doxorubicin and rhodomycins. The enzyme from *Streptomyces purpurascens* is an FAD monooxygenase.

References:

- Filippini, S., Solinas, M.M., Breme, U., Schluter, M.B., Gabellini, D., Biamonti, G., Colombo, A.L. and Garofano, L. *Streptomyces peucetius* daunorubicin biosynthesis gene, *dnrF*: sequence and heterologous expression. *Microbiology* 141 (1995) 1007-1016. [PMID: [7773378](#)]
- Niemi, J., Wang, Y., Airas, K., Ylihonko, K., Hakala, J. and Mantsala, P. Characterization of aklavinone-11-hydroxylase from *Streptomyces purpurascens*. *Biochim. Biophys. Acta* 1430 (1999) 57-64. [PMID: [10082933](#)]

[EC 1.14.13.180 created 2013]

EC 1.14.13.181**Accepted name:** 13-deoxydaunorubicin hydroxylase

Reaction: (1) 13-deoxydaunorubicin + NADPH + H⁺ + O₂ = 13-dihydrodaunorubicin + NADP⁺ + H₂O
 (2) 13-dihydrodaunorubicin + NADPH + H⁺ + O₂ = daunorubicin + NADP⁺ + 2 H₂O

For diagram of reaction [click here](#).

Glossary: 13-dihydrodaunorubicin = daunorubicinol = (1*S*,3*S*)-3,5,12-trihydroxy-3-(1-hydroxyethyl)-10-methoxy-6,11-dioxo-1,2,3,4,6,11-hexahydrotetracene-1-yl 3-amino-2,3,6-trideoxy- α -L-lyxo-hexopyranoside
 13-deoxydaunorubicin = (1*S*,3*S*)-3-ethyl-3,5,12-trihydroxy-10-methoxy-6,11-dioxo-1,2,3,4,6,11-hexahydrotetracene-1-yl 3-amino-2,3,6-trideoxy- α -L-lyxo-hexopyranoside
 daunorubicin = (1*S*,3*S*)-3-acetyl-3,5,12-trihydroxy-10-methoxy-6,11-dioxo-1,2,3,4,6,11-hexahydrotetracene-1-yl 3-amino-2,3,6-trideoxy- α -L-lyxo-hexopyranoside

Other name(s): DoxA**Systematic name:** 13-deoxydaunorubicin,NADPH:oxygen oxidoreductase (13-hydroxylating)

Comments: The enzymes from the Gram-positive bacteria *Streptomyces* sp. C5 and *Streptomyces peucetius* show broad substrate specificity for structures based on an anthracycline aglycone, but have a strong preference for 4-methoxy anthracycline intermediates (13-deoxydaunorubicin and 13-dihydrodaunorubicin) over their 4-hydroxy analogues (13-deoxycarminomycin and 13-dihydrocarminomycin), as well as a preference for substrates hydroxylated at the C-13 rather than the C-14 position.

References:

1. Walczak, R.J., Dickens, M.L., Priestley, N.D. and Strohl, W.R. Purification, properties, and characterization of recombinant *Streptomyces* sp. strain C5 DoxA, a cytochrome *P*-450 catalyzing multiple steps in doxorubicin biosynthesis. *J. Bacteriol.* 181 (1999) 298-304. [PMID: [9864343](#)]
2. Dickens, M.L., Priestley, N.D. and Strohl, W.R. *In vivo* and *in vitro* bioconversion of ϵ -rhodomycinone glycoside to doxorubicin: functions of DauP, DauK, and DoxA. *J. Bacteriol.* 179 (1997) 2641-2650. [PMID: [9098063](#)]

[EC 1.14.13.181 created 2013]

EC 1.14.13.182

Accepted name: 2-heptyl-3-hydroxy-4(1*H*)-quinolone synthase**Reaction:** 2-heptyl-4(1*H*)-quinolone + NADH + H⁺ + O₂ = 2-heptyl-3-hydroxy-4(1*H*)-quinolone + NAD⁺ + H₂O

Glossary: 2-heptyl-4(1*H*)-quinolone = 2-heptyl-4-hydroxyquinoline
 2-heptyl-3-hydroxy-4(1*H*)-quinolone = 2-heptyl-3,4-dihydroxyquinoline

Other name(s): PqsH; 2-heptyl-3,4-dihydroxyquinoline synthase**Systematic name:** 2-heptyl-4(1*H*)-quinolone:NADH:oxygen oxidoreductase (3-hydroxylating)**Comments:** The enzyme from the bacterium *Pseudomonas aeruginosa* catalyses the terminal step in biosynthesis of the signal molecule 2-heptyl-3,4-dihydroxyquinoline that plays a role in regulation of virulence genes.**References:**

1. Schertzer, J.W., Brown, S.A. and Whiteley, M. Oxygen levels rapidly modulate *Pseudomonas aeruginosa* social behaviours via substrate limitation of PqsH. *Mol. Microbiol.* 77 (2010) 1527-1538. [PMID: [20662781](#)]

[EC 1.14.13.182 created 2013]

EC 1.14.14.14

Accepted name: aromatase**Reaction:** (1) testosterone + 3 O₂ + 3 reduced flavoproteins = 17 β -estradiol + formate + 4 H₂O + 3 oxidized flavoproteins (overall reaction)(1a) testosterone + O₂ + a reduced flavoprotein = 19-hydroxytestosterone + H₂O + an oxidized flavoprotein(1b) 19-hydroxytestosterone + O₂ + a reduced flavoprotein = 19-oxotestosterone + 2 H₂O + an oxidized flavoprotein(1c) 19-oxotestosterone + O₂ + a reduced flavoprotein = 17 β -estradiol + formate + H₂O + an oxidized flavoprotein(2) androst-4-ene-3,17-dione + 3 O₂ + 3 reduced flavoproteins = estrone + formate + 4 H₂O + 3 oxidized flavoproteins (overall reaction)(2a) androst-4-ene-3,17-dione + O₂ + a reduced flavoprotein = 19-hydroxyandrost-4-ene-3,17-dione + H₂O + an oxidized flavoprotein(2b) 19-hydroxyandrost-4-ene-3,17-dione + O₂ + a reduced flavoprotein = 19-oxo-androst-4-ene-3,17-dione + 2 H₂O + an oxidized flavoprotein(2c) 19-oxoandrost-4-ene-3,17-dione + O₂ + a reduced flavoprotein = estrone + formate + H₂O + an oxidized flavoprotein**Other name(s):** CYP19A1 (gene name); estrogen synthetase (incorrect)**Systematic name:** testosterone monooxygenase (17 β -estradiol-forming)**Comments:** A cytochrome P450. The enzyme catalyses three sequential hydroxylations of the androgens androst-4-ene-3,17-dione and testosterone, resulting in their aromatization and forming the estrogens estrone and 17 β -estradiol, respectively.**References:**

1. Thompson, E.A., Jr. and Siiteri, P.K. The involvement of human placental microsomal cytochrome *P*-450 in aromatization. *J. Biol. Chem.* 249 (1974) 5373-5378. [PMID: [4370479](#)]
2. Fishman, J. and Goto, J. Mechanism of estrogen biosynthesis. Participation of multiple enzyme sites in placental aromatase hydroxylations. *J. Biol. Chem.* 256 (1981) 4466-4471. [PMID: [7217091](#)]
3. Kellis, J.T., Jr. and Vickery, L.E. Purification and characterization of human placental aromatase cytochrome *P*-450. *J. Biol. Chem.* 262 (1987) 4413-4420. [PMID: [3104339](#)]
4. Ghosh, D., Griswold, J., Erman, M. and Pangborn, W. Structural basis for androgen specificity and oestrogen synthesis in human aromatase. *Nature* 457 (2009) 219-223. [PMID: [19129847](#)]

[EC 1.14.14.14 created 2013]

EC 1.14.99.48

Accepted name: heme oxygenase (staphylobilin-producing)**Reaction:** (1) protoheme + 4 AH₂ + 4 O₂ = 5-oxo- δ -bilirubin + Fe²⁺ + CO + 4 A + 4 H₂O(2) protoheme + 4 AH₂ + 4 O₂ = 15-oxo- β -bilirubin + Fe²⁺ + CO + 4 A + 4 H₂O**Glossary:** staphylobilins = 5-oxo- δ -bilirubin and 15-oxo- β -bilirubin**Other name(s):** haem oxygenase (ambiguous); heme oxygenase (decyclizing) (ambiguous); heme oxidase (ambiguous); haem oxidase (ambiguous); heme oxygenase (ambiguous); *isdG* (gene name); *isdI* (gene name)**Systematic name:** protoheme:hydrogen-donor:oxygen oxidoreductase (δ/β -methene-oxidizing, hydroxylating)**Comments:** This enzyme, which is found in pathogenic bacteria, is involved in an iron acquisition system that catabolizes the host's hemoglobin. The two enzymes from the bacterium *Staphylococcus aureus*, encoded by the *isdG* and *isdI* genes, produce 67.5 % and 56.2 % 5-oxo- δ -bilirubin, respectively.**References:**

1. Reniere, M.L., Ukpabi, G.N., Harry, S.R., Stec, D.F., Krull, R., Wright, D.W., Bachmann, B.O., Murphy, M.E. and Skaar, E.P. The IsdG-family of haem oxygenases degrades haem to a novel chromophore. *Mol. Microbiol.* 75 (2010) 1529-1538. [PMID: [20180905](#)]

[EC 1.14.99.48 created 2013]

*EC 2.1.1.44

Accepted name: L-histidine *N*^α-methyltransferase

Reaction: 3 *S*-adenosyl-L-methionine + L-histidine = 3 *S*-adenosyl-L-homocysteine + hercynine (overall reaction)

(1a) *S*-adenosyl-L-methionine + L-histidine = *S*-adenosyl-L-homocysteine + *N*^α-methyl-L-histidine

(1b) *S*-adenosyl-L-methionine + *N*^α-methyl-L-histidine = *S*-adenosyl-L-homocysteine + *N*^α,*N*^α-dimethyl-L-histidine

(1c) *S*-adenosyl-L-methionine + *N*^α,*N*^α-dimethyl-L-histidine = *S*-adenosyl-L-homocysteine + hercynine

Glossary: hercynine = *N*^α,*N*^α,*N*^α-trimethyl-L-histidine

Other name(s): dimethylhistidine *N*-methyltransferase; dimethylhistidine methyltransferase; histidine- α -*N*-methyltransferase; *S*-adenosyl-L-methionine: α -*N*, α -*N*-dimethyl-L-histidine α -*N*-methyltransferase; *S*-adenosyl-L-methionine:*N*^α,*N*^α-dimethyl-L-histidine *N*^α-methyltransferase

Systematic name: *S*-adenosyl-L-methionine:L-histidine *N*^α-methyltransferase (hercynine-forming)

Comments: Part of the biosynthetic pathway of ergothioneine.

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 62213-53-0

References:

1. Ishikawa, Y. and Melville, D.B. The enzymatic α -*N*-methylation of histidine. *J. Biol. Chem.* 245 (1970) 5967-5973. [PMID: [5484456](#)]

2. Seebeck, F.P. *In vitro* reconstitution of mycobacterial ergothioneine biosynthesis. *J. Am. Chem. Soc.* 132 (2010) 6632-6633. [PMID: [20420449](#)]

[EC 2.1.1.44 created 1976, modified 2013]

[EC 2.1.1.66 Deleted entry: rRNA (adenosine-2'-*O*)-methyltransferase. Now covered by [EC 2.1.1.230](#), 23S rRNA (adenosine¹⁰⁶⁷-2'-*O*)-methyltransferase. (EC 2.1.1.66 created 1984, deleted 2013)]

EC 2.1.1.288

Accepted name: aklanonic acid methyltransferase

Reaction: *S*-adenosyl-L-methionine + aklanonate = *S*-adenosyl-L-homocysteine + methyl aklanonate

For diagram of reaction [click here](#).

Glossary: methyl aklanonate = methyl [1,4,5-trihydroxy-9,10-dioxo-3-(3-oxopentanoyl)-9,10-dihydroanthracen-2-yl]acetate
aklanonate = [4,5-dihydroxy-9,10-dioxo-3-(3-oxopentanoyl)-9,10-dihydroanthracen-2-yl]acetic acid

Other name(s): DauC; AAMT

Systematic name: *S*-adenosyl-L-methionine:aklanonate *O*-methyltransferase

Comments: The enzyme from the Gram-positive bacterium *Streptomyces* sp. C5 is involved in the biosynthesis of the anthracycline daunorubicin.

References:

1. Dickens, M.L., Ye, J. and Strohl, W.R. Analysis of clustered genes encoding both early and late steps in daunomycin biosynthesis by *Streptomyces* sp. strain C5. *J. Bacteriol.* 177 (1995) 536-543. [PMID: [7836284](#)]

[EC 2.1.1.288 created 2013]

EC 2.1.3.13

Accepted name: ATP carbamoyltransferase

Reaction: carbamoyl phosphate + ATP + H₂O = diphosphate + *O*-carbamoyladenylate + phosphate

For diagram of reaction [click here](#).

Other name(s): TobZ (ambiguous)

Systematic name: carbamoyl phosphate:ATP carbamoyl-transferase

Comments: The enzyme from the bacterium *Streptoalloteichus tenebrarius* catalyses the activation of carbamoyl phosphate to *O*-carbamoyladenylate, and the subsequent carbamoylation of kanamycin and tobramycin. cf. [EC 2.1.3.14](#), tobramycin carbamoyltransferase.

References:

1. Parthier, C., Gorlich, S., Jaenecke, F., Breithaupt, C., Brauer, U., Fandrich, U., Clausnitzer, D., Wehmeier, U.F., Botcher, C., Scheel, D. and Stubbs, M.T. The *O*-carbamoyltransferase TobZ catalyzes an ancient enzymatic reaction. *Angew. Chem. Int. Ed. Engl.* 51 (2012) 4046-4052. [PMID: [22383337](#)]

[EC 2.1.3.13 created 2013]

EC 2.1.3.14

Accepted name: tobramycin carbamoyltransferase

Reaction: (1) *O*-carbamoyladenylate + tobramycin = AMP + nebramycin 5'

(2) *O*-carbamoyladenylate + kanamycin A = AMP + 6"-*O*-carbamoylkanamycin A

Glossary: tobramycin = (1*S*,2*S*,3*R*,4*S*,6*R*)-4,6-diamino-3-(2,6-diamino-2,3,6-trideoxy- α -D-ribo-hexopyranosyloxy)-2-hydroxycyclohexyl 3-amino-3-deoxy- α -D-glucopyranoside
 nebramycin 5' = (1*S*,2*S*,3*R*,4*S*,6*R*)-4,6-diamino-3-[(2,6-diamino-2,3,6-trideoxy- α -D-ribo-hexopyranosyl)oxy]-2-hydroxycyclohexyl 3-amino-6-*O*-carbamoyl-3-deoxy- α -D-glucopyranoside
 kanamycin A = (1*S*,2*R*,3*R*,4*S*,6*R*)-4,6-diamino-3-(6-amino-6-deoxy-D-glucopyranosyloxy)-2-hydroxycyclohexyl 3-amino-3-deoxy-D-glucopyranoside
 6'-*O*-carbamoylkanamycin A = (1*S*,2*R*,3*R*,4*S*,6*R*)-4,6-diamino-3-[(6-amino-6-deoxy- α -D-glucopyranosyl)oxy]-2-hydroxycyclohexyl 3-amino-6-*O*-carbamoyl-3-deoxy- α -D-glucopyranoside

For diagram of reaction [click here](#).

Other name(s): TobZ (ambiguous)

Systematic name: carbamoyl phosphate:tobramycin 6'-*O*-carbamoyl-transferase

Comments: Binds iron. The enzyme from the bacterium *Streptoalloteichus tenebrarius* catalyses the activation of carbamoyl phosphate to *O*-carbamoyladenylate (see [EC 2.1.3.13](#), ATP carbamoyltransferase), and the subsequent carbamoylation of kanamycin and tobramycin.

References:

1. Parthier, C., Gorlich, S., Jaenecke, F., Breithaupt, C., Brauer, U., Fandrich, U., Clausnitzer, D., Wehmeier, U.F., Bottcher, C., Scheel, D. and Stubbs, M.T. The *O*-carbamoyltransferase TobZ catalyzes an ancient enzymatic reaction. *Angew. Chem. Int. Ed. Engl.* 51 (2012) 4046-4052. [PMID: [22383337](#)]

[EC 2.1.3.14 created 2013]

EC 2.3.1.227

Accepted name: GDP-perosamine *N*-acetyltransferase

Reaction: acetyl-CoA + GDP-4-amino-4,6-dideoxy- α -D-mannose = CoA + GDP-4-acetamido-4,6-dideoxy- α -D-mannose

Glossary: GDP-4-amino-4,6-dideoxy- α -D-mannose = GDP- α -D-perosamine
 GDP-4-acetamido-4,6-dideoxy- α -D-mannose = GDP-*N*-acetyl- α -D-perosamine

Other name(s): *perB* (gene name); GDP- α -D-perosamine *N*-acetyltransferase

Systematic name: acetyl-CoA:GDP-4-amino-4,6-dideoxy- α -D-mannose *N*-acetyltransferase

Comments: D-Perosamine is one of several dideoxy sugars found in the O-antigen component of the outer membrane lipopolysaccharides of Gram-negative bacteria.

References:

1. Albermann, C. and Beuttler, H. Identification of the GDP-*N*-acetyl-D-perosamine producing enzymes from *Escherichia coli* O157:H7. *FEBS Lett* 582 (2008) 479-484. [PMID: [18201574](#)]

[EC 2.3.1.227 created 2013]

EC 2.3.1.228

Accepted name: isovaleryl-homoserine lactone synthase

Reaction: isovaleryl-CoA + *S*-adenosyl-L-methionine = CoA + *S*-methyl-5'-thioadenosine + *N*-isovaleryl-L-homoserine lactone

Other name(s): IV-HSL synthase; BjaI

Systematic name: isovaleryl-CoA:*S*-adenosyl-L-methionine isovaleryltransferase (lactone-forming, methylthioadenosine-releasing)

Comments: The enzyme, found in the bacterium *Bradyrhizobium japonicum*, does not accept isovaleryl-[acyl-carrier protein] as acyl donor (*cf.* [EC 2.3.1.184](#), acyl-homoserine-lactone synthase).

References:

1. Lindemann, A., Pessi, G., Schaefer, A.L., Mattmann, M.E., Christensen, Q.H., Kessler, A., Hennecke, H., Blackwell, H.E., Greenberg, E.P. and Harwood, C.S. Isovaleryl-homoserine lactone, an unusual branched-chain quorum-sensing signal from the soybean symbiont *Bradyrhizobium japonicum*. *Proc. Natl. Acad. Sci. USA* 108 (2011) 16765-16770. [PMID: [21949379](#)]

[EC 2.3.1.228 created 2013]

EC 2.3.1.229

Accepted name: 4-coumaroyl-homoserine lactone synthase

Reaction: 4-coumaroyl-CoA + *S*-adenosyl-L-methionine = CoA + *S*-methyl-5'-thioadenosine + *N*-(4-coumaroyl)-L-homoserine lactone

Other name(s): *p*-coumaryl-homoserine lactone synthase; RpaI

Systematic name: 4-coumaroyl-CoA:*S*-adenosyl-L-methionine *trans*-4-coumaroyltransferase (lactone-forming, methylthioadenosine-releasing)

Comments: The enzyme is found in the bacterium *Rhodopseudomonas palustris*, which produces *N*-(4-coumaroyl)-L-homoserine lactone as a quorum-sensing signal.

References:

1. Schaefer, A.L., Greenberg, E.P., Oliver, C.M., Oda, Y., Huang, J.J., Bittan-Banin, G., Peres, C.M., Schmidt, S., Juhaszova, K., Sufrin, J.R. and Harwood, C.S. A new class of homoserine lactone quorum-sensing signals. *Nature* 454 (2008) 595-599. [PMID: [18563084](#)]

[EC 2.3.1.229 created 2013]

*EC 2.3.2.3

Accepted name: lysyltransferase

Reaction: L-lysyl-tRNA^{Lys} + phosphatidylglycerol = tRNA^{Lys} + 3-O-L-lysyl-1-O-phosphatidylglycerol

Other name(s): L-lysyl-tRNA:phosphatidylglycerol 3-O-lysyltransferase

Systematic name: L-lysyl-tRNA^{Lys}:phosphatidylglycerol 3-O-lysyltransferase

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 37257-20-8

References:

1. Lennarz, W.J., Bensen, P.P.M. and van Deenan, L.L.M. Substrate specificity of O-L-lysylphosphatidylglycerol synthetase. Enzymatic studies on the structure of O-L-lysylphosphatidylglycerol. *Biochemistry* 6 (1967) 2307-2312. [PMID: [6049461](#)]

[EC 2.3.2.3 created 1972, modified 2013]

***EC 2.3.2.6**

Accepted name: leucyltransferase

Reaction: L-leucyl-tRNA^{Leu} + protein = tRNA^{Leu} + L-leucyl-[protein]

Other name(s): leucyl, phenylalanine-tRNA-protein transferase; leucyl-phenylalanine-transfer ribonucleate-protein aminoacyltransferase; leucyl-phenylalanine-transfer ribonucleate-protein transferase; L-leucyl-tRNA:protein leucyltransferase

Systematic name: L-leucyl-tRNA^{Leu}:protein leucyltransferase

Comments: Also transfers phenylalanyl groups. Requires a univalent cation. Peptides and proteins containing an N-terminal arginine, lysine or histidine residue can act as acceptors.

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), [PDB](#), CAS registry number: 37257-22-0

References:

1. Leibowitz, M.J. and Soffer, R.L. A soluble enzyme from *Escherichia coli* which catalyzes the transfer of leucine and phenylalanine from tRNA to acceptor proteins. *Biochem. Biophys. Res. Commun.* 36 (1969) 47-53. [PMID: [4894363](#)]

2. Leibowitz, M.J. and Soffer, R.L. Enzymatic modification of proteins. 3. Purification and properties of a leucyl, phenylalanyl transfer ribonucleic acid protein transferase from *Escherichia coli*. *J. Biol. Chem.* 245 (1970) 2066-2073. [PMID: [4909560](#)]

3. Soffer, R.L. Peptide acceptors in the leucine, phenylalanine transfer reaction. *J. Biol. Chem.* 248 (1973) 8424-8428. [PMID: [4587124](#)]

[EC 2.3.2.6 created 1972, modified 1976, modified 2013]

***EC 2.3.2.8**

Accepted name: arginyltransferase

Reaction: L-arginyl-tRNA^{Arg} + protein = tRNA^{Arg} + L-arginyl-[protein]

Other name(s): arginine transferase; arginyl-transfer ribonucleate-protein aminoacyltransferase; arginyl-transfer ribonucleate-protein transferase; arginyl-tRNA protein transferase; L-arginyl-tRNA:protein arginyltransferase

Systematic name: L-arginyl-tRNA^{Arg}:protein arginyltransferase

Comments: Requires mercaptoethanol and a univalent cation. Peptides and proteins containing an N-terminal glutamate, aspartate or cystine residue can act as acceptors.

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 37257-24-2

References:

1. Soffer, R.L. Enzymatic modification of proteins. II. Purification and properties of the arginyl transfer ribonucleic acid-protein transferase from rabbit liver cytoplasm. *J. Biol. Chem.* 245 (1970) 731-737. [PMID: [5416661](#)]

2. Soffer, R.L. Peptide acceptors in the arginine transfer reaction. *J. Biol. Chem.* 248 (1973) 2918-2921. [PMID: [4572514](#)]

3. Soffer, R.L. and Horinishi, H. Enzymic modification of proteins. I. General characteristics of the arginine-transfer reaction in rabbit liver cytoplasm. *J. Mol. Biol.* 43 (1969) 163-175. [PMID: [5811819](#)]

[EC 2.3.2.8 created 1972, modified 1976, modified 2013]

***EC 2.3.2.10**

Accepted name: UDP-N-acetylmuramoylpentapeptide-lysine N⁶-alanyltransferase

Reaction: L-alanyl-tRNA^{Ala} + UDP-N-acetyl-α-D-muramoyl-L-alanyl-D-glutamyl-L-lysyl-D-alanyl-D-alanine = tRNA^{Ala} + UDP-N-acetyl-α-D-muramoyl-L-alanyl-D-glutamyl-L-lysyl-D-alanyl-D-alanine N⁶-(L-alanyl)-L-lysyl-D-alanyl-D-alanine

Other name(s): alanyl-transfer ribonucleate-uridine diphosphoacetylmuramoylpentapeptide transferase; UDP-N-acetylmuramoylpentapeptide lysine N⁶-alanyltransferase; uridine diphosphoacetylmuramoylpentapeptide lysine N⁶-alanyltransferase; L-alanyl-tRNA:UDP-N-acetylmuramoyl-L-alanyl-D-glutamyl-L-lysyl-D-alanyl-D-alanine 6-N-alanyltransferase; L-alanyl-tRNA:UDP-N-acetylmuramoyl-L-alanyl-D-glutamyl-L-lysyl-D-alanyl-D-alanine N⁶-alanyltransferase

Systematic name: L-alanyl-tRNA^{Ala}:UDP-N-acetyl-α-D-muramoyl-L-alanyl-D-glutamyl-L-lysyl-D-alanyl-D-alanine N⁶-alanyltransferase

Comments: Also acts on L-seryl-tRNA^{Ser}.

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 37257-26-4

References:

1. Plapp, R. and Strominger, J.L. Biosynthesis of the peptidoglycan of bacterial cell walls. 18. Purification and properties of L-alanyl transfer ribonucleic acid-uridine diphosphate-*N*-acetylmuramyl-pentapeptide transferase from *Lactobacillus viridescens*. *J. Biol. Chem.* 245 (1970) 3675-3682. [PMID: [4248527](#)]

[EC 2.3.2.10 created 1972, modified 2013]

***EC 2.3.2.11**

Accepted name: alanylphosphatidylglycerol synthase

Reaction: L-alanyl-tRNA^{Ala} + phosphatidylglycerol = tRNA^{Ala} + 3-*O*-L-alanyl-1-*O*-phosphatidylglycerol

Other name(s): *O*-alanylphosphatidylglycerol synthase; alanyl phosphatidylglycerol synthetase

Systematic name: L-alanyl-tRNA^{Ala}:phosphatidylglycerol alanyltransferase

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 37257-27-5

References:

1. Gould, R.M., Thornton, M.P., Liepkalns, V. and Lennarz, W.J. Participation of aminoacyl transfer ribonucleic acid in aminoacyl phosphatidylglycerol synthesis. II. Specificity of alanyl phosphatidylglycerol synthetase. *J. Biol. Chem.* 243 (1968) 3096-3104. [PMID: [4297471](#)]

[EC 2.3.2.11 created 1972, modified 2013]

***EC 2.4.1.229**

Accepted name: [Skp1-protein]-hydroxyproline *N*-acetylglucosaminyltransferase

Reaction: UDP-*N*-acetylglucosamine + [Skp1-protein]-*trans*-4-hydroxy-L-proline = UDP + [Skp1-protein]-*O*-(*N*-acetyl-D-glucosaminyl)-*trans*-4-hydroxy-L-proline

Other name(s): Skp1-HyPro GlcNAc-transferase; UDP-*N*-acetylglucosamine (GlcNAc):hydroxyproline polypeptide GlcNAc-transferase; UDP-GlcNAc:Skp1-hydroxyproline GlcNAc-transferase; UDP-GlcNAc:hydroxyproline polypeptide GlcNAc-transferase; UDP-*N*-acetyl-D-glucosamine:[Skp1-protein]-hydroxyproline *N*-acetyl-D-glucosaminyl-transferase

Systematic name: UDP-*N*-acetyl-D-glucosamine:[Skp1-protein]-*trans*-4-hydroxy-L-proline *N*-acetyl-D-glucosaminyl-transferase

Comments: Skp1 is a cytoplasmic and nuclear protein required for the ubiquitination of cell cycle regulatory proteins and transcriptional factors. In *Dictyostelium* Skp1 is modified by the linear pentasaccharide Galα1-6Galα1-L-Fuca1-2Galβ1-3GlcNAc, which is attached to a hydroxyproline residue at position 143. This enzyme catalyses the first step in the building up of the pentasaccharide by attaching an *N*-acetylglucosaminyl group to the hydroxyproline residue. It requires dithiothreitol and a divalent cation for activity.

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 256531-81-4

References:

1. van der Wel, H., Morris, H.R., Panico, M., Paxton, T., Dell, A., Kaplan, L. and West, C.M. Molecular cloning and expression of a UDP-*N*-acetylglucosamine (GlcNAc):hydroxyproline polypeptide GlcNAc-transferase that modifies Skp1 in the cytoplasm of *Dictyostelium*. *J. Biol. Chem.* 277 (2002) 46328-46337. [PMID: [12244115](#)]
2. Teng-umnuay, P., van der Wel, H. and West, C.M. Identification of a UDP-GlcNAc:Skp1-hydroxyproline GlcNAc-transferase in the cytoplasm of *Dictyostelium*. *J. Biol. Chem.* 274 (1999) 36392-36402. [PMID: [10593934](#)]
3. West, C.M., van der Wel, H. and Gaucher, E.A. Complex glycosylation of Skp1 in *Dictyostelium*: implications for the modification of other eukaryotic cytoplasmic and nuclear proteins. *Glycobiology* 12 (2002) 17. [PMID: [11886837](#)]

[EC 2.4.1.229 created 2003, modified 2013]

***EC 2.4.1.245**

Accepted name: α,α-trehalose synthase

Reaction: NDP-α-D-glucose + D-glucose = α,α-trehalose + NDP

Glossary: NDP = a nucleoside diphosphate

Other name(s): trehalose synthase; trehalose synthetase; UDP-glucose:glucose 1-glucosyltransferase; TreT; PhGT; ADP-glucose:D-glucose 1-α-D-glucosyltransferase

Systematic name: NDP-α-D-glucose:D-glucose 1-α-D-glucosyltransferase

Comments: Requires Mg²⁺ for maximal activity [1]. The enzyme-catalysed reaction is reversible [1]. In the reverse direction to that shown above, the enzyme is specific for α,α-trehalose as substrate, as it cannot use α- or β-paranitrophenyl glucosides, maltose, sucrose, lactose or cellobiose [1]. While the enzymes from the thermophilic bacterium *Rubrobacter xylanophilus* and the hyperthermophilic archaeon *Pyrococcus horikoshii* can use ADP-, UDP- and GDP-α-D-glucose to the same extent [2,3], that from the hyperthermophilic archaeon *Thermococcus litoralis* has a marked preference for ADP-α-D-glucose [1] and that from the hyperthermophilic archaeon *Thermoproteus tenax* has a marked preference for UDP-α-D-glucose [4].

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number:

References:

1. Qu, Q., Lee, S.J. and Boos, W. TreT, a novel trehalose glycosyltransferring synthase of the hyperthermophilic archaeon *Thermococcus litoralis*. *J. Biol. Chem.* 279 (2004) 47890-47897. [PMID: [15364950](#)]
2. Ryu, S.I., Park, C.S., Cha, J., Woo, E.J. and Lee, S.B. A novel trehalose-synthesizing glycosyltransferase from *Pyrococcus horikoshii*: molecular cloning and characterization. *Biochem. Biophys. Res. Commun.* 329 (2005) 429-436. [PMID: [15737605](#)]
3. Nobre, A., Alarico, S., Fernandes, C., Empadinhas, N. and da Costa, M.S. A unique combination of genetic systems for the synthesis of trehalose in *Rubrobacter xylanophilus*: properties of a rare actinobacterial TreT. *J. Bacteriol.* 190 (2008) 7939-7946. [PMID: [18835983](#)]
4. Kouril, T., Zaparty, M., Marrero, J., Brinkmann, H. and Siebers, B. A novel trehalose synthesizing pathway in the hyperthermophilic Crenarchaeon *Thermoproteus tenax*: the unidirectional TreT pathway. *Arch. Microbiol.* 190 (2008) 355-369. [PMID: [18483808](#)]

[EC 2.4.1.245 created 2008, modified 2013]

EC 2.5.1.16*Accepted name:** spermidine synthase**Reaction:** *S*-adenosyl 3-(methylthio)propylamine + putrescine = *S*-methyl-5'-thioadenosine + spermidineFor diagram of reaction [click here](#).**Glossary:** spermidine = *N*-(3-aminopropyl)butane-1,4-diaminespermine = *N,N'*-bis(3-aminopropyl)butane-1,4-diamine

putrescine = butane-1,4-diamine

S-adenosyl 3-(methylthio)propylamine = (3-aminopropyl){[(2*S*,3*S*,4*R*,5*R*)-5-(6-amino-9*H*-purin-9-yl)-3,4-dihydroxytetrahydrofuran-2-yl]methyl}methylsulfonium**Other name(s):** aminopropyltransferase; putrescine aminopropyltransferase; spermidine synthetase; SpeE; *S*-adenosylmethioninamine:putrescine 3-aminopropyltransferase**Systematic name:** *S*-adenosyl 3-(methylthio)propylamine:putrescine 3-aminopropyltransferase**Comments:** The enzymes from the plant *Glycine max* and from mammalia are highly specific for putrescine as the amine acceptor [2,7]. The enzymes from the bacteria *Escherichia coli* and *Thermotoga maritima* prefer putrescine but are more tolerant towards other amine acceptors, such as spermidine and cadaverine [5,6]. *cf.* [EC 2.5.1.22](#) (spermine synthase) and [EC 2.5.1.23](#) (*sym*-norspermidine synthase).**Links to other databases:** [BRENDA](#), [EXPASY](#), [KEGG](#), [MetaCyc](#), [PDB](#), CAS registry number: 37277-82-0**References:**

1. Hannonen, P., Janne, J. and Raina, A. Partial purification and characterization of spermine synthase from rat brain. *Biochim. Biophys. Acta* 289 (1972) 225-231. [PMID: [4564056](#)]
2. Pegg, A.E., Shuttleworth, K. and Hibasami, H. Specificity of mammalian spermidine synthase and spermine synthase. *Biochem. J.* 197 (1981) 315-320. [PMID: [6798961](#)]
3. Tabor, C.W. Propylamine transferase (spermidine synthesis). *Methods Enzymol.* 5 (1962) 761-765.
4. Tabor, H. and Tabor, C.W. Biosynthesis and metabolism of 1,4-diaminobutane, spermidine, spermine, and related amines. *Adv. Enzymol. Relat. Areas Mol. Biol.* 36 (1972) 203-268. [PMID: [4628436](#)]
5. Bowman, W.H., Tabor, C.W. and Tabor, H. Spermidine biosynthesis. Purification and properties of propylamine transferase from *Escherichia coli*. *J. Biol. Chem.* 248 (1973) 2480-2486. [PMID: [4572733](#)]
6. Korolev, S., Ikeguchi, Y., Skarina, T., Beasley, S., Arrowsmith, C., Edwards, A., Joachimiak, A., Pegg, A.E. and Savchenko, A. The crystal structure of spermidine synthase with a multisubstrate adduct inhibitor. *Nat. Struct. Biol.* 9 (2002) 27-31. [PMID: [11731804](#)]
7. Yoon, S.O., Lee, Y.S., Lee, S.H. and Cho, Y.D. Polyamine synthesis in plants: isolation and characterization of spermidine synthase from soybean (*Glycine max*) axes. *Biochim. Biophys. Acta* 1475 (2000) 17-26. [PMID: [10806333](#)]

[EC 2.5.1.16 created 1972, modified 1982, modified 2013]

EC 2.5.1.22*Accepted name:** spermine synthase**Reaction:** *S*-adenosyl 3-(methylthio)propylamine + spermidine = *S*-methyl-5'-thioadenosine + spermineFor diagram of reaction [click here](#).**Glossary:** spermidine = *N*-(3-aminopropyl)butane-1,4-diaminespermine = *N,N'*-bis(3-aminopropyl)butane-1,4-diamine*S*-adenosyl 3-(methylthio)propylamine = (3-aminopropyl){[(2*S*,3*S*,4*R*,5*R*)-5-(6-amino-9*H*-purin-9-yl)-3,4-dihydroxytetrahydrofuran-2-yl]methyl}methylsulfonium**Other name(s):** spermidine aminopropyltransferase; spermine synthetase; *S*-adenosylmethioninamine:spermidine 3-aminopropyltransferase**Systematic name:** *S*-adenosyl 3-(methylthio)propylamine:spermidine 3-aminopropyltransferase**Comments:** The enzyme from mammalia is highly specific for spermidine [2,3]. *cf.* [EC 2.5.1.16](#) (spermidine synthase) and [EC 2.5.1.23](#) (*sym*-norspermidine synthase).**Links to other databases:** [BRENDA](#), [EXPASY](#), [KEGG](#), [MetaCyc](#), [PDB](#), CAS registry number: 74812-43-4**References:**

1. Hibasami, H., Borchardt, R.T., Chen, S.-Y., Coward, J.K. and Pegg, A.E. Studies of inhibition of rat spermidine synthase and spermine synthase. *Biochem. J.* 187 (1980) 419-428. [PMID: [7396856](#)]
2. Pajula, R.-L., Raina, A. and Eloranta, T. Polyamine synthesis in mammalian tissues. Isolation and characterization of spermine synthase from bovine brain. *Eur. J. Biochem.* 101 (1979) 619-626. [PMID: [520313](#)]
3. Pegg, A.E., Shuttleworth, K. and Hibasami, H. Specificity of mammalian spermidine synthase and spermine synthase. *Biochem. J.* 197 (1981) 315-320. [PMID: [6798961](#)]

[EC 2.5.1.22 created 1982, modified 2013]

EC 2.5.1.23*Accepted name:** *sym*-norspermidine synthase**Reaction:** *S*-adenosyl 3-(methylthio)propylamine + propane-1,3-diamine = *S*-methyl-thioadenosine + bis(3-aminopropyl)amine**Glossary:** *S*-adenosyl 3-(methylthio)propylamine = (3-aminopropyl){[(2*S*,3*S*,4*R*,5*R*)-5-(6-amino-9*H*-purin-9-yl)-3,4-dihydroxytetrahydrofuran-2-yl]methyl}methylsulfonium**Other name(s):** *S*-adenosylmethioninamine:propane-1,3-diamine 3-aminopropyltransferase

Systematic name: S-adenosyl 3-(methylthio)propylamine:propane-1,3-diamine 3-aminopropyltransferase

Comments: The enzyme has been originally characterized from the protist *Euglena gracilis* [1,2]. The enzyme from the archaeon *Sulfolobus solfataricus* can transfer the propylamine moiety from S-adenosyl 3-(methylthio)propylamine to putrescine, sym-norspermidine and spermidine with lower efficiency [3]. cf. [EC 2.5.1.16](#) (spermidine synthase) and [EC 2.5.1.22](#) (spermine synthase).

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number:

References:

1. Aleksijevic, A., Grove, J. and Schuber, F. Studies on polyamine biosynthesis in *Euglena gracilis*. *Biochim. Biophys. Acta* 565 (1979) 199-207. [PMID: [116684](#)]
2. Villanueva, V.R., Adlakha, R.C. and Calbayrac, R. Biosynthesis of polyamines in *Euglena gracilis*. *Phytochemistry* 19 (1980) 787-790.
3. Cacciapuoti, G., Porcelli, M., Carteni-Farina, M., Gambacorta, A. and Zappia, V. Purification and characterization of propylamine transferase from *Sulfolobus solfataricus*, an extreme thermophilic archaeobacterium. *Eur. J. Biochem.* 161 (1986) 263-271. [PMID: [3096734](#)]

[EC 2.5.1.23 created 1983, modified 2013]

EC 2.5.1.111

Accepted name: 4-hydroxyphenylpyruvate 3-dimethylallyltransferase

Reaction: dimethylallyl diphosphate + 4-hydroxyphenylpyruvate = diphosphate + 3-dimethylallyl-4-hydroxyphenylpyruvate

Glossary: 3-dimethylallyl-4-hydroxyphenylpyruvate = 3-[4-hydroxy-3-(2-methylprop-1-en-1-yl)phenyl]-2-oxopropanoate

Other name(s): CloQ; 4HPP dimethylallyltransferase; NovQ

Systematic name: dimethylallyl diphosphate:4-hydroxyphenylpyruvate 3-dimethylallyltransferase

Comments: The enzyme is involved in the biosynthesis of the 3-dimethylallyl-4-hydroxyphenylpyruvate moiety of the aminocoumarin antibiotics clorobiocin and novobiocin [1].

References:

1. Pojer, F., Wemakor, E., Kammerer, B., Chen, H., Walsh, C.T., Li, S.M. and Heide, L. CloQ, a prenyltransferase involved in clorobiocin biosynthesis. *Proc. Natl. Acad. Sci. USA* 100 (2003) 2316-2321. [PMID: [12618544](#)]
2. Keller, S., Pojer, F., Heide, L. and Lawson, D.M. Crystallization and preliminary X-ray analysis of the aromatic prenyltransferase CloQ from the clorobiocin biosynthetic cluster of *Streptomyces roseochromogenes*. *Acta Crystallogr. Sect. F Struct. Biol. Cryst. Commun.* 62 (2006) 1153-1155. [PMID: [17077503](#)]
3. Metzger, U., Keller, S., Stevenson, C.E., Heide, L. and Lawson, D.M. Structure and mechanism of the magnesium-independent aromatic prenyltransferase CloQ from the clorobiocin biosynthetic pathway. *J. Mol. Biol.* 404 (2010) 611-626. [PMID: [20946900](#)]
4. Ozaki, T., Mishima, S., Nishiyama, M. and Kuzuyama, T. NovQ is a prenyltransferase capable of catalyzing the addition of a dimethylallyl group to both phenylpropanoids and flavonoids. *J. Antibiot. (Tokyo)* 62 (2009) 385-392. [PMID: [19557032](#)]

[EC 2.5.1.111 created 2013]

EC 3.1.1.95

Accepted name: aclacinomycin methylesterase

Reaction: aclacinomycin T + H₂O = 15-demethylaclacinomycin T + methanol

For diagram of reaction [click here](#).

Glossary: aclacinomycin T = 2-ethyl-1,2,3,4,6,11-hexahydro-2,5,7-trihydroxy-6,11-dioxo-4-{{[2,3,6-trideoxy-3-(dimethylamino)-α-L-lyxo-hexopyranosyl]oxy}}-1-naphthacene-carboxylic acid methyl ester = methyl (1R,2R,4S)-2-ethyl-2,5,7-trihydroxy-6,11-dioxo-4-{{[2,3,6-trideoxy-3-(dimethylamino)-α-L-lyxo-hexopyranosyl]oxy}}-1,2,3,4,6,11-hexahydro-tetracene-1-carboxylate
15-demethoxyaclacinomycin T = (1R,2R,4S)-2-ethyl-1,2,3,4,6,11-hexahydro-2,5,7-trihydroxy-6,11-dioxo-4-{{[2,3,6-trideoxy-3-(dimethylamino)-α-L-lyxo-hexopyranosyl]oxy}}-1-naphthacene-carboxylic acid = (1R,2R,4S)-2-ethyl-2,5,7-trihydroxy-6,11-dioxo-4-{{[2,3,6-trideoxy-3-(dimethylamino)-α-L-lyxo-hexopyranosyl]oxy}}-1,2,3,4,6,11-hexahydro-tetracene-1-carboxylic acid

Other name(s): RdmC; aclacinomycin methyl esterase

Systematic name: aclacinomycin T acylhydrolase

Comments: The enzyme is involved in the modification of the aklavinone skeleton in the biosynthesis of anthracyclines in *Streptomyces* species.

References:

1. Wang, Y., Niemi, J., Airas, K., Ylihonko, K., Hakala, J. and Mantsala, P. Modifications of aclacinomycin T by aclacinomycin methyl esterase (RdmC) and aclacinomycin-10-hydroxylase (RdmB) from *Streptomyces purpurascens*. *Biochim. Biophys. Acta* 1480 (2000) 191-200. [PMID: [11004563](#)]
2. Jansson, A., Niemi, J., Mantsala, P. and Schneider, G. Crystal structure of aclacinomycin methylesterase with bound product analogues: implications for anthracycline recognition and mechanism. *J. Biol. Chem.* 278 (2003) 39006-39013. [PMID: [12878604](#)]

[EC 3.1.1.95 created 2013]

EC 3.1.3.91

Accepted name: 7-methylguanosine nucleotidase

Reaction: (1) N⁷-methyl-GMP + H₂O = N⁷-methyl-guanosine + phosphate
(2) CMP + H₂O = cytidine + phosphate

Other name(s): cytosolic nucleotidase III-like; cNIII-like; N⁷-methylguanylate 5'-phosphatase

Systematic name: *N*⁷-methyl-GMP phosphohydrolase

Comments: The enzyme also has low activity with *N*⁷-methyl-GDP, producing *N*⁷-methyl-GMP. Does not accept AMP or GMP, and has low activity with UMP.

References:

1. Buschmann, J., Moritz, B., Jeske, M., Lilie, H., Schierhorn, A. and Wahle, E. Identification of *Drosophila* and human 7-methyl GMP-specific nucleotidases. *J. Biol. Chem.* 288 (2013) 2441-2451. [PMID: [23223233](#)]

[EC 3.1.3.91 created 2013]

EC 3.1.3.92

Accepted name: kanosamine-6-phosphate phosphatase

Reaction: kanosamine 6-phosphate + H₂O = kanosamine + phosphate

For diagram of reaction [click here](#).

Glossary: kanosamine = 3-amino-3-deoxy-D-glucose

Other name(s): *ntdB* (gene name)

Systematic name: kanosamine-6-phosphate phosphohydrolase

Comments: The enzyme, found in the bacterium *Bacillus subtilis*, is involved in a kanosamine biosynthesis pathway.

References:

1. Vetter, N.D., Langill, D.M., Anjum, S., Boisvert-Martel, J., Jagdhane, R.C., Omene, E., Zheng, H., van Straaten, K.E., Asiamah, I., Krol, E.S., Sanders, D.A. and Palmer, D.R. A previously unrecognized kanosamine biosynthesis pathway in *Bacillus subtilis*. *J. Am. Chem. Soc.* 135 (2013) 5970-5973. [PMID: [23586652](#)]

[EC 3.1.3.92 created 2013]

EC 3.2.1.186

Accepted name: protodioscin 26-*O*-β-D-glucosidase

Reaction: protodioscin + H₂O = 26-deglucoprotodioscin + D-glucose

For diagram of reaction [click here](#).

Other name(s): F26G; torvosidase; CSF26G1; furostanol glycoside 26-*O*-β-D-glucosidase; furostanol 26-*O*-β-D-glucoside glucosylhydrolase

Systematic name: protodioscin glucosylhydrolase

Comments: The enzyme has been characterized from the plants *Cheilostocys speciosus* and *Solanum torvum*. It also hydrolyses the 26-β-D-glucose group from related steroid glucosides such as protogracillin, torvoside A and torvoside H.

References:

1. Inoue, K. and Ebizuka, Y. Purification and characterization of furostanol glycoside 26-*O*-β-glucosidase from *Costus speciosus* rhizomes. *FEBS Lett* 378 (1996) 157-160. [PMID: [8549824](#)]

2. Arthan, D., Kittakoop, P., Esen, A. and Svasti, J. Furostanol glycoside 26-*O*-β-glucosidase from the leaves of *Solanum torvum*. *Phytochemistry* 67 (2006) 27-33. [PMID: [16289258](#)]

[EC 3.2.1.186 created 2013]

EC 3.6.3.55

Accepted name: tungstate-importing ATPase

Reaction: ATP + H₂O + tungstate_[side 1] = ADP + phosphate + tungstate_[side 2]

Other name(s): tungstate transporter; WtpABC; TupABC; tungstate-specific ABC transporter

Systematic name: ATP phosphohydrolase (tungstate-importing)

Comments: An ABC-type (ATP-binding cassette-type) ATPase. The enzymes from the archaeon *Pyrococcus furiosus*, the Gram-positive bacterium *Eubacterium acidaminophilum* and the Gram-negative bacterium *Campylobacter jejuni* transport tungsten into the cell for incorporation into tungsten-dependent enzymes.

References:

1. Makdessi, K., Andreessen, J.R. and Pich, A. Tungstate Uptake by a highly specific ABC transporter in *Eubacterium acidaminophilum*. *J. Biol. Chem.* 276 (2001) 24557-24564. [PMID: [11292832](#)]

2. Bevers, L.E., Hagedoorn, P.L., Krijger, G.C. and Hagen, W.R. Tungsten transport protein A (WtpA) in *Pyrococcus furiosus*: the first member of a new class of tungstate and molybdate transporters. *J. Bacteriol.* 188 (2006) 6498-6505. [PMID: [16952940](#)]

3. Smart, J.P., Cliff, M.J. and Kelly, D.J. A role for tungsten in the biology of *Campylobacter jejuni*: tungstate stimulates formate dehydrogenase activity and is transported via an ultra-high affinity ABC system distinct from the molybdate transporter. *Mol. Microbiol.* 74 (2009) 742-757. [PMID: [19818021](#)]

[EC 3.6.3.55 created 2013]

*EC 3.7.1.9

Accepted name: 2-hydroxymuconate-6-semialdehyde hydrolase

Reaction: 2-hydroxymuconate-6-semialdehyde + H₂O = formate + 2-oxopent-4-enoate

For diagram of reaction [click here](#).

Glossary: 2-hydroxymuconate-6-semialdehyde = (2Z,4E)-2-hydroxy-6-oxohexa-2,4-dienoate

Other name(s): 2-hydroxy-6-oxohepta-2,4-dienoate hydrolase; 2-hydroxymuconic semialdehyde hydrolase; HMSH; HOD hydrolase; *xyIF* (gene name); 2-hydroxymuconate-semialdehyde formylhydrolase; 2-hydroxymuconate-semialdehyde hydrolase

Systematic name: 2-hydroxymuconate-6-semialdehyde formylhydrolase

Comments: The enzyme is involved in the degradation of catechols.

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), [UM-BBD](#), CAS registry number: 54004-61-4

References:

1. Sala-Trepat, J.M. and Evans, W.C. The meta cleavage of catechol by *Azotobacter* species. 4-Oxalocrotonate pathway. *Eur. J. Biochem.* 20 (1971) 400-413. [PMID: [4325686](#)]
2. Harayama, S., Rekik, M., Wasserfallen, A. and Bairoch, A. Evolutionary relationships between catabolic pathways for aromatics: conservation of gene order and nucleotide sequences of catechol oxidation genes of pWW0 and NAH7 plasmids. *MGG Mol. Gen. Genet.* 210 (1987) 241-247. [PMID: [3481421](#)]
3. Diaz, E. and Timmis, K.N. Identification of functional residues in a 2-hydroxymuconic semialdehyde hydrolase. A new member of the α/β hydrolase-fold family of enzymes which cleaves carbon-carbon bonds. *J. Biol. Chem.* 270 (1995) 6403-6411. [PMID: [7890778](#)]

[EC 3.7.1.9 created 1990, modified 2013]

*EC 4.1.2.33

Accepted name: fucosterol-epoxide lyase

Reaction: (24R,24'R)-fucosterol epoxide = desmosterol + acetaldehyde

Glossary: (24R,24'R)-fucosterol epoxide = (3 β ,24R,28R)-24,28-epoxystigmast-5-en-3-ol

Other name(s): (24R,24'R)-fucosterol-epoxide acetaldehyde-lyase; (24R,24'R)-fucosterol-epoxide acetaldehyde-lyase (desmosterol-forming)

Systematic name: (24R,24'R)-fucosterol-epoxide acetaldehyde-lyase (desmosterol-forming)

Comments: The insect enzyme is involved in the conversion of sitosterol into cholesterol.

Links to other databases: [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), CAS registry number: 99676-42-3

References:

1. Prestwich, G.D., Angelastro, M., De Palma, A. and Perino, M.A. Fucosterol epoxide lyase of insects: synthesis of labeled substrates and development of a partition assay. *Anal. Biochem.* 151 (1985) 315-326. [PMID: [3913328](#)]

[EC 4.1.2.33 created 1989, modified 2013]

EC 4.1.2.54

Accepted name: L-threo-3-deoxy-hexulosonate aldolase

Reaction: 2-dehydro-3-deoxy-L-galactonate = pyruvate + L-glyceraldehyde

Other name(s): GAAC; LGA1

Systematic name: 2-dehydro-3-deoxy-L-galactonate L-glyceraldehyde-lyase (pyruvate-forming)

Comments: The enzyme takes part in a D-galacturonate degradation pathway in the fungi *Aspergillus niger* and *Trichoderma reesei* (*Hypocrea jecorina*).

References:

1. Hilditch, S., Berghall, S., Kalkkinen, N., Penttila, M. and Richard, P. The missing link in the fungal D-galacturonate pathway: identification of the L-threo-3-deoxy-hexulosonate aldolase. *J. Biol. Chem.* 282 (2007) 26195-26201. [PMID: [17609199](#)]
2. Martens-Uzunova, E.S. and Schaap, P.J. An evolutionary conserved D-galacturonic acid metabolic pathway operates across filamentous fungi capable of pectin degradation. *Fungal Genet. Biol.* 45 (2008) 1449-1457. [PMID: [18768163](#)]

[EC 4.1.2.54 created 2013]

EC 4.1.3.44

Accepted name: tRNA 4-demethylwyosine synthase (AdoMet-dependent)

Reaction: N¹-methylguanine³⁷ in tRNA^{Phe} + pyruvate + S-adenosyl-L-methionine = 4-demethylwyosine³⁷ in tRNA^{Phe} + L-methionine + 5'-deoxyadenosine + CO₂ + H₂O

Glossary: 4-demethylwyosine = imG-14 = 6-methyl-3-(β -D-ribofuranosyl)-3,5-dihydro-9H-imidazo[1,2-a]purin-9-one

Other name(s): TYW1

Systematic name: tRNA^{Phe} N¹-methylguanine,pyruvate acetaldehyde-lyase (tRNA^{Phe} 4-demethylwyosine-forming, decarboxylating, dehydrating)

Comments: This enzyme, which is a member of the superfamily of S-adenosyl-L-methionine-dependent radical (radical AdoMet) enzymes, binds two [4Fe-4S] clusters [3,4]. Carbons C₂ and C₃ from pyruvate are incorporated into 4-demethylwyosine [3]. The enzyme is found in eukaryotes where it is part of the pathway for wybutosine synthesis, and in archaea, where it is involved in the biosynthesis of archaeal wye bases, such as wyosine, isowyosine, and methylwyosine.

References:

1. Goto-Ito, S., Ishii, R., Ito, T., Shibata, R., Fusatomi, E., Sekine, S.I., Bessho, Y. and Yokoyama, S. Structure of an archaeal TYW1, the enzyme catalyzing the second step of wye-base biosynthesis. *Acta Crystallogr. D Biol. Crystallogr.* 63 (2007) 1059-1068. [PMID: [17881823](#)]
2. Suzuki, Y., Noma, A., Suzuki, T., Senda, M., Senda, T., Ishitani, R. and Nureki, O. Crystal structure of the radical SAM enzyme catalyzing tricyclic modified base formation in tRNA. *J. Mol. Biol.* 372 (2007) 1204-1214. [PMID: [17727881](#)]
3. Young, A.P. and Bandarian, V. Pyruvate is the source of the two carbons that are required for formation of the imidazoline ring of 4-demethylwyosine. *Biochemistry* 50 (2011) 10573-10575. [PMID: [22026549](#)]
4. Perche-Letuvé, P., Kathirvelu, V., Berggren, G., Clemancey, M., Latour, J.M., Maurel, V., Douki, T., Armengaud, J., Mulliez, E., Fontecave, M., Garcia-Serres, R., Gambarelli, S. and Atta, M. 4-Demethylwyosine synthase from *Pyrococcus abyssi* is a radical-S-adenosyl-L-methionine enzyme with an additional [4Fe-4S]²⁺ cluster that interacts with the pyruvate co-substrate. *J. Biol. Chem.* 287 (2012) 41174-41185. [PMID: [23043105](#)]

[EC 4.1.3.44 created 2013]

[EC 4.2.1.4 Deleted entry: citrate dehydratase. Now known to be a partial reaction catalysed by EC 4.2.1.3, aconitate hydratase. (EC 4.2.1.4 created 1961, deleted 2013)]

EC 4.2.1.145

Accepted name: capreomycin synthase**Reaction:** (2S,3S)-3-hydroxyarginine = (2S,3R)-capreomycin + H₂O**Glossary:** (2S,3R)-capreomycin = (S)-2-amino-2-[(R)-2-imino-6-hydroxypyrimidin-4-yl]acetic acid**Other name(s):** VioD (ambiguous)**Systematic name:** (2S,3S)-3-hydroxyarginine hydrolyase (cyclizing, (2S,3R)-capreomycin-forming)**Comments:** A pyridoxal 5'-phosphate protein. The enzyme is involved in the biosynthesis of the cyclic pentapeptide antibiotic viomycin.**References:**

1. Yin, X., McPhail, K.L., Kim, K.J. and Zabriskie, T.M. Formation of the nonproteinogenic amino acid (2S,3R)-capreomycin by VioD from the viomycin biosynthesis pathway. *ChemBioChem.* 5 (2004) 1278-1281. [PMID: [15368581](#)]
2. Ju, J., Ozanick, S.G., Shen, B. and Thomas, M.G. Conversion of (2S)-arginine to (2S,3R)-capreomycin by VioC and VioD from the viomycin biosynthetic pathway of *Streptomyces* sp. strain ATCC11861. *ChemBioChem.* 5 (2004) 1281-1285. [PMID: [15368582](#)]

[EC 4.2.1.145 created 2013]

EC 4.2.1.146

Accepted name: L-galactonate dehydratase**Reaction:** L-galactonate = 2-dehydro-3-deoxy-L-galactonate + H₂O**Other name(s):** LGD1**Systematic name:** L-galactonate hydro-lyase (2-dehydro-3-deoxy-L-galactonate-forming)**Comments:** The enzyme takes part in a D-galacturonate degradation pathway in the fungi *Trichoderma reesei* (*Hypocrea jecorina*) and *Aspergillus niger*.**References:**

1. Kuorelahti, S., Jouhten, P., Maaheimo, H., Penttilä, M. and Richard, P. L-Galactonate dehydratase is part of the fungal path for D-galacturonic acid catabolism. *Mol. Microbiol.* 61 (2006) 1060-1068. [PMID: [16879654](#)]
2. Martens-Uzunova, E.S. and Schaap, P.J. An evolutionary conserved D-galacturonic acid metabolic pathway operates across filamentous fungi capable of pectin degradation. *Fungal Genet. Biol.* 45 (2008) 1449-1457. [PMID: [18768163](#)]

[EC 4.2.1.146 created 2013]

EC 4.2.3.144

Accepted name: geranylgeranyl synthase**Reaction:** geranylgeranyl diphosphate + H₂O = (E,E)-geranylgeranyl + diphosphateFor diagram of reaction [click here](#).**Glossary:** geranylgeranyl diphosphate = (2E,6E,10E)-3,7,11,15-tetramethylhexadeca-2,6,10,14-tetraen-1-yl diphosphate
(E,E)-geranylgeranyl = (6E,10E)-3,7,11,15-tetramethylhexadeca-1,6,10,14-tetraen-3-ol**Other name(s):** TPS4/GES; GES**Systematic name:** geranylgeranyl diphosphate diphosphate-lyase ((E,E)-geranylgeranyl-forming)**Comments:** The enzyme is a component of the herbivore-induced indirect defense system. The product, (E,E)-geranylgeranyl, is a precursor to the volatile compound 4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT), which is released by many plants in response to damage.**References:**

1. Herde, M., Gartner, K., Kollner, T.G., Fode, B., Boland, W., Gershenzon, J., Gatz, C. and Tholl, D. Identification and regulation of TPS4/GES, an *Arabidopsis* geranylgeranyl synthase catalyzing the first step in the formation of the insect-induced volatile C¹⁶-homoterpene TMTT. *Plant Cell* 20 (2008) 1152-1168. [PMID: [18398052](#)]
2. Attaran, E., Rostas, M. and Zeier, J. *Pseudomonas syringae* elicits emission of the terpenoid (E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene in *Arabidopsis* leaves via jasmonate signaling and expression of the terpene synthase TPS4. *Mol Plant Microbe Interact* 21 (2008) 1482-1497. [PMID: [18842097](#)]

[EC 4.2.3.144 created 2013]

EC 4.4.1.27

Accepted name: carbon disulfide lyase**Reaction:** carbon disulfide + 2 H₂O = CO₂ + 2 hydrogen sulfide (overall reaction)(1a) carbon disulfide + H₂O = carbonyl sulfide + hydrogen sulfide(1b) carbonyl sulfide + H₂O = CO₂ + hydrogen sulfide**Other name(s):** CS₂ hydrolase (misleading); carbon disulfide hydrolase (misleading); CS₂-converting enzyme; carbon disulphide-lyase (decarboxylating)**Systematic name:** carbon disulfide-lyase (hydrogen sulfide-producing)**Comments:** The enzyme contains Zn²⁺. The hyperthermophilic archaeon *Acidianus* sp. A1-3 obtains energy by the conversion of carbon disulfide to hydrogen sulfide, with carbonyl sulfide as an intermediate.**References:**

1. Smeulders, M.J., Barends, T.R., Pol, A., Scherer, A., Zandvoort, M.H., Udvarhelyi, A., Khadem, A.F., Menzel, A., Hermans, J., Shoeman, R.L., Wessels, H.J., van den Heuvel, L.P., Russ, L., Schlichting, I., Jetten, M.S. and Op den Camp, H.J. Evolution of a new enzyme for carbon disulphide conversion by an acidothermophilic archaeon. *Nature* 478 (2011) 412-416. [PMID: [22012399](#)]

[EC 4.4.1.27 created 2013]

EC 5.1.3.26

Accepted name: *N*-acetyl- α -D-glucosaminyl-diphospho-*ditrans*,*octakis*-undecaprenol 4-epimerase**Reaction:** *N*-acetyl- α -D-glucosaminyl-diphospho-*ditrans*,*octakis*-undecaprenol = *N*-acetyl- α -D-galactosaminyl-diphospho-*ditrans*,*octakis*-undecaprenol**Other name(s):** GlcNAc-P-P-Und epimerase; GlcNAc-P-P-Und 4-epimerase; *gne* (gene name)**Systematic name:** *N*-acetyl- α -D-glucosaminyl-diphospho-*ditrans*,*octakis*-undecaprenol 4-epimerase**Comments:** The enzyme is involved in biosynthesis of the repeating tetrasaccharide unit of the O-antigen produced by some Gram-negative bacteria.**References:**

1. Rush, J.S., Alaimo, C., Robbani, R., Wacker, M. and Waechter, C.J. A novel epimerase that converts GlcNAc-P-P-undecaprenol to GalNAc-P-P-undecaprenol in *Escherichia coli* O157. *J. Biol. Chem.* 285 (2010) 1671-1680. [PMID: [19923219](#)]

[EC 5.1.3.26 created 2013]

EC 5.3.1.29

Accepted name: ribose 1,5-bisphosphate isomerase**Reaction:** α -D-ribose 1,5-bisphosphate = D-ribulose 1,5-bisphosphate**Other name(s):** R15P isomerase; ribulose 1,5-bisphosphate synthase; RuBP synthase**Systematic name:** α -D-ribose 1,5-bisphosphate aldose-ketose-isomerase**Comments:** This archaeal enzyme is involved in AMP metabolism and CO₂ fixation through type III RubisCO enzymes. The enzyme is activated by cAMP [2].**References:**

1. Sato, T., Atomi, H. and Imanaka, T. Archaeal type III RuBisCOs function in a pathway for AMP metabolism. *Science* 315 (2007) 1003-1006. [PMID: [17303759](#)]
2. Aono, R., Sato, T., Yano, A., Yoshida, S., Nishitani, Y., Miki, K., Imanaka, T. and Atomi, H. Enzymatic characterization of AMP phosphorylase and ribose-1,5-bisphosphate isomerase functioning in an archaeal AMP metabolic pathway. *J. Bacteriol.* 194 (2012) 6847-6855. [PMID: [23065974](#)]
3. Nakamura, A., Fujihashi, M., Aono, R., Sato, T., Nishiba, Y., Yoshida, S., Yano, A., Atomi, H., Imanaka, T. and Miki, K. Dynamic, ligand-dependent conformational change triggers reaction of ribose-1,5-bisphosphate isomerase from *Thermococcus kodakarensis* KOD1. *J. Biol. Chem.* 287 (2012) 20784-20796. [PMID: [22511789](#)]

[EC 5.3.1.29 created 2013]

EC 5.4.99.59

Accepted name: dTDP-fucopyranose mutase**Reaction:** dTDP- α -D-fucopyranose = dTDP- β -D-fucofuranoseFor diagram of reaction [click here](#).**Other name(s):** Fcf2**Systematic name:** dTDP- α -D-fucopyranose furanomutase**Comments:** The enzyme is involved in the biosynthesis of the *Escherichia coli* O52 O antigen.**References:**

1. Wang, Q., Ding, P., Perepelov, A.V., Xu, Y., Wang, Y., Knirel, Y.A., Wang, L. and Feng, L. Characterization of the dTDP-D-fucofuranose biosynthetic pathway in *Escherichia coli* O52. *Mol. Microbiol.* 70 (2008) 1358-1367. [PMID: [19019146](#)]

[EC 5.4.99.59 created 2013]

EC 5.5.1.23

Accepted name: aklanonic acid methyl ester cyclase**Reaction:** methyl aklanonate = aklaviketoneFor diagram of reaction [click here](#).**Glossary:** aklaviketone = methyl (1*R*,2*R*)-2-ethyl-2,5,7-trihydroxy-4,6,11-trioxo-1,2,3,4,6,11-hexahydrotetracene-1-carboxylate
methyl aklanonate = methyl [4,5-dihydroxy-9,10-dioxo-3-(3-oxopentanoyl)-9,10-dihydroanthracen-2-yl]acetate**Other name(s):** *dauD* (gene name); *aknH* (gene name); *dnrD* (gene name); methyl aklanonate cyclase**Systematic name:** methyl aklanonate-aklaviketone isomerase (cyclizing)**Comments:** The enzyme is involved in the biosynthesis of aklaviketone, an intermediate in the biosynthetic pathways leading to formation of several anthracycline antibiotics, including aclacinomycin, daunorubicin and doxorubicin.**References:**

- Dickens, M.L., Ye, J. and Strohl, W.R. Analysis of clustered genes encoding both early and late steps in daunomycin biosynthesis by *Streptomyces* sp. strain C5. *J. Bacteriol.* 177 (1995) 536-543. [PMID: [7836284](#)]
- Kendrew, S.G., Katayama, K., Deutsch, E., Madduri, K. and Hutchinson, C.R. DnrD cyclase involved in the biosynthesis of doxorubicin: purification and characterization of the recombinant enzyme. *Biochemistry* 38 (1999) 4794-4799. [PMID: [10200167](#)]
- Kallio, P., Sultana, A., Niemi, J., Mantsala, P. and Schneider, G. Crystal structure of the polyketide cyclase AknH with bound substrate and product analogue: implications for catalytic mechanism and product stereoselectivity. *J. Mol. Biol.* 357 (2006) 210-220. [PMID: [16414075](#)]

[EC 5.5.1.23 created 2013]

[EC 6.3.1.16 Transferred entry: carbapenam-3-carboxylate synthetase. The enzyme was discovered at the public-review stage to have been misclassified and so was withdrawn. See [EC 6.3.3.6](#), carbapenam-3-carboxylate synthase (EC 6.3.1.16 created 2013, deleted 2013)]

EC 6.3.3.6

Accepted name: carbapenam-3-carboxylate synthase**Reaction:** ATP + (2*S*,5*S*)-5-carboxymethylproline = AMP + diphosphate + (3*S*,5*S*)-carbapenam 3-carboxylate**Other name(s):** CarA (ambiguous); CPS (ambiguous); carbapenam-3-carboxylate ligase**Systematic name:** 6-methyl-(2*S*,5*S*)-5-carboxymethylproline cyclo-ligase (AMP-forming)**Comments:** The enzyme is involved in the biosynthesis of the carbapenem β -lactam antibiotic (5*R*)-carbapen-2-em-3-carboxylate in the bacterium *Pectobacterium carotovorum*.**References:**

- Gerrata, B., Stapon, A. and Townsend, C.A. Inhibition and alternate substrate studies on the mechanism of carbapenam synthetase from *Erwinia carotovora*. *Biochemistry* 42 (2003) 7836-7847. [PMID: [12820893](#)]
- Miller, M.T., Gerrata, B., Stapon, A., Townsend, C.A. and Rosenzweig, A.C. Crystal structure of carbapenam synthetase (CarA). *J. Biol. Chem.* 278 (2003) 40996-41002. [PMID: [12890666](#)]
- Raber, M.L., Arnett, S.O. and Townsend, C.A. A conserved tyrosyl-glutamyl catalytic dyad in evolutionarily linked enzymes: carbapenam synthetase and β -lactam synthetase. *Biochemistry* 48 (2009) 4959-4971. [PMID: [19371088](#)]
- Arnett, S.O., Gerrata, B. and Townsend, C.A. Rate-limiting steps and role of active site Lys⁴⁴³ in the mechanism of carbapenam synthetase. *Biochemistry* 46 (2007) 9337-9345. [PMID: [17658887](#)]

[EC 6.3.3.6 created 2013 as 6.3.1.16, transferred 2013 to EC 6.3.3.6]

*EC 6.5.1.4

Accepted name: RNA 3'-terminal-phosphate cyclase (ATP)**Reaction:** ATP + RNA 3'-terminal-phosphate = AMP + diphosphate + RNA terminal-2',3'-cyclic-phosphate**Other name(s):** RNA cyclase (ambiguous); RNA-3'-phosphate cyclase (ambiguous)**Systematic name:** RNA-3'-phosphate:RNA ligase (cyclizing, AMP-forming)**Comments:** Adenosine 5'-(γ -thio)triphosphate can act instead of ATP. *cf.* [EC 6.5.1.5](#), RNA-3'-phosphate cyclase (GTP).**Links to other databases:** [BRENDA](#), [EXPASY](#), [KEGG](#), [Metacyc](#), [PDB](#), CAS registry number: 85638-41-1**References:**

- Filipowicz, W., Konarska, M., Gross, H.J. and Shatkin, A.J. RNA 3'-terminal phosphate cyclase activity and RNA ligation in HeLa cell extract. *Nucleic Acids Res.* 11 (1983) 1405-1418. [PMID: [6828385](#)]
- Reinberg, D., Arenas, J. and Hurwitz, J. The enzymatic conversion of 3'-phosphate terminated RNA chains to 2',3'-cyclic phosphate derivatives. *J. Biol. Chem.* 260 (1985) 6088-6097. [PMID: [2581947](#)]

[EC 6.5.1.4 created 1986, modified 1989, modified 2013]

EC 6.5.1.5

Accepted name: RNA 3'-terminal-phosphate cyclase (GTP)

Reaction: GTP + RNA 3'-terminal-phosphate = GMP + diphosphate + RNA terminal-2',3'-cyclic-phosphate

Other name(s): Pf-Rtc; RNA-3'-phosphate cyclase (GTP)

Systematic name: RNA-3'-phosphate:RNA ligase (cyclizing, GMP-forming)

Comments: The enzyme from the archaeon *Pyrococcus furiosus* is activated by Mg^{2+} . cf. [EC 6.5.1.4](#), RNA-3'-phosphate cyclase (ATP).

References:

1. Sato, A., Soga, T., Igarashi, K., Takesue, K., Tomita, M. and Kanai, A. GTP-dependent RNA 3'-terminal phosphate cyclase from the hyperthermophilic archaeon *Pyrococcus furiosus*. *Genes Cells* 16 (2011) 1190-1199. [PMID: [22074260](#)]

[EC 6.5.1.5 created 2013]

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