

The Enzyme List

Class 1 — Oxidoreductases

Nomenclature Committee
of the
International Union of Biochemistry and Molecular Biology
(NC-IUBMB)

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EC 1.1 Acting on the CH-OH group of donors

This subclass contains dehydrogenases that act on primary alcohols, secondary alcohols and hemi-acetals. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.1.1), a cytochrome (EC 1.1.2), oxygen (EC 1.1.3), a disulfide (EC 1.1.4), a quinone or similar compound (EC 1.1.5), or some other acceptor (EC 1.1.99).

EC 1.1.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.1.1.1

- Accepted name:** alcohol dehydrogenase
Reaction: (1) a primary alcohol + NAD⁺ = an aldehyde + NADH + H⁺
(2) a secondary alcohol + NAD⁺ = a ketone + NADH + H⁺
Other name(s): aldehyde reductase; ADH; alcohol dehydrogenase (NAD); aliphatic alcohol dehydrogenase; ethanol dehydrogenase; NAD-dependent alcohol dehydrogenase; NAD-specific aromatic alcohol dehydrogenase; NADH-alcohol dehydrogenase; NADH-aldehyde dehydrogenase; primary alcohol dehydrogenase; yeast alcohol dehydrogenase
Systematic name: alcohol:NAD⁺ oxidoreductase
Comments: A zinc protein. Acts on primary or secondary alcohols or hemi-acetals with very broad specificity; however the enzyme oxidizes methanol much more poorly than ethanol. The animal, but not the yeast, enzyme acts also on cyclic secondary alcohols.
References: [385, 1777, 2756, 3735, 3860]

[EC 1.1.1.1 created 1961, modified 2011]

EC 1.1.1.2

- Accepted name:** alcohol dehydrogenase (NADP⁺)
Reaction: an alcohol + NADP⁺ = an aldehyde + NADPH + H⁺
Other name(s): aldehyde reductase (NADPH₂); NADP-alcohol dehydrogenase; NADP⁺-aldehyde reductase; NADP⁺-dependent aldehyde reductase; NADPH-aldehyde reductase; NADPH-dependent aldehyde reductase; nonspecific succinic semialdehyde reductase; ALR 1; low-*K_m* aldehyde reductase; high-*K_m* aldehyde reductase; alcohol dehydrogenase (NADP)
Systematic name: alcohol:NADP⁺ oxidoreductase
Comments: A zinc protein. Some members of this group oxidize only primary alcohols; others act also on secondary alcohols. May be identical with EC 1.1.1.19 (L-glucuronate reductase), EC 1.1.1.33 [mevaldate reductase (NADPH)] and EC 1.1.1.55 [lactaldehyde reductase (NADPH)]. *Re*-specific with respect to NADPH.
References: [361, 790, 3156, 3768]

[EC 1.1.1.2 created 1961]

EC 1.1.1.3

- Accepted name:** homoserine dehydrogenase
Reaction: L-homoserine + NAD(P)⁺ = L-aspartate 4-semialdehyde + NAD(P)H + H⁺
Other name(s): HSDH; HSD
Systematic name: L-homoserine:NAD(P)⁺ oxidoreductase
Comments: The yeast enzyme acts most rapidly with NAD⁺; the *Neurospora* enzyme with NADP⁺. The enzyme from *Escherichia coli* is a multi-functional protein, which also catalyses the reaction of EC 2.7.2.4 (aspartate kinase).
References: [310, 3624, 4036]

[EC 1.1.1.3 created 1961, modified 1976]

EC 1.1.1.4

- Accepted name:** (*R,R*)-butanediol dehydrogenase
Reaction: (*R,R*)-butane-2,3-diol + NAD⁺ = (*R*)-acetoin + NADH + H⁺

Other name(s): butyleneglycol dehydrogenase; D-butanediol dehydrogenase; D-(–)-butanediol dehydrogenase; butylene glycol dehydrogenase; diacetyl (acetoin) reductase; D-aminopropanol dehydrogenase; 1-amino-2-propanol dehydrogenase; 2,3-butanediol dehydrogenase; D-1-amino-2-propanol dehydrogenase; (R)-diacetyl reductase; (R)-2,3-butanediol dehydrogenase; D-1-amino-2-propanol:NAD⁺ oxidoreductase; 1-amino-2-propanol oxidoreductase; aminopropanol oxidoreductase
Systematic name: (R,R)-butane-2,3-diol:NAD⁺ oxidoreductase
Comments: Also converts diacetyl into acetoin with NADH as reductant.
References: [3674, 3834]

[EC 1.1.1.4 created 1961 (EC 1.1.1.74 created 1972, incorporated 1976)]

[1.1.1.5 *Transferred entry. acetoin dehydrogenase. Now EC 1.1.1.303, diacetyl reductase [(R)-acetoin forming] and EC 1.1.1.304, diacetyl reductase [(S)-acetoin forming]]*

[EC 1.1.1.5 created 1961, modified 1976, deleted 2010]

EC 1.1.1.6

Accepted name: glycerol dehydrogenase
Reaction: glycerol + NAD⁺ = glycerone + NADH + H⁺
Other name(s): glycerin dehydrogenase; NAD-linked glycerol dehydrogenase
Systematic name: glycerol:NAD⁺ 2-oxidoreductase
Comments: Also acts on propane-1,2-diol.
References: [133, 456, 2253]

[EC 1.1.1.6 created 1961]

EC 1.1.1.7

Accepted name: propanediol-phosphate dehydrogenase
Reaction: propane-1,2-diol 1-phosphate + NAD⁺ = hydroxyacetone phosphate + NADH + H⁺
Other name(s): PDP dehydrogenase; 1,2-propanediol-1-phosphate:NAD⁺ oxidoreductase; propanediol phosphate dehydrogenase
Systematic name: propane-1,2-diol-1-phosphate:NAD⁺ oxidoreductase
References: [3439]

[EC 1.1.1.7 created 1961]

EC 1.1.1.8

Accepted name: glycerol-3-phosphate dehydrogenase (NAD⁺)
Reaction: *sn*-glycerol 3-phosphate + NAD⁺ = glycerone phosphate + NADH + H⁺
Other name(s): α-glycerol phosphate dehydrogenase (NAD⁺); α-glycerophosphate dehydrogenase (NAD⁺); glycerol 1-phosphate dehydrogenase; glycerol phosphate dehydrogenase (NAD⁺); glycerophosphate dehydrogenase (NAD⁺); hydroglycerophosphate dehydrogenase; L-α-glycerol phosphate dehydrogenase; L-α-glycerophosphate dehydrogenase; L-glycerol phosphate dehydrogenase; L-glycerophosphate dehydrogenase (ambiguous); NAD⁺-α-glycerophosphate dehydrogenase; NAD⁺-dependent glycerol phosphate dehydrogenase; NAD⁺-dependent glycerol-3-phosphate dehydrogenase; NAD⁺-L-glycerol-3-phosphate dehydrogenase; NAD⁺-linked glycerol 3-phosphate dehydrogenase; NADH-dihydroxyacetone phosphate reductase; glycerol-3-phosphate dehydrogenase (NAD⁺); L-glycerol-3-phosphate dehydrogenase (ambiguous)
Systematic name: *sn*-glycerol-3-phosphate:NAD⁺ 2-oxidoreductase
Comments: Also acts on propane-1,2-diol phosphate and glycerone sulfate (but with a much lower affinity).
References: [195, 411, 2836, 4133, 54, 1993]

[EC 1.1.1.8 created 1961, modified 2005]

EC 1.1.1.9

Accepted name: D-xylulose reductase
Reaction: xylitol + NAD⁺ = D-xylulose + NADH + H⁺
Other name(s): NAD⁺-dependent xylitol dehydrogenase; xylitol dehydrogenase (ambiguous); erythritol dehydrogenase; 2,3-*cis*-polyol(DPN) dehydrogenase (C3-5); pentitol-DPN dehydrogenase (ambiguous); xylitol-2-dehydrogenase
Systematic name: xylitol:NAD⁺ 2-oxidoreductase (D-xylulose-forming)
Comments: Also acts as an L-erythrulose reductase.
References: [588, 1489, 1714]

[EC 1.1.1.9 created 1961]

EC 1.1.1.10

Accepted name: L-xylulose reductase
Reaction: xylitol + NADP⁺ = L-xylulose + NADPH + H⁺
Other name(s): xylitol dehydrogenase (ambiguous)
Systematic name: xylitol:NADP⁺ 4-oxidoreductase (L-xylulose-forming)
References: [861, 1489, 1544, 3917]

[EC 1.1.1.10 created 1961]

EC 1.1.1.11

Accepted name: D-arabinitol 4-dehydrogenase
Reaction: D-arabinitol + NAD⁺ = D-xylulose + NADH + H⁺
Other name(s): D-arabitol dehydrogenase; arabitol dehydrogenase
Systematic name: D-arabinitol:NAD⁺ 4-oxidoreductase
References: [2252, 4250]

[EC 1.1.1.11 created 1961]

EC 1.1.1.12

Accepted name: L-arabinitol 4-dehydrogenase
Reaction: L-arabinitol + NAD⁺ = L-xylulose + NADH + H⁺
Other name(s): pentitol-DPN dehydrogenase (ambiguous); L-arabitol dehydrogenase
Systematic name: L-arabinitol:NAD⁺ 4-oxidoreductase (L-xylulose-forming)
References: [588, 589]

[EC 1.1.1.12 created 1961]

EC 1.1.1.13

Accepted name: L-arabinitol 2-dehydrogenase
Reaction: L-arabinitol + NAD⁺ = L-ribulose + NADH + H⁺
Other name(s): L-arabinitol dehydrogenase (ribulose-forming); L-arabinitol (ribulose-forming) dehydrogenase
Systematic name: L-arabinitol:NAD⁺ 2-oxidoreductase (L-ribulose-forming)
References: [589]

[EC 1.1.1.13 created 1961]

EC 1.1.1.14

Accepted name: L-iditol 2-dehydrogenase
Reaction: L-iditol + NAD⁺ = L-sorbose + NADH + H⁺

Other name(s): polyol dehydrogenase; sorbitol dehydrogenase; L-idoitol:NAD⁺ 5-oxidoreductase; L-idoitol (sorbitol) dehydrogenase; glucitol dehydrogenase; L-idoitol:NAD⁺ oxidoreductase; NAD⁺-dependent sorbitol dehydrogenase; NAD⁺-sorbitol dehydrogenase
Systematic name: L-idoitol:NAD⁺ 2-oxidoreductase
Comments: This enzyme is widely distributed and has been described in archaea, bacteria, yeast, plants and animals. It acts on a number of sugar alcohols, including (but not limited to) L-idoitol, D-glucitol, D-xylitol, and D-galactitol. Enzymes from different organisms or tissues display different substrate specificity. The enzyme is specific to NAD⁺ and can not use NADP⁺.
References: [165, 449, 2195, 2757, 2835, 2775]

[EC 1.1.1.14 created 1961, modified 2011]

EC 1.1.1.15

Accepted name: D-idoitol 2-dehydrogenase
Reaction: D-idoitol + NAD⁺ = D-sorbose + NADH + H⁺
Other name(s): D-sorbitol dehydrogenase
Systematic name: D-idoitol:NAD⁺ 2-oxidoreductase
Comments: Also converts xylitol into L-xylulose and L-glucitol into L-fructose.
References: [3466]

[EC 1.1.1.15 created 1961]

EC 1.1.1.16

Accepted name: galactitol 2-dehydrogenase
Reaction: galactitol + NAD⁺ = D-tagatose + NADH + H⁺
Other name(s): dulcitol dehydrogenase; AtuSorbD (gene name); galactitol:NAD⁺ 2-oxidoreductase
Systematic name: galactitol:NAD⁺ 2-oxidoreductase (D-tagatose-forming)
Comments: Also converts other alditols containing an L-*threo*-configuration adjacent to a primary alcohol group into the corresponding sugars. The enzyme from *Agrobacterium fabrum* C58 is part of D-altritol and galactitol degradation pathways.
References: [3466, 4202]

[EC 1.1.1.16 created 1961]

EC 1.1.1.17

Accepted name: mannitol-1-phosphate 5-dehydrogenase
Reaction: D-mannitol 1-phosphate + NAD⁺ = D-fructose 6-phosphate + NADH + H⁺
Other name(s): hexose reductase; mannitol 1-phosphate dehydrogenase; D-mannitol-1-phosphate dehydrogenase; fructose 6-phosphate reductase
Systematic name: D-mannitol-1-phosphate:NAD⁺ 5-oxidoreductase
References: [2403, 4237, 4238]

[EC 1.1.1.17 created 1961]

EC 1.1.1.18

Accepted name: inositol 2-dehydrogenase
Reaction: *myo*-inositol + NAD⁺ = 2,4,6/3,5-pentahydroxycyclohexanone + NADH + H⁺
Other name(s): *myo*-inositol 2-dehydrogenase; *myo*-inositol:NAD⁺ oxidoreductase; inositol dehydrogenase; *myo*-inositol dehydrogenase
Systematic name: *myo*-inositol:NAD⁺ 2-oxidoreductase
References: [270, 2141, 4042]

[EC 1.1.1.18 created 1961]

EC 1.1.1.19

Accepted name: glucuronate reductase
Reaction: L-gulonate + NADP⁺ = D-glucuronate + NADPH + H⁺
Other name(s): aldehyde reductase; L-hexonate:NADP dehydrogenase; TPN-L-gulonate dehydrogenase; aldehyde reductase II; NADP-L-gulonate dehydrogenase; D-glucuronate dehydrogenase; D-glucuronate reductase; L-glucuronate reductase (incorrect)
Systematic name: L-gulonate:NADP⁺ 6-oxidoreductase
Comments: Also reduces D-galacturonate. May be identical with EC 1.1.1.2 [alcohol dehydrogenase (NADP⁺)].
References: [3544, 4062, 4373]

[EC 1.1.1.19 created 1961]

EC 1.1.1.20

Accepted name: glucuronolactone reductase
Reaction: L-gulono-1,4-lactone + NADP⁺ = D-glucurono-3,6-lactone + NADPH + H⁺
Other name(s): GRase; gulonolactone dehydrogenase
Systematic name: L-gulono-1,4-lactone:NADP⁺ 1-oxidoreductase
References: [3751]

[EC 1.1.1.20 created 1961]

EC 1.1.1.21

Accepted name: aldehyde reductase
Reaction: alditol + NAD(P)⁺ = aldose + NAD(P)H + H⁺
Other name(s): aldose reductase; polyol dehydrogenase (NADP⁺); ALR2; alditol:NADP oxidoreductase; alditol:NADP⁺ 1-oxidoreductase; NADPH-aldopentose reductase; NADPH-aldose reductase
Systematic name: alditol:NAD(P)⁺ 1-oxidoreductase
Comments: Has wide specificity.
References: [137, 334, 1481, 3360]

[EC 1.1.1.21 created 1961 (EC 1.1.1.139 created 1972, incorporated 1978)]

EC 1.1.1.22

Accepted name: UDP-glucose 6-dehydrogenase
Reaction: UDP- α -D-glucose + 2 NAD⁺ + H₂O = UDP- α -D-glucuronate + 2 NADH + 2 H⁺
Other name(s): UDP-glucose dehydrogenase; uridine diphosphoglucose dehydrogenase; UDPG dehydrogenase; UDPG:NAD oxidoreductase; UDP- α -D-glucose:NAD oxidoreductase; UDP-glucose:NAD⁺ oxidoreductase; uridine diphosphate glucose dehydrogenase; UDP-D-glucose dehydrogenase; uridine diphosphate D-glucose dehydrogenase
Systematic name: UDP- α -D-glucose:NAD⁺ 6-oxidoreductase
Comments: Also acts on UDP- α -D-2-deoxyglucose.
References: [875, 2471, 3687, 3688]

[EC 1.1.1.22 created 1961]

EC 1.1.1.23

Accepted name: histidinol dehydrogenase
Reaction: L-histidinol + 2 NAD⁺ + H₂O = L-histidine + 2 NADH + 3 H⁺
Other name(s): L-histidinol dehydrogenase
Systematic name: L-histidinol:NAD⁺ oxidoreductase
Comments: Also oxidizes L-histidinal. The *Neurospora* enzyme also catalyses the reactions of EC 3.5.4.19 (phosphoribosyl-AMP cyclohydrolase) and EC 3.6.1.31 (phosphoribosyl-ATP diphosphatase).
References: [18, 19, 2296, 4396]

[EC 1.1.1.23 created 1961]

EC 1.1.1.24

Accepted name: quinate dehydrogenase
Reaction: L-quinatate + NAD⁺ = 3-dehydroquinatate + NADH + H⁺
Other name(s): quinic dehydrogenase; quinate:NAD oxidoreductase; quinate 5-dehydrogenase; quinate:NAD⁺ 5-oxidoreductase
Systematic name: L-quinatate:NAD⁺ 3-oxidoreductase
Comments: The enzyme is specific for quinate as substrate; phenylpyruvate, phenylalanine, cinnamate and shikimate will not act as substrates. NAD⁺ cannot be replaced by NADP⁺.
References: [1148, 2566]

[EC 1.1.1.24 created 1961, modified 1976, modified 2004]

EC 1.1.1.25

Accepted name: shikimate dehydrogenase
Reaction: shikimate + NADP⁺ = 3-dehydroshikimate + NADPH + H⁺
Other name(s): dehydroshikimic reductase; shikimate oxidoreductase; shikimate:NADP⁺ oxidoreductase; 5-dehydroshikimate reductase; shikimate 5-dehydrogenase; 5-dehydroshikimic reductase; DHS reductase; shikimate:NADP⁺ 5-oxidoreductase; AroE
Systematic name: shikimate:NADP⁺ 3-oxidoreductase
Comments: NAD⁺ cannot replace NADP⁺ [4347]. In higher organisms, this enzyme forms part of a multienzyme complex with EC 4.2.1.10, 3-dehydroquinatate dehydratase [557].
References: [181, 2566, 4347, 557, 98, 4354]

[EC 1.1.1.25 created 1961, modified 1976, modified 2004]

EC 1.1.1.26

Accepted name: glyoxylate reductase
Reaction: glycolate + NAD⁺ = glyoxylate + NADH + H⁺
Other name(s): NADH-glyoxylate reductase; glyoxylic acid reductase; NADH-dependent glyoxylate reductase
Systematic name: glycolate:NAD⁺ oxidoreductase
Comments: Reduces glyoxylate to glycolate or hydroxypyruvate to D-glycerate.
References: [4431, 4432]

[EC 1.1.1.26 created 1961]

EC 1.1.1.27

Accepted name: L-lactate dehydrogenase
Reaction: (S)-lactate + NAD⁺ = pyruvate + NADH + H⁺
Other name(s): lactic acid dehydrogenase; L(+)-nLDH; L-(+)-lactate dehydrogenase; L-lactic dehydrogenase; L-lactic acid dehydrogenase; lactate dehydrogenase; lactate dehydrogenase NAD-dependent; lactic dehydrogenase; NAD-lactate dehydrogenase
Systematic name: (S)-lactate:NAD⁺ oxidoreductase
Comments: Also oxidizes other (S)-2-hydroxymonocarboxylic acids. NADP⁺ also acts, more slowly, with the animal, but not the bacterial, enzyme.
References: [797, 972, 1536, 3350]

[EC 1.1.1.27 created 1961]

EC 1.1.1.28

Accepted name: D-lactate dehydrogenase

Reaction: (R)-lactate + NAD⁺ = pyruvate + NADH + H⁺
Other name(s): lactic acid dehydrogenase; lactic acid dehydrogenase; D-specific lactic dehydrogenase; D-(-)-lactate dehydrogenase (NAD); D-lactic acid dehydrogenase; D-lactic dehydrogenase
Systematic name: (R)-lactate:NAD⁺ oxidoreductase
References: [797]

[EC 1.1.1.28 created 1961]

EC 1.1.1.29

Accepted name: glycerate dehydrogenase
Reaction: D-glycerate + NAD⁺ = hydroxypyruvate + NADH + H⁺
Other name(s): D-glycerate dehydrogenase; hydroxypyruvate reductase; (R)-glycerate:NAD⁺ oxidoreductase
Systematic name: D-glycerate:NAD⁺ oxidoreductase
References: [1551, 3618]

[EC 1.1.1.29 created 1961]

EC 1.1.1.30

Accepted name: 3-hydroxybutyrate dehydrogenase
Reaction: (R)-3-hydroxybutanoate + NAD⁺ = acetoacetate + NADH + H⁺
Other name(s): NAD-β-hydroxybutyrate dehydrogenase; hydroxybutyrate oxidoreductase; β-hydroxybutyrate dehydrogenase; D-β-hydroxybutyrate dehydrogenase; D-3-hydroxybutyrate dehydrogenase; D-(-)-3-hydroxybutyrate dehydrogenase; β-hydroxybutyric acid dehydrogenase; 3-D-hydroxybutyrate dehydrogenase; β-hydroxybutyric dehydrogenase
Systematic name: (R)-3-hydroxybutanoate:NAD⁺ oxidoreductase
Comments: Also oxidizes other 3-hydroxymonocarboxylic acids.
References: [268, 786, 2189]

[EC 1.1.1.30 created 1961]

EC 1.1.1.31

Accepted name: 3-hydroxyisobutyrate dehydrogenase
Reaction: 3-hydroxy-2-methylpropanoate + NAD⁺ = 2-methyl-3-oxopropanoate + NADH + H⁺
Other name(s): β-hydroxyisobutyrate dehydrogenase
Systematic name: 3-hydroxy-2-methylpropanoate:NAD⁺ oxidoreductase
References: [3204]

[EC 1.1.1.31 created 1961]

EC 1.1.1.32

Accepted name: mevaldate reductase
Reaction: (R)-mevalonate + NAD⁺ = mevaldate + NADH + H⁺
Other name(s): mevalonic dehydrogenase
Systematic name: (R)-mevalonate:NAD⁺ oxidoreductase
References: [3371]

[EC 1.1.1.32 created 1961]

EC 1.1.1.33

Accepted name: mevaldate reductase (NADPH)
Reaction: (R)-mevalonate + NADP⁺ = mevaldate + NADPH + H⁺
Other name(s): mevaldate (reduced nicotinamide adenine dinucleotide phosphate) reductase; mevaldate reductase (NADPH₂)

Systematic name: (*R*)-mevalonate:NADP⁺ oxidoreductase
Comments: May be identical with EC 1.1.1.2 [alcohol dehydrogenase (NADP⁺)].
References: [653, 4062]

[EC 1.1.1.33 created 1961]

EC 1.1.1.34

Accepted name: hydroxymethylglutaryl-CoA reductase (NADPH)
Reaction: (*R*)-mevalonate + CoA + 2 NADP⁺ = (*S*)-3-hydroxy-3-methylglutaryl-CoA + 2 NADPH + 2 H⁺
Other name(s): hydroxymethylglutaryl coenzyme A reductase (reduced nicotinamide adenine dinucleotide phosphate); 3-hydroxy-3-methylglutaryl-CoA reductase; β-hydroxy-β-methylglutaryl coenzyme A reductase; hydroxymethylglutaryl CoA reductase (NADPH); *S*-3-hydroxy-3-methylglutaryl-CoA reductase; NADPH-hydroxymethylglutaryl-CoA reductase; HMGC_oA reductase-mevalonate:NADP-oxidoreductase (acetylating-CoA); 3-hydroxy-3-methylglutaryl CoA reductase (NADPH); hydroxymethylglutaryl-CoA reductase (NADPH₂)
Systematic name: (*R*)-mevalonate:NADP⁺ oxidoreductase (CoA-acylating)
Comments: The enzyme is inactivated by EC 2.7.11.31 [hydroxymethylglutaryl-CoA reductase (NADPH)] kinase and reactivated by EC 3.1.3.47 [hydroxymethylglutaryl-CoA reductase (NADPH)]-phosphatase.
References: [439, 893, 1856]

[EC 1.1.1.34 created 1961]

EC 1.1.1.35

Accepted name: 3-hydroxyacyl-CoA dehydrogenase
Reaction: (*S*)-3-hydroxyacyl-CoA + NAD⁺ = 3-oxoacyl-CoA + NADH + H⁺
Other name(s): β-hydroxyacyl dehydrogenase; β-keto-reductase; 3-keto reductase; 3-hydroxyacyl coenzyme A dehydrogenase; β-hydroxyacyl-coenzyme A synthetase; β-hydroxyacylcoenzyme A dehydrogenase; β-hydroxybutyrylcoenzyme A dehydrogenase; 3-hydroxyacetyl-coenzyme A dehydrogenase; L-3-hydroxyacyl coenzyme A dehydrogenase; L-3-hydroxyacyl CoA dehydrogenase; β-hydroxyacyl CoA dehydrogenase; 3β-hydroxyacyl coenzyme A dehydrogenase; 3-hydroxybutyryl-CoA dehydrogenase; β-ketoacyl-CoA reductase; β-hydroxy acid dehydrogenase; 3-L-hydroxyacyl-CoA dehydrogenase; 3-hydroxyisobutyryl-CoA dehydrogenase; 1-specific DPN-linked β-hydroxybutyric dehydrogenase
Systematic name: (*S*)-3-hydroxyacyl-CoA:NAD⁺ oxidoreductase
Comments: Also oxidizes *S*-3-hydroxyacyl-*N*-acylthioethanolamine and *S*-3-hydroxyacyl-hydrolipoate. Some enzymes act, more slowly, with NADP⁺. Broad specificity to acyl chain-length (*cf.* EC 1.1.1.211 [long-chain-3-hydroxyacyl-CoA dehydrogenase]).
References: [1504, 2188, 3641, 4083]

[EC 1.1.1.35 created 1961]

EC 1.1.1.36

Accepted name: acetoacetyl-CoA reductase
Reaction: (*R*)-3-hydroxyacyl-CoA + NADP⁺ = 3-oxoacyl-CoA + NADPH + H⁺
Other name(s): acetoacetyl coenzyme A reductase; hydroxyacyl coenzyme-A dehydrogenase; NADP-linked acetoacetyl CoA reductase; NADPH:acetoacetyl-CoA reductase; D(-)-β-hydroxybutyryl CoA-NADP oxidoreductase; short chain β-ketoacetyl(acetoacetyl)-CoA reductase; β-ketoacyl-CoA reductase; D-3-hydroxyacyl-CoA reductase; (*R*)-3-hydroxyacyl-CoA dehydrogenase
Systematic name: (*R*)-3-hydroxyacyl-CoA:NADP⁺ oxidoreductase
References: [4082]

[EC 1.1.1.36 created 1961]

EC 1.1.1.37

Accepted name: malate dehydrogenase
Reaction: (S)-malate + NAD⁺ = oxaloacetate + NADH + H⁺
Other name(s): malic dehydrogenase; L-malate dehydrogenase; NAD-L-malate dehydrogenase; malic acid dehydrogenase; NAD-dependent malic dehydrogenase; NAD-malate dehydrogenase; NAD-malic dehydrogenase; malate (NAD) dehydrogenase; NAD-dependent malate dehydrogenase; NAD-specific malate dehydrogenase; NAD-linked malate dehydrogenase; MDH; L-malate-NAD⁺ oxidoreductase
Systematic name: (S)-malate:NAD⁺ oxidoreductase
Comments: Also oxidizes some other 2-hydroxydicarboxylic acids.
References: [188, 1309, 2492, 4239]

[EC 1.1.1.37 created 1961]

EC 1.1.1.38

Accepted name: malate dehydrogenase (oxaloacetate-decarboxylating)
Reaction: (1) (S)-malate + NAD⁺ = pyruvate + CO₂ + NADH
(2) oxaloacetate = pyruvate + CO₂
Other name(s): 'malic' enzyme (ambiguous); pyruvic-malic carboxylase (ambiguous); NAD⁺-specific malic enzyme; NAD⁺-malic enzyme; NAD⁺-linked malic enzyme
Systematic name: (S)-malate:NAD⁺ oxidoreductase (oxaloacetate-decarboxylating)
Comments: Unlike EC 1.1.1.39, malate dehydrogenase (decarboxylating), this enzyme can also decarboxylate oxaloacetate. *cf.* EC 1.1.1.40, malate dehydrogenase (oxaloacetate-decarboxylating) (NADP⁺).
References: [1853, 4305]

[EC 1.1.1.38 created 1961]

EC 1.1.1.39

Accepted name: malate dehydrogenase (decarboxylating)
Reaction: (S)-malate + NAD⁺ = pyruvate + CO₂ + NADH
Other name(s): 'malic' enzyme (ambiguous); pyruvic-malic carboxylase (ambiguous); NAD-specific malic enzyme (ambiguous); NAD-malic enzyme (ambiguous); malate dehydrogenase (decarboxylating) (ambiguous)
Systematic name: (S)-malate:NAD⁺ oxidoreductase (decarboxylating)
Comments: There are several forms of malate dehydrogenases that differ in their use of substrates and cofactors. This particular form is found only in the plant kingdom. Unlike EC 1.1.1.38, which catalyses a similar reaction, this enzyme can not bind oxaloacetate, and thus does not decarboxylate exogenously-added oxaloacetate. *cf.* EC 1.1.1.37, malate dehydrogenase; EC 1.1.1.38, malate dehydrogenase (oxaloacetate-decarboxylating); and EC 1.1.1.83, D-malate dehydrogenase (decarboxylating).
References: [2350, 1304, 4156, 4155]

[EC 1.1.1.39 created 1961]

EC 1.1.1.40

Accepted name: malate dehydrogenase (oxaloacetate-decarboxylating) (NADP⁺)
Reaction: (1) (S)-malate + NADP⁺ = pyruvate + CO₂ + NADPH
(2) oxaloacetate = pyruvate + CO₂
Other name(s): 'malic' enzyme (ambiguous); pyruvic-malic carboxylase (ambiguous); malate dehydrogenase (decarboxylating, NADP⁺); NADP⁺-linked decarboxylating malic enzyme; NADP⁺-malic enzyme; NADP⁺-specific malic enzyme; NADP⁺-specific malate dehydrogenase; malate dehydrogenase (NADP⁺, decarboxylating); L-malate:NADP⁺ oxidoreductase
Systematic name: (S)-malate:NADP⁺ oxidoreductase (oxaloacetate-decarboxylating)
Comments: The enzyme catalyses the oxidative decarboxylation of (S)-malate in the presence of NADP⁺ and divalent metal ions, and the decarboxylation of oxaloacetate. *cf.* EC 1.1.1.38, malate dehydrogenase (oxaloacetate-decarboxylating), and EC 1.1.1.39, malate dehydrogenase (decarboxylating).
References: [1392, 2839, 3265, 3645, 3646, 4086]

[EC 1.1.1.40 created 1961, modified 1976]

EC 1.1.1.41

- Accepted name:** isocitrate dehydrogenase (NAD⁺)
Reaction: isocitrate + NAD⁺ = 2-oxoglutarate + CO₂ + NADH
Other name(s): isocitric dehydrogenase; β-ketoglutaric-isocitric carboxylase; isocitric acid dehydrogenase; NAD dependent isocitrate dehydrogenase; NAD isocitrate dehydrogenase; NAD-linked isocitrate dehydrogenase; NAD-specific isocitrate dehydrogenase; NAD isocitric dehydrogenase; isocitrate dehydrogenase (NAD); IDH (ambiguous); nicotinamide adenine dinucleotide isocitrate dehydrogenase
- Systematic name:** isocitrate:NAD⁺ oxidoreductase (decarboxylating)
Comments: Requires Mn²⁺ or Mg²⁺ for activity. Unlike EC 1.1.1.42, isocitrate dehydrogenase (NADP⁺), oxalosuccinate cannot be used as a substrate. In eukaryotes, isocitrate dehydrogenase exists in two forms: an NAD⁺-linked enzyme found only in mitochondria and displaying allosteric properties, and a non-allosteric, NADP⁺-linked enzyme that is found in both mitochondria and cytoplasm [481]. The enzyme from some species can also use NADP⁺ but much more slowly [1651].
References: [1421, 2035, 3021, 3022, 3116, 4040, 481, 1926, 1651]

[EC 1.1.1.41 created 1961, modified 2005]

EC 1.1.1.42

- Accepted name:** isocitrate dehydrogenase (NADP⁺)
Reaction: isocitrate + NADP⁺ = 2-oxoglutarate + CO₂ + NADPH + H⁺ (overall reaction)
(1a) isocitrate + NADP⁺ = oxalosuccinate + NADPH + H⁺
(1b) oxalosuccinate = 2-oxoglutarate + CO₂
Other name(s): oxalosuccinate decarboxylase; oxalosuccinic decarboxylase; isocitrate (NADP) dehydrogenase; isocitrate (nicotinamide adenine dinucleotide phosphate) dehydrogenase; NADP-specific isocitrate dehydrogenase; NADP-linked isocitrate dehydrogenase; NADP-dependent isocitrate dehydrogenase; NADP isocitric dehydrogenase; isocitrate dehydrogenase (NADP-dependent); NADP-dependent isocitric dehydrogenase; triphosphopyridine nucleotide-linked isocitrate dehydrogenase-oxalosuccinate carboxylase; NADP⁺-linked isocitrate dehydrogenase; IDH (ambiguous); dual-cofactor-specific isocitrate dehydrogenase; NADP⁺-ICDH; NADP⁺-IDH; IDP; IDP1; IDP2; IDP3
- Systematic name:** isocitrate:NADP⁺ oxidoreductase (decarboxylating)
Comments: Requires Mn²⁺ or Mg²⁺ for activity. Unlike EC 1.1.1.41, isocitrate dehydrogenase (NAD⁺), oxalosuccinate can be used as a substrate. In eukaryotes, isocitrate dehydrogenase exists in two forms: an NAD⁺-linked enzyme found only in mitochondria and displaying allosteric properties, and a non-allosteric, NADP⁺-linked enzyme that is found in both mitochondria and cytoplasm [481]. The enzyme from some species can also use NAD⁺ but much more slowly [481, 3627].
References: [34, 2643, 3021, 3527, 4040, 481, 3627, 2001, 527]

[EC 1.1.1.42 created 1961, modified 2005]

EC 1.1.1.43

- Accepted name:** phosphogluconate 2-dehydrogenase
Reaction: 6-phospho-D-gluconate + NAD(P)⁺ = 6-phospho-2-dehydro-D-gluconate + NAD(P)H + H⁺
Other name(s): 6-phosphogluconic dehydrogenase; phosphogluconate dehydrogenase; gluconate 6-phosphate dehydrogenase; 6-phosphogluconate dehydrogenase (NAD); 2-keto-6-phosphogluconate reductase
- Systematic name:** 6-phospho-D-gluconate:NAD(P)⁺ 2-oxidoreductase
References: [1049]

[EC 1.1.1.43 created 1961]

EC 1.1.1.44

- Accepted name:** phosphogluconate dehydrogenase (NADP⁺-dependent, decarboxylating)

Reaction: 6-phospho-D-gluconate + NADP⁺ = D-ribulose 5-phosphate + CO₂ + NADPH + H⁺
Other name(s): phosphogluconic acid dehydrogenase; 6-phosphogluconic dehydrogenase; 6-phosphogluconic carboxylase; 6-phosphogluconate dehydrogenase (decarboxylating); 6-phospho-D-gluconate dehydrogenase
Systematic name: 6-phospho-D-gluconate:NADP⁺ 2-oxidoreductase (decarboxylating)
Comments: The enzyme participates in the oxidative branch of the pentose phosphate pathway, whose main purpose is to produce NADPH and pentose for biosynthetic reactions. Highly specific for NADP⁺. *cf.* EC 1.1.1.343, phosphogluconate dehydrogenase (NAD⁺-dependent, decarboxylating).
References: [816, 3038, 3416, 3417, 400, 4371, 4423]

[EC 1.1.1.44 created 1961, modified 2013]

EC 1.1.1.45

Accepted name: L-gulonate 3-dehydrogenase
Reaction: L-gulonate + NAD⁺ = 3-dehydro-L-gulonate + NADH + H⁺
Other name(s): L-3-aldonate dehydrogenase; L-3-aldonic dehydrogenase; L-gulonic acid dehydrogenase; L-β-hydroxyacid dehydrogenase; L-β-hydroxy-acid-NAD-oxidoreductase; L-3-hydroxyacid dehydrogenase
Systematic name: L-gulonate:NAD⁺ 3-oxidoreductase
Comments: Also oxidizes other L-3-hydroxyacids.
References: [896, 3555]

[EC 1.1.1.45 created 1961]

EC 1.1.1.46

Accepted name: L-arabinose 1-dehydrogenase
Reaction: L-arabinose + NAD⁺ = L-arabinono-1,4-lactone + NADH + H⁺
Systematic name: L-arabinose:NAD⁺ 1-oxidoreductase
References: [4164]

[EC 1.1.1.46 created 1961]

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⁺).
References: [189, 401, 2966, 3675, 3877, 1101]

[EC 1.1.1.47 created 1961, modified 2013]

EC 1.1.1.48

Accepted name: D-galactose 1-dehydrogenase
Reaction: D-galactose + NAD⁺ = D-galactono-1,4-lactone + NADH + H⁺
Other name(s): D-galactose dehydrogenase; β-galactose dehydrogenase (ambiguous); NAD⁺-dependent D-galactose dehydrogenase
Systematic name: D-galactose:NAD⁺ 1-oxidoreductase
Comments: This enzyme is part of the De Ley-Doudoroff pathway, which is used by some bacteria during growth on D-galactose.
References: [2220, 1588]

[EC 1.1.1.48 created 1961, modified 2011]

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⁺
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)⁺] and EC 1.1.1.388, glucose-6-phosphate dehydrogenase (NAD⁺).
References: [949, 1219, 1783, 2812, 2528, 2870, 1375, 1624, 1697, 606]

[EC 1.1.1.49 created 1961, modified 2013, modified 2015]

EC 1.1.1.50

- Accepted name:** 3 α -hydroxysteroid 3-dehydrogenase (*Si*-specific)
Reaction: a 3 α -hydroxysteroid + NAD(P)⁺ = a 3-oxosteroid + NAD(P)H + H⁺
Other name(s): hydroxyprostaglandin dehydrogenase; 3 α -hydroxysteroid oxidoreductase; sterognost 3 α ; 3 α -hydroxysteroid dehydrogenase (B-specific); 3 α -hydroxysteroid 3-dehydrogenase (B-specific); 3 α -hydroxysteroid:NAD(P)⁺ 3-oxidoreductase (B-specific)
Systematic name: 3 α -hydroxysteroid:NAD(P)⁺ 3-oxidoreductase (*Si*-specific)
Comments: The enzyme acts on androsterone and other 3 α -hydroxysteroids and on 9-, 11- and 15-hydroxyprostaglandin. *Si*-specific with respect to NAD⁺ or NADP⁺. *cf.* EC 1.1.1.213, 3 α -hydroxysteroid 3-dehydrogenase (*Re*-specific).
References: [1724, 1986, 2395, 2979]

[EC 1.1.1.50 created 1961, modified 1986, modified 1990, modified 2012, modified 2013]

EC 1.1.1.51

- Accepted name:** 3(or 17) β -hydroxysteroid dehydrogenase
Reaction: testosterone + NAD(P)⁺ = androstenedione + NAD(P)H + H⁺
Other name(s): β -hydroxy steroid dehydrogenase; 17-ketoreductase; 17 β -hydroxy steroid dehydrogenase; 3 β -hydroxysteroid dehydrogenase; 3 β -hydroxy steroid dehydrogenase
Systematic name: 3(or 17) β -hydroxysteroid:NAD(P)⁺ oxidoreductase
Comments: Also acts on other 3 β - or 17 β -hydroxysteroids. *cf.* EC 1.1.1.209 3(or 17) α -hydroxysteroid dehydrogenase.
References: [720, 2326, 2395, 3400, 3798]

[EC 1.1.1.51 created 1961]

EC 1.1.1.52

- Accepted name:** 3 α -hydroxycho lanate dehydrogenase (NAD⁺)
Reaction: lithocholate + NAD⁺ = 3-oxo-5 β -cholan-24-oate + NADH + H⁺
Other name(s): α -hydroxy-cho lanate dehydrogenase; lithocholate:NAD⁺ oxidoreductase; 3 α -hydroxycho lanate dehydrogenase
Systematic name: lithocholate:NAD⁺ 3-oxidoreductase
Comments: Also acts on other 3 α -hydroxysteroids with an acidic side-chain. *cf.* EC 1.1.1.392, 3 α -hydroxycho lanate dehydrogenase (NADP⁺).
References: [1434]

[EC 1.1.1.52 created 1961, modified 1976, modified 2016]

EC 1.1.1.53

Accepted name: 3 α (or 20 β)-hydroxysteroid dehydrogenase
Reaction: androstan-3 α ,17 β -diol + NAD⁺ = 17 β -hydroxyandrostan-3-one + NADH + H⁺
Other name(s): cortisone reductase; (*R*)-20-hydroxysteroid dehydrogenase; dehydrogenase, 20 β -hydroxy steroid; Δ^4 -3-ketosteroid hydrogenase; 20 β -hydroxysteroid dehydrogenase; 3 α ,20 β -hydroxysteroid:NAD⁺-oxidoreductase; NADH-20 β -hydroxysteroid dehydrogenase; 20 β -HSD
Systematic name: 3 α (or 20 β)-hydroxysteroid:NAD⁺ oxidoreductase
Comments: The 3 α -hydroxy group or 20 β -hydroxy group of pregnane and androstane steroids can act as donor.
References: [923, 1600, 1601, 2326, 3679, 3762]

[EC 1.1.1.53 created 1961, modified 1986]

EC 1.1.1.54

Accepted name: allyl-alcohol dehydrogenase
Reaction: allyl alcohol + NADP⁺ = acrolein + NADPH + H⁺
Systematic name: allyl-alcohol:NADP⁺ oxidoreductase
Comments: Also acts on saturated primary alcohols.
References: [2910]

[EC 1.1.1.54 created 1965]

EC 1.1.1.55

Accepted name: lactaldehyde reductase (NADPH)
Reaction: propane-1,2-diol + NADP⁺ = L-lactaldehyde + NADPH + H⁺
Other name(s): lactaldehyde (reduced nicotinamide adenine dinucleotide phosphate) reductase; NADP-1,2-propanediol dehydrogenase; propanediol dehydrogenase; 1,2-propanediol:NADP⁺ oxidoreductase; lactaldehyde reductase (NADPH₂)
Systematic name: propane-1,2-diol:NADP⁺ oxidoreductase
Comments: May be identical with EC 1.1.1.2 alcohol dehydrogenase (NADP⁺).
References: [1319]

[EC 1.1.1.55 created 1965]

EC 1.1.1.56

Accepted name: ribitol 2-dehydrogenase
Reaction: ribitol + NAD⁺ = D-ribulose + NADH + H⁺
Other name(s): adonitol dehydrogenase; ribitol dehydrogenase A (wild type); ribitol dehydrogenase B (mutant enzyme with different properties); ribitol dehydrogenase D (mutant enzyme with different properties)
Systematic name: ribitol:NAD⁺ 2-oxidoreductase
References: [1544, 2817, 4250]

[EC 1.1.1.56 created 1965]

EC 1.1.1.57

Accepted name: fructuronate reductase
Reaction: D-mannonate + NAD⁺ = D-fructuronate + NADH + H⁺
Other name(s): mannonate oxidoreductase; mannonic dehydrogenase; D-mannonate dehydrogenase; D-mannonate:NAD oxidoreductase
Systematic name: D-mannonate:NAD⁺ 5-oxidoreductase
Comments: Also reduces D-tagaturonate.
References: [1490, 1905]

[EC 1.1.1.57 created 1965]

EC 1.1.1.58

Accepted name: tagaturonate reductase
Reaction: D-altronate + NAD⁺ = D-tagaturonate + NADH + H⁺
Other name(s): altronic oxidoreductase; altronate oxidoreductase; TagUAR; altronate dehydrogenase; D-tagaturonate reductase
Systematic name: D-altronate:NAD⁺ 3-oxidoreductase
References: [1490]

[EC 1.1.1.58 created 1965]

EC 1.1.1.59

Accepted name: 3-hydroxypropionate dehydrogenase
Reaction: 3-hydroxypropanoate + NAD⁺ = 3-oxopropanoate + NADH + H⁺
Systematic name: 3-hydroxypropanoate:NAD⁺ oxidoreductase
References: [792]

[EC 1.1.1.59 created 1965]

EC 1.1.1.60

Accepted name: 2-hydroxy-3-oxopropionate reductase
Reaction: D-glycerate + NAD(P)⁺ = 2-hydroxy-3-oxopropanoate + NAD(P)H + H⁺
Other name(s): tartronate semialdehyde reductase; (*R*)-glycerate:NAD(P)⁺ oxidoreductase
Systematic name: D-glycerate:NAD(P)⁺ oxidoreductase
References: [1249]

[EC 1.1.1.60 created 1965]

EC 1.1.1.61

Accepted name: 4-hydroxybutyrate dehydrogenase
Reaction: 4-hydroxybutanoate + NAD⁺ = succinate semialdehyde + NADH + H⁺
Other name(s): γ-hydroxybutyrate dehydrogenase
Systematic name: 4-hydroxybutanoate:NAD⁺ oxidoreductase
References: [2790]

[EC 1.1.1.61 created 1965]

EC 1.1.1.62

Accepted name: 17β-estradiol 17-dehydrogenase
Reaction: 17β-estradiol + NAD(P)⁺ = estrone + NAD(P)H + H⁺
Other name(s): 20α-hydroxysteroid dehydrogenase; 17β,20α-hydroxysteroid dehydrogenase; 17β-estradiol dehydrogenase; estradiol dehydrogenase; estrogen 17-oxidoreductase; 17β-HSD; HSD17B7
Systematic name: 17β-estradiol:NAD(P)⁺ 17-oxidoreductase
Comments: The enzyme oxidizes or reduces the hydroxy/keto group on C₁₇ of estrogens and androgens in mammals and regulates the biological potency of these steroids. The mammalian enzyme is bifunctional and also catalyses EC 1.1.1.270, 3β-hydroxysteroid 3-dehydrogenase [2398]. The enzyme also acts on (*S*)-20-hydroxypregn-4-en-3-one and related compounds, oxidizing the (*S*)-20-group, but unlike EC 1.1.1.149, 20α-hydroxysteroid dehydrogenase, it is *Si*-specific with respect to NAD(P)⁺.
References: [1855, 2133, 2398]

[EC 1.1.1.62 created 1965, modified 1983, modified 1986, modified 2012]

[1.1.1.63 Transferred entry. testosterone 17 β -dehydrogenase. Now EC 1.1.1.239, 3 α (17 β)-hydroxysteroid dehydrogenase (NAD⁺)]

[EC 1.1.1.63 created 1965, deleted 2012]

EC 1.1.1.64

Accepted name: testosterone 17 β -dehydrogenase (NADP⁺)
Reaction: testosterone + NADP⁺ = androstenedione + NADPH + H⁺
Other name(s): 17-ketoreductase; NADP-dependent testosterone-17 β -oxidoreductase; testosterone 17 β -dehydrogenase (NADP)
Systematic name: 17 β -hydroxysteroid:NADP⁺ 17-oxidoreductase
Comments: Also oxidizes 3-hydroxyhexobarbital to 3-oxohexobarbital.
References: [946, 3761, 4046]

[EC 1.1.1.64 created 1965]

EC 1.1.1.65

Accepted name: pyridoxine 4-dehydrogenase
Reaction: pyridoxine + NADP⁺ = pyridoxal + NADPH + H⁺
Other name(s): pyridoxin dehydrogenase; pyridoxol dehydrogenase; pyridoxine dehydrogenase
Systematic name: pyridoxine:NADP⁺ 4-oxidoreductase
Comments: Also oxidizes pyridoxine phosphate.
References: [1552]

[EC 1.1.1.65 created 1965, modified 1976]

EC 1.1.1.66

Accepted name: ω -hydroxydecanoate dehydrogenase
Reaction: 10-hydroxydecanoate + NAD⁺ = 10-oxodecanoate + NADH + H⁺
Systematic name: 10-hydroxydecanoate:NAD⁺ 10-oxidoreductase
Comments: Also acts, more slowly, on 9-hydroxynonanoate and 11-hydroxyundecanoate.
References: [1803, 2569]

[EC 1.1.1.66 created 1965]

EC 1.1.1.67

Accepted name: mannitol 2-dehydrogenase
Reaction: D-mannitol + NAD⁺ = D-fructose + NADH + H⁺
Other name(s): D-mannitol dehydrogenase; mannitol dehydrogenase
Systematic name: D-mannitol:NAD⁺ 2-oxidoreductase
References: [2417]

[EC 1.1.1.67 created 1965]

[1.1.1.68 Transferred entry. 5,10-methylenetetrahydrofolate reductase. Now EC 1.5.1.20, methylenetetrahydrofolate reductase [NAD(P)H]]

[EC 1.1.1.68 created 1965, deleted 1978 [transferred to EC 1.1.99.15, deleted 1980]]

EC 1.1.1.69

Accepted name: gluconate 5-dehydrogenase
Reaction: D-gluconate + NAD(P)⁺ = 5-dehydro-D-gluconate + NAD(P)H + H⁺
Other name(s): 5-keto-D-gluconate 5-reductase; 5-keto-D-gluconate 5-reductase; 5-ketogluconate 5-reductase; 5-ketogluconate reductase; 5-keto-D-gluconate reductase

Systematic name: D-gluconate:NAD(P)⁺ 5-oxidoreductase

References: [69, 2219, 2862]

[EC 1.1.1.69 created 1965, modified 1976]

[1.1.1.70 Deleted entry. D-glucuronolactone dehydrogenase. Now included with EC 1.2.1.3 aldehyde dehydrogenase (NAD⁺)]

[EC 1.1.1.70 created 1965, deleted 1978]

EC 1.1.1.71

Accepted name: alcohol dehydrogenase [NAD(P)⁺]

Reaction: an alcohol + NAD(P)⁺ = an aldehyde + NAD(P)H + H⁺

Other name(s): retinal reductase (ambiguous); aldehyde reductase (NADPH/NADH); alcohol dehydrogenase [NAD(P)]

Systematic name: alcohol:NAD(P)⁺ oxidoreductase

Comments: Reduces aliphatic aldehydes of carbon chain length from 2 to 14, with greatest activity on C₄, C₆ and C₈ aldehydes; also reduces retinal to retinol.

References: [1009]

[EC 1.1.1.71 created 1972]

EC 1.1.1.72

Accepted name: glycerol dehydrogenase (NADP⁺)

Reaction: glycerol + NADP⁺ = D-glyceraldehyde + NADPH + H⁺

Other name(s): glycerol dehydrogenase (NADP)

Systematic name: glycerol:NADP⁺ oxidoreductase

References: [2034, 3900]

[EC 1.1.1.72 created 1972]

EC 1.1.1.73

Accepted name: octanol dehydrogenase

Reaction: octan-1-ol + NAD⁺ = octanal + NADH + H⁺

Other name(s): 1-octanol dehydrogenase; octanol:NAD⁺ oxidoreductase

Systematic name: octan-1-ol:NAD⁺ oxidoreductase

Comments: Acts, less rapidly, on other long-chain alcohols.

References: [3206]

[EC 1.1.1.73 created 1972]

[1.1.1.74 Deleted entry. D-aminopropanol dehydrogenase (reaction due to EC 1.1.1.4 (R,R)-butanediol dehydrogenase)]

[EC 1.1.1.74 created 1972, deleted 1976]

EC 1.1.1.75

Accepted name: (R)-aminopropanol dehydrogenase

Reaction: (R)-1-aminopropan-2-ol + NAD⁺ = aminoacetone + NADH + H⁺

Other name(s): L-aminopropanol dehydrogenase; 1-aminopropan-2-ol-NAD⁺ dehydrogenase; L(+)-1-aminopropan-2-ol:NAD⁺ oxidoreductase; 1-aminopropan-2-ol-dehydrogenase; DL-1-aminopropan-2-ol: NAD⁺ dehydrogenase; L(+)-1-aminopropan-2-ol-NAD/NADP oxidoreductase

Systematic name: (R)-1-aminopropan-2-ol:NAD⁺ oxidoreductase

Comments: Requires K⁺.

References: [781, 3950, 3951]

[EC 1.1.1.75 created 1972]

EC 1.1.1.76

Accepted name: (*S,S*)-butanediol dehydrogenase
Reaction: (2*S,3S*)-butane-2,3-diol + NAD⁺ = (*S*)-acetoin + NADH + H⁺
Other name(s): L-butanediol dehydrogenase; L-BDH; L(+)-2,3-butanediol dehydrogenase (L-acetoin forming); (*S*)-acetoin reductase [(*S,S*)-butane-2,3-diol forming]
Systematic name: (*S,S*)-butane-2,3-diol:NAD⁺ oxidoreductase
Comments: This enzyme catalyses the reversible reduction of (*S*)-acetoin to (*S,S*)-butane-2,3-diol. It can also catalyse the irreversible reduction of diacetyl to (*S*)-acetoin.
References: [3834, 501, 3797]

[EC 1.1.1.76 created 1972, modified 2010]

EC 1.1.1.77

Accepted name: lactaldehyde reductase
Reaction: (*R*)[or (*S*)]-propane-1,2-diol + NAD⁺ = (*R*)[or (*S*)]-lactaldehyde + NADH + H⁺
Other name(s): propanediol:nicotinamide adenine dinucleotide (NAD) oxidoreductase; L-lactaldehyde:propanediol oxidoreductase
Systematic name: (*R*)[or (*S*)]-propane-1,2-diol:NAD⁺ oxidoreductase
References: [3893]

[EC 1.1.1.77 created 1972]

EC 1.1.1.78

Accepted name: methylglyoxal reductase (NADH)
Reaction: (*R*)-lactaldehyde + NAD⁺ = 2-oxopropanal + NADH + H⁺
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), by its coenzyme requirement, reaction direction, and enantiomeric preference.
References: [3892, 3140]

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

EC 1.1.1.79

Accepted name: glyoxylate reductase (NADP⁺)
Reaction: glycolate + NADP⁺ = glyoxylate + NADPH + H⁺
Other name(s): NADPH-glyoxylate reductase; glyoxylate reductase (NADP)
Systematic name: glycolate:NADP⁺ oxidoreductase
Comments: Also reduces hydroxypyruvate to glycerate; has some affinity for NAD⁺.
References: [514, 1962]

[EC 1.1.1.79 created 1972]

EC 1.1.1.80

Accepted name: isopropanol dehydrogenase (NADP⁺)
Reaction: propan-2-ol + NADP⁺ = acetone + NADPH + H⁺
Other name(s): isopropanol dehydrogenase (NADP)
Systematic name: propan-2-ol:NADP⁺ oxidoreductase
Comments: Also acts on other short-chain secondary alcohols and, slowly, on primary alcohols.
References: [1577, 1578]

[EC 1.1.1.80 created 1972]

EC 1.1.1.81

Accepted name: hydroxypyruvate reductase
Reaction: D-glycerate + NAD(P)⁺ = hydroxypyruvate + NAD(P)H + H⁺
Other name(s): β-hydroxypyruvate reductase; NADH:hydroxypyruvate reductase; D-glycerate dehydrogenase
Systematic name: D-glycerate:NADP⁺ 2-oxidoreductase
References: [1960, 1961, 2006]

[EC 1.1.1.81 created 1972]

EC 1.1.1.82

Accepted name: malate dehydrogenase (NADP⁺)
Reaction: (S)-malate + NADP⁺ = oxaloacetate + NADPH + H⁺
Other name(s): NADP-malic enzyme; NADP-malate dehydrogenase; malic dehydrogenase (nicotinamide adenine dinucleotide phosphate); malate NADP dehydrogenase; NADP malate dehydrogenase; NADP-linked malate dehydrogenase; malate dehydrogenase (NADP)
Systematic name: (S)-malate:NADP⁺ oxidoreductase
Comments: Activated by light.
References: [649, 1758, 1759]

[EC 1.1.1.82 created 1972]

EC 1.1.1.83

Accepted name: D-malate dehydrogenase (decarboxylating)
Reaction: (R)-malate + NAD⁺ = pyruvate + CO₂ + NADH
Other name(s): D-malate dehydrogenase; D-malic enzyme; bifunctional L(+)-tartrate dehydrogenase-D(+)-malate (decarboxylating)
Systematic name: (R)-malate:NAD⁺ oxidoreductase (decarboxylating)
References: [3642]

[EC 1.1.1.83 created 1972]

EC 1.1.1.84

Accepted name: dimethylmalate dehydrogenase
Reaction: (R)-3,3-dimethylmalate + NAD⁺ = 3-methyl-2-oxobutanoate + CO₂ + NADH
Other name(s): β,β-dimethylmalate dehydrogenase
Systematic name: (R)-3,3-dimethylmalate:NAD⁺ oxidoreductase (decarboxylating)
Comments: Requires K⁺ or NH₄⁺ and Mn²⁺ or Co²⁺; also acts on (R)-malate.
References: [2360]

[EC 1.1.1.84 created 1972]

EC 1.1.1.85

Accepted name: 3-isopropylmalate dehydrogenase
Reaction: (2R,3S)-3-isopropylmalate + NAD⁺ = 4-methyl-2-oxopentanoate + CO₂ + NADH + H⁺ (overall reaction)
(1a) (2R,3S)-3-isopropylmalate + NAD⁺ = (2S)-2-isopropyl-3-oxosuccinate + NADH + H⁺
(1b) (2S)-2-isopropyl-3-oxosuccinate = 4-methyl-2-oxopentanoate + CO₂ (spontaneous)
Other name(s): β-isopropylmalic enzyme; β-isopropylmalate dehydrogenase; *threo*-D₅-3-isopropylmalate dehydrogenase; 3-carboxy-2-hydroxy-4-methylpentanoate:NAD⁺ oxidoreductase
Systematic name: (2R,3S)-3-isopropylmalate:NAD⁺ oxidoreductase

Comments: The product decarboxylates spontaneously to yield 4-methyl-2-oxopentanoate.

References: [451, 2949, 2762, 480]

[EC 1.1.1.85 created 1972, modified 1976]

EC 1.1.1.86

Accepted name: ketol-acid reductoisomerase (NADP⁺)

Reaction: (2*R*)-2,3-dihydroxy-3-methylbutanoate + NADP⁺ = (2*S*)-2-hydroxy-2-methyl-3-oxobutanoate + NADPH + H⁺

Other name(s): dihydroxyisovalerate dehydrogenase (isomerizing); acetoxy acid isomeroreductase; ketol acid reductoisomerase; α-keto-β-hydroxyacyl reductoisomerase; 2-hydroxy-3-keto acid reductoisomerase; acetoxy acid reductoisomerase; acetolactate reductoisomerase; dihydroxyisovalerate (isomerizing) dehydrogenase; isomeroreductase; reductoisomerase; ketol-acid reductoisomerase; (*R*)-2,3-dihydroxy-3-methylbutanoate:NADP⁺ oxidoreductase (isomerizing)

Systematic name: (2*R*)-2,3-dihydroxy-3-methylbutanoate:NADP⁺ oxidoreductase (isomerizing)

Comments: Also catalyses the reduction of 2-ethyl-2-hydroxy-3-oxobutanoate to 2,3-dihydroxy-3-methylpentanoate. The enzyme, found in many bacteria and archaea, is specific for NADPH (*cf.* EC 1.1.1.382, ketol-acid reductoisomerase (NAD⁺) and EC 1.1.1.383, ketol-acid reductoisomerase [NAD(P)⁺]).

References: [118, 1501, 1938, 3324, 403]

[EC 1.1.1.86 created 1972, modified 1976, modified 1981 (EC 1.1.1.89 created 1972, incorporated 1976), modified 2015]

EC 1.1.1.87

Accepted name: homoisocitrate dehydrogenase

Reaction: (1*R*,2*S*)-1-hydroxybutane-1,2,4-tricarboxylate + NAD⁺ = 2-oxoadipate + CO₂ + NADH + H⁺

Other name(s): 2-hydroxy-3-carboxyadipate dehydrogenase; 3-carboxy-2-hydroxyadipate dehydrogenase; homoisocitric dehydrogenase; (-)-1-hydroxy-1,2,4-butanetricarboxylate:NAD⁺ oxidoreductase (decarboxylating); 3-carboxy-2-hydroxyadipate:NAD⁺ oxidoreductase (decarboxylating); HICDH

Systematic name: (1*R*,2*S*)-1-hydroxybutane-1,2,4-tricarboxylate:NAD⁺ oxidoreductase (decarboxylating)

Comments: Forms part of the lysine biosynthesis pathway in fungi [4418].

References: [3669, 3243, 4418]

[EC 1.1.1.87 created 1972 (EC 1.1.1.155 created 1976, incorporated 2004)]

EC 1.1.1.88

Accepted name: hydroxymethylglutaryl-CoA reductase

Reaction: (*R*)-mevalonate + CoA + 2 NAD⁺ = 3-hydroxy-3-methylglutaryl-CoA + 2 NADH + 2 H⁺

Other name(s): β-hydroxy-β-methylglutaryl coenzyme A reductase; β-hydroxy-β-methylglutaryl CoA-reductase; 3-hydroxy-3-methylglutaryl coenzyme A reductase; hydroxymethylglutaryl coenzyme A reductase

Systematic name: (*R*)-mevalonate:NAD⁺ oxidoreductase (CoA-acylating)

References: [1017]

[EC 1.1.1.88 created 1972, modified 2002]

[1.1.1.89 Deleted entry. dihydroxyisovalerate dehydrogenase (isomerizing). Now included with EC 1.1.1.86 ketol-acid reductoisomerase]

[EC 1.1.1.89 created 1972, deleted 1976]

EC 1.1.1.90

Accepted name: aryl-alcohol dehydrogenase

Reaction: an aromatic alcohol + NAD⁺ = an aromatic aldehyde + NADH + H⁺

Other name(s): *p*-hydroxybenzyl alcohol dehydrogenase; benzyl alcohol dehydrogenase; coniferyl alcohol dehydrogenase
Systematic name: aryl-alcohol:NAD⁺ oxidoreductase
Comments: A group of enzymes with broad specificity towards primary alcohols with an aromatic or cyclohex-1-ene ring, but with low or no activity towards short-chain aliphatic alcohols.
References: [3720, 4321]

[EC 1.1.1.90 created 1972, modified 1989]

EC 1.1.1.91

Accepted name: aryl-alcohol dehydrogenase (NADP⁺)
Reaction: an aromatic alcohol + NADP⁺ = an aromatic aldehyde + NADPH + H⁺
Other name(s): aryl alcohol dehydrogenase (nicotinamide adenine dinucleotide phosphate); coniferyl alcohol dehydrogenase; NADPH-linked benzaldehyde reductase; aryl-alcohol dehydrogenase (NADP)
Systematic name: aryl-alcohol:NADP⁺ oxidoreductase
Comments: Also acts on some aliphatic aldehydes, but cinnamaldehyde was the best substrate found.
References: [1300]

[EC 1.1.1.91 created 1972]

EC 1.1.1.92

Accepted name: oxaloglycolate reductase (decarboxylating)
Reaction: D-glycerate + NAD(P)⁺ + CO₂ = 2-hydroxy-3-oxosuccinate + NAD(P)H + 2 H⁺
Systematic name: D-glycerate:NAD(P)⁺ oxidoreductase (carboxylating)
Comments: Also reduces hydroxypyruvate to D-glycerate and glyoxylate to glycolate.
References: [2005]

[EC 1.1.1.92 created 1972]

EC 1.1.1.93

Accepted name: tartrate dehydrogenase
Reaction: tartrate + NAD⁺ = oxaloglycolate + NADH + H⁺
Other name(s): mesotartrate dehydrogenase
Systematic name: tartrate:NAD⁺ oxidoreductase
Comments: *meso*-tartrate and (*R,R*)-tartrate act as substrates. Requires Mn²⁺ and a monovalent cation.
References: [2008]

[EC 1.1.1.93 created 1972]

EC 1.1.1.94

Accepted name: glycerol-3-phosphate dehydrogenase [NAD(P)⁺]
Reaction: *sn*-glycerol 3-phosphate + NAD(P)⁺ = glycerone phosphate + NAD(P)H + H⁺
Other name(s): L-glycerol-3-phosphate:NAD(P) oxidoreductase; glycerol phosphate dehydrogenase (nicotinamide adenine dinucleotide (phosphate)); glycerol 3-phosphate dehydrogenase (NADP); glycerol-3-phosphate dehydrogenase [NAD(P)]
Systematic name: *sn*-glycerol-3-phosphate:NAD(P)⁺ 2-oxidoreductase
Comments: The enzyme from *Escherichia coli* shows specificity for the B side of NADPH.
References: [1950, 917, 918, 919]

[EC 1.1.1.94 created 1972, modified 2005]

EC 1.1.1.95

Accepted name: phosphoglycerate dehydrogenase
Reaction: 3-phospho-D-glycerate + NAD⁺ = 3-phosphooxypyruvate + NADH + H⁺
Other name(s): PHGDH (gene name); D-3-phosphoglycerate:NAD⁺ oxidoreductase; α-phosphoglycerate dehydrogenase; 3-phosphoglycerate dehydrogenase; 3-phosphoglyceric acid dehydrogenase; D-3-phosphoglycerate dehydrogenase; glycerate 3-phosphate dehydrogenase; glycerate-1,3-phosphate dehydrogenase; phosphoglycerate oxidoreductase; phosphoglyceric acid dehydrogenase; SerA; 3-phosphoglycerate:NAD⁺ 2-oxidoreductase; SerA 3PG dehydrogenase; 3PHP reductase
Systematic name: 3-phospho-D-glycerate:NAD⁺ 2-oxidoreductase
Comments: This enzyme catalyses the first committed and rate-limiting step in the phosphoserine pathway of serine biosynthesis. The reaction occurs predominantly in the direction of reduction. The enzyme from the bacterium *Escherichia coli* also catalyses the activity of EC 1.1.1.399, 2-oxoglutarate reductase [4459].
References: [3018, 4098, 3550, 3710, 3397, 4459, 8, 810]

[EC 1.1.1.95 created 1972, modified 2006, modified 2016]

EC 1.1.1.96

Accepted name: diiodophenylpyruvate reductase
Reaction: 3-(3,5-diiodo-4-hydroxyphenyl)lactate + NAD⁺ = 3-(3,5-diiodo-4-hydroxyphenyl)pyruvate + NADH + H⁺
Other name(s): aromatic α-keto acid; KAR; 2-oxo acid reductase
Systematic name: 3-(3,5-diiodo-4-hydroxyphenyl)lactate:NAD⁺ oxidoreductase
Comments: Substrates contain an aromatic ring with a pyruvate side chain. The most active substrates are halogenated derivatives. Compounds with hydroxy or amino groups in the 3 or 5 position are inactive.
References: [4426]

[EC 1.1.1.96 created 1972]

EC 1.1.1.97

Accepted name: 3-hydroxybenzyl-alcohol dehydrogenase
Reaction: 3-hydroxybenzyl alcohol + NADP⁺ = 3-hydroxybenzaldehyde + NADPH + H⁺
Other name(s): *m*-hydroxybenzyl alcohol dehydrogenase; *m*-hydroxybenzyl alcohol (NADP) dehydrogenase; *m*-hydroxybenzylalcohol dehydrogenase
Systematic name: 3-hydroxybenzyl-alcohol:NADP⁺ oxidoreductase
References: [1037]

[EC 1.1.1.97 created 1972]

EC 1.1.1.98

Accepted name: (*R*)-2-hydroxy-fatty-acid dehydrogenase
Reaction: (*R*)-2-hydroxystearate + NAD⁺ = 2-oxostearate + NADH + H⁺
Other name(s): D-2-hydroxy fatty acid dehydrogenase; 2-hydroxy fatty acid oxidase
Systematic name: (*R*)-2-hydroxystearate:NAD⁺ oxidoreductase
References: [2212]

[EC 1.1.1.98 created 1972]

EC 1.1.1.99

Accepted name: (*S*)-2-hydroxy-fatty-acid dehydrogenase
Reaction: (*S*)-2-hydroxystearate + NAD⁺ = 2-oxostearate + NADH + H⁺
Other name(s): dehydrogenase, L-2-hydroxy fatty acid; L-2-hydroxy fatty acid dehydrogenase; 2-hydroxy fatty acid oxidase
Systematic name: (*S*)-2-hydroxystearate:NAD⁺ oxidoreductase
References: [2212]

[EC 1.1.1.99 created 1972]

EC 1.1.1.100

- Accepted name:** 3-oxoacyl-[acyl-carrier-protein] reductase
Reaction: a (3*R*)-3-hydroxyacyl-[acyl-carrier protein] + NADP⁺ = a 3-oxoacyl-[acyl-carrier protein] + NADPH + H⁺
Other name(s): β-ketoacyl-[acyl-carrier protein](ACP) reductase; β-ketoacyl acyl carrier protein (ACP) reductase; β-ketoacyl reductase; β-ketoacyl thioester reductase; β-ketoacyl-ACP reductase; β-ketoacyl-acyl carrier protein reductase; 3-ketoacyl acyl carrier protein reductase; NADPH-specific 3-oxoacyl-[acyl carrier protein] reductase; 3-oxoacyl-[ACP] reductase; (3*R*)-3-hydroxyacyl-[acyl-carrier-protein]:NADP⁺ oxidoreductase
Systematic name: (3*R*)-3-hydroxyacyl-[acyl-carrier protein]:NADP⁺ oxidoreductase
Comments: Exhibits a marked preference for acyl-carrier-protein derivatives over CoA derivatives as substrates.
References: [3058, 3496, 3913]

[EC 1.1.1.100 created 1972, modified 1976]

EC 1.1.1.101

- Accepted name:** acylglycerone-phosphate reductase
Reaction: 1-palmitoylglycerol 3-phosphate + NADP⁺ = palmitoylglycerone phosphate + NADPH + H⁺
Other name(s): palmitoyldihydroxyacetone-phosphate reductase; palmitoyl dihydroxyacetone phosphate reductase; palmitoyl-dihydroxyacetone-phosphate reductase; acyldihydroxyacetone phosphate reductase; palmitoyl dihydroxyacetone phosphate reductase
Systematic name: 1-palmitoylglycerol-3-phosphate:NADP⁺ oxidoreductase
Comments: Also acts on alkylglycerone 3-phosphate and alkylglycerol 3-phosphate.
References: [2108]

[EC 1.1.1.101 created 1972, modified 1976]

EC 1.1.1.102

- Accepted name:** 3-dehydrosphinganine reductase
Reaction: sphinganine + NADP⁺ = 3-dehydrosphinganine + NADPH + H⁺
Other name(s): D-3-dehydrosphinganine reductase; D-3-oxosphinganine reductase; DSR; 3-oxosphinganine reductase; 3-oxosphinganine:NADPH oxidoreductase; D-3-oxosphinganine:B-NADPH oxidoreductase
Systematic name: D-erythro-dihydrosphingosine:NADP⁺ 3-oxidoreductase
References: [3656, 3657]

[EC 1.1.1.102 created 1972]

EC 1.1.1.103

- Accepted name:** L-threonine 3-dehydrogenase
Reaction: L-threonine + NAD⁺ = L-2-amino-3-oxobutanoate + NADH + H⁺
Other name(s): L-threonine dehydrogenase; threonine 3-dehydrogenase; threonine dehydrogenase; TDH
Systematic name: L-threonine:NAD⁺ oxidoreductase
Comments: This enzyme acts in concert with EC 2.3.1.29, glycine C-acetyltransferase, in the degradation of threonine to glycine. This threonine-degradation pathway is common to prokaryotic and eukaryotic cells and the two enzymes involved form a complex [1402]. In aqueous solution, the product L-2-amino-3-oxobutanoate can spontaneously decarboxylate to form aminoacetone.
References: [1272, 1402, 2774, 959]

[EC 1.1.1.103 created 1972]

EC 1.1.1.104

Accepted name: 4-oxoproline reductase
Reaction: 4-hydroxy-L-proline + NAD⁺ = 4-oxoproline + NADH + H⁺
Other name(s): hydroxy-L-proline oxidase
Systematic name: 4-hydroxy-L-proline:NAD⁺ oxidoreductase
References: [3566]

[EC 1.1.1.104 created 1972]

EC 1.1.1.105

Accepted name: *all-trans*-retinol dehydrogenase (NAD⁺)
Reaction: *all-trans*-retinol—[cellular-retinol-binding-protein] + NAD⁺ = *all-trans*-retinal—[cellular-retinol-binding-protein] + NADH + H⁺
Other name(s): retinol (vitamin A₁) dehydrogenase; MDR; microsomal retinol dehydrogenase; retinol dehydrogenase (misleading); retinal reductase (ambiguous); retinene reductase; epidermal retinol dehydrogenase 2; SDR16C5 (gene name); RDH16 (gene name)
Systematic name: *all-trans* retinol:NAD⁺ oxidoreductase
Comments: The enzyme recognizes *all-trans*-retinol and *all-trans*-retinal as substrates and exhibits a strong preference for NAD⁺/NADH as cofactors. Recognizes the substrate both in free form and when bound to cellular-retinol-binding-protein (CRBP1), but has higher affinity for the bound form [1252]. No activity with 11-*cis*-retinol or 11-*cis*-retinal (*cf.* EC 1.1.1.315, 11-*cis* retinol dehydrogenase). Also active with 3 α -hydroxysteroids [1252].
References: [1995, 1252, 2465, 2178]

[EC 1.1.1.105 created 1972, modified 2011]

EC 1.1.1.106

Accepted name: pantoate 4-dehydrogenase
Reaction: (*R*)-pantoate + NAD⁺ = (*R*)-4-dehydropantoate + NADH + H⁺
Other name(s): pantoate dehydrogenase; pantothenase; D-pantoate:NAD⁺ 4-oxidoreductase
Systematic name: (*R*)-pantoate:NAD⁺ 4-oxidoreductase
References: [1241]

[EC 1.1.1.106 created 1972, modified 1976]

EC 1.1.1.107

Accepted name: pyridoxal 4-dehydrogenase
Reaction: pyridoxal + NAD⁺ = 4-pyridoxolactone + NADH + H⁺
Other name(s): pyridoxal dehydrogenase
Systematic name: pyridoxal:NAD⁺ 4-oxidoreductase
Comments: The enzyme acts on the hemiacetal form of the substrate.
References: [445]

[EC 1.1.1.107 created 1972]

EC 1.1.1.108

Accepted name: carnitine 3-dehydrogenase
Reaction: carnitine + NAD⁺ = 3-dehydrocarnitine + NADH + H⁺
Systematic name: carnitine:NAD⁺ 3-oxidoreductase
References: [142, 3392]

[EC 1.1.1.108 created 1972]

[1.1.1.109] Transferred entry. 2,3-dihydro-2,3-dihydroxybenzoate dehydrogenase. Now EC 1.3.1.28, 2,3-dihydro-2,3-dihydroxybenzoate

dehydrogenase]

[EC 1.1.1.109 created 1972, deleted 1976]

EC 1.1.1.110

- Accepted name:** aromatic 2-oxoacid reductase
Reaction: (1) *(R)*-3-(phenyl)lactate + NAD⁺ = 3-phenylpyruvate + NADH + H⁺
(2) *(R)*-3-(4-hydroxyphenyl)lactate + NAD⁺ = 3-(4-hydroxyphenyl)pyruvate + NADH + H⁺
(3) *(R)*-(indol-3-yl)lactate + NAD⁺ = (indol-3-yl)pyruvate + NADH + H⁺
Other name(s): *(R)*-aromatic lactate dehydrogenase; *(R)*-4-hydroxyphenyllactate dehydrogenase; indolelactate:NAD⁺ oxidoreductase; indolelactate dehydrogenase; *fldH* (gene name); (indol-3-yl)lactate:NAD⁺ oxidoreductase
Systematic name: aromatic 2-oxoacid:NAD⁺ oxidoreductase
Comments: The enzymes from anaerobic bacteria such as *Clostridium sporogenes* participate in the fermentation pathways of L-phenylalanine, L-tyrosine and L-tryptophan. The enzyme from the yeast *Candida maltosa* has similar activity, but, unlike the bacterial enzyme, requires Mn²⁺ and can also use NADPH with lower activity.
References: [1727, 1202, 327, 819, 847]

[EC 1.1.1.110 created 1972 (EC 1.1.1.222 created 2000, incorporated 2018), modified 2018]

EC 1.1.1.111

- Accepted name:** 3-(imidazol-5-yl)lactate dehydrogenase
Reaction: *(S)*-3-(imidazol-5-yl)lactate + NAD(P)⁺ = 3-(imidazol-5-yl)pyruvate + NAD(P)H + H⁺
Other name(s): imidazol-5-yl lactate dehydrogenase
Systematic name: *(S)*-3-(imidazol-5-yl)lactate:NAD(P)⁺ oxidoreductase
References: [659, 668]

[EC 1.1.1.111 created 1972]

EC 1.1.1.112

- Accepted name:** indanol dehydrogenase
Reaction: indan-1-ol + NAD(P)⁺ = indanone + NAD(P)H + H⁺
Systematic name: indan-1-ol:NAD(P)⁺ 1-oxidoreductase
Comments: 3(20) α -Hydroxysteroids are also oxidized, more slowly.
References: [298, 1386]

[EC 1.1.1.112 created 1972]

EC 1.1.1.113

- Accepted name:** L-xylose 1-dehydrogenase
Reaction: L-xylose + NADP⁺ = L-xylono-1,4-lactone + NADPH + H⁺
Other name(s): L-xylose dehydrogenase; NADPH-xylose reductase
Systematic name: L-xylose:NADP⁺ 1-oxidoreductase
Comments: Also oxidizes D-arabinose and D-lyxose.
References: [3963]

[EC 1.1.1.113 created 1972]

EC 1.1.1.114

- Accepted name:** apiose 1-reductase
Reaction: D-apiitol + NAD⁺ = D--apiose + NADH + H⁺
Other name(s): D-apirose reductase; D-apiitol reductase

Systematic name: D-apiitol:NAD⁺ 1-oxidoreductase
References: [1371, 2750]

[EC 1.1.1.114 created 1972]

EC 1.1.1.115

Accepted name: ribose 1-dehydrogenase (NADP⁺)
Reaction: D-ribose + NADP⁺ + H₂O = D-ribonate + NADPH + H⁺
Other name(s): D-ribose dehydrogenase (NADP⁺); NADP-pentose-dehydrogenase; ribose 1-dehydrogenase (NADP)
Systematic name: D-ribose:NADP⁺ 1-oxidoreductase
Comments: Also acts, more slowly, on D-xylose and other pentoses.
References: [3360, 3367]

[EC 1.1.1.115 created 1972]

EC 1.1.1.116

Accepted name: D-arabinose 1-dehydrogenase (NAD⁺)
Reaction: D-arabinose + NAD⁺ = D-arabinono-1,4-lactone + NADH + H⁺
Other name(s): NAD⁺-pentose-dehydrogenase; arabinose(fucose)dehydrogenase
Systematic name: D-arabinose:NAD⁺ 1-oxidoreductase
References: [2926, 3367]

[EC 1.1.1.116 created 1972]

EC 1.1.1.117

Accepted name: D-arabinose 1-dehydrogenase [NAD(P)⁺]
Reaction: D-arabinose + NAD(P)⁺ = D-arabinono-1,4-lactone + NAD(P)H + H⁺
Other name(s): D-arabinose 1-dehydrogenase [NAD(P)]
Systematic name: D-arabinose:NAD(P)⁺ 1-oxidoreductase
Comments: Also acts on L-galactose, 6-deoxy- and 3,6-dideoxy-L-galactose.
References: [637, 635, 636]

[EC 1.1.1.117 created 1972]

EC 1.1.1.118

Accepted name: glucose 1-dehydrogenase (NAD⁺)
Reaction: D-glucose + NAD⁺ = D-glucono-1,5-lactone + NADH + H⁺
Other name(s): D-glucose:NAD oxidoreductase; D-aldohehexose dehydrogenase; glucose 1-dehydrogenase (NAD)
Systematic name: D-glucose:NAD⁺ 1-oxidoreductase
References: [1588]

[EC 1.1.1.118 created 1972, modified 1976]

EC 1.1.1.119

Accepted name: glucose 1-dehydrogenase (NADP⁺)
Reaction: D-glucose + NADP⁺ = D-glucono-1,5-lactone + NADPH + H⁺
Other name(s): nicotinamide adenine dinucleotide phosphate-linked aldohexose dehydrogenase; NADP-linked aldohexose dehydrogenase; NADP-dependent glucose dehydrogenase; glucose 1-dehydrogenase (NADP)
Systematic name: D-glucose:NADP⁺ 1-oxidoreductase
Comments: Also oxidizes D-mannose, 2-deoxy-D-glucose and 2-amino-2-deoxy-D-mannose.
References: [13, 143]

[EC 1.1.1.119 created 1972]

EC 1.1.1.120

Accepted name: galactose 1-dehydrogenase (NADP⁺)
Reaction: D-galactose + NADP⁺ = D-galactono-1,5-lactone + NADPH + H⁺
Other name(s): D-galactose dehydrogenase (NADP⁺); galactose 1-dehydrogenase (NADP)
Systematic name: D-galactose:NADP⁺ 1-oxidoreductase
Comments: Also acts on L-arabinose, 6-deoxy- and 2-deoxy-D-galactose.
References: [637, 635, 636, 3366]

[EC 1.1.1.120 created 1972]

EC 1.1.1.121

Accepted name: aldose 1-dehydrogenase (NAD⁺)
Reaction: D-aldose + NAD⁺ = D-aldonolactone + NADH + H⁺
Other name(s): aldose dehydrogenase; D-aldohexose dehydrogenase; aldose 1-dehydrogenase
Systematic name: D-aldose:NAD⁺ 1-oxidoreductase
Comments: Acts on D-glucose, 2-deoxy- and 6-deoxy-D-glucose, D-galactose, 6-deoxy-D-galactose, 2-deoxy-L-arabinose and D-xylose.
References: [637, 635, 636]

[EC 1.1.1.121 created 1972]

EC 1.1.1.122

Accepted name: D-threo-aldose 1-dehydrogenase
Reaction: a D-threo-aldose + NAD⁺ = a D-threo-aldono-1,5-lactone + NADH + H⁺
Other name(s): L-fucose dehydrogenase; (2S,3R)-aldose dehydrogenase; dehydrogenase, L-fucose; L-fucose (D-arabinose) dehydrogenase
Systematic name: D-threo-aldose:NAD⁺ 1-oxidoreductase
Comments: Acts on L-fucose, D-arabinose and L-xylose; the animal enzyme was also shown to act on L-arabinose, and the enzyme from *Pseudomonas caryophylli* on L-glucose.
References: [3315, 3346]

[EC 1.1.1.122 created 1972]

EC 1.1.1.123

Accepted name: sorbose 5-dehydrogenase (NADP⁺)
Reaction: L-sorbose + NADP⁺ = 5-dehydro-D-fructose + NADPH + H⁺
Other name(s): 5-ketofructose reductase; 5-keto-D-fructose reductase; sorbose (nicotinamide adenine dinucleotide phosphate) dehydrogenase; reduced nicotinamide adenine dinucleotide phosphate-linked reductase; sorbose 5-dehydrogenase (NADP⁺)
Systematic name: L-sorbose:NADP⁺ 5-oxidoreductase
References: [951]

[EC 1.1.1.123 created 1972, modified 1976]

EC 1.1.1.124

Accepted name: fructose 5-dehydrogenase (NADP⁺)
Reaction: D-fructose + NADP⁺ = 5-dehydro-D-fructose + NADPH + H⁺
Other name(s): 5-ketofructose reductase (NADP); 5-keto-D-fructose reductase (NADP⁺); fructose 5-(nicotinamide adenine dinucleotide phosphate) dehydrogenase; D-(-)fructose:(NADP⁺) 5-oxidoreductase; fructose 5-dehydrogenase (NADP)

Systematic name: D-fructose:NADP⁺ 5-oxidoreductase
References: [73, 145]

[EC 1.1.1.124 created 1972, modified 1976]

EC 1.1.1.125

Accepted name: 2-deoxy-D-gluconate 3-dehydrogenase
Reaction: 2-deoxy-D-gluconate + NAD⁺ = 3-dehydro-2-deoxy-D-gluconate + NADH + H⁺
Other name(s): 2-deoxygluconate dehydrogenase
Systematic name: 2-deoxy-D-gluconate:NAD⁺ 3-oxidoreductase
References: [931]

[EC 1.1.1.125 created 1972]

EC 1.1.1.126

Accepted name: 2-dehydro-3-deoxy-D-gluconate 6-dehydrogenase
Reaction: 2-dehydro-3-deoxy-D-gluconate + NADP⁺ = (4S,5S)-4,5-dihydroxy-2,6-dioxohexanoate + NADPH + H⁺
Other name(s): 2-keto-3-deoxy-D-gluconate dehydrogenase; 2-keto-3-deoxygluconate dehydrogenase
Systematic name: 2-dehydro-3-deoxy-D-gluconate:NADP⁺ 6-oxidoreductase
References: [3055]

[EC 1.1.1.126 created 1972]

EC 1.1.1.127

Accepted name: 2-dehydro-3-deoxy-D-gluconate 5-dehydrogenase
Reaction: 2-dehydro-3-deoxy-D-gluconate + NAD⁺ = (4S)-4,6-dihydroxy-2,5-dioxohexanoate + NADH + H⁺
Other name(s): 2-keto-3-deoxygluconate 5-dehydrogenase; 2-keto-3-deoxy-D-gluconate dehydrogenase; 2-keto-3-deoxygluconate (nicotinamide adenine dinucleotide (phosphate)) dehydrogenase; 2-keto-3-deoxy-D-gluconate (3-deoxy-D-glycero-2,5-hexodiulosonic acid) dehydrogenase
Systematic name: 2-dehydro-3-deoxy-D-gluconate:NAD⁺ 5-oxidoreductase
Comments: The enzyme from *Pseudomonas* acts equally well on NAD⁺ or NADP⁺, while that from *Erwinia chrysanthemi* and *Escherichia coli* is more specific for NAD⁺.
References: [647, 3056]

[EC 1.1.1.127 created 1972, modified 1976, modified 1989]

[1.1.1.128 Deleted entry. L-idonate 2-dehydrogenase. The reaction described is covered by EC 1.1.1.264.]

[EC 1.1.1.128 created 1972, modified 1976, deleted 2012]

EC 1.1.1.129

Accepted name: L-threonate 3-dehydrogenase
Reaction: L-threonate + NAD⁺ = 3-dehydro-L-erythronate + NADH + H⁺
Other name(s): threonate dehydrogenase; L-threonic acid dehydrogenase
Systematic name: L-threonate:NAD⁺ 3-oxidoreductase
References: [134]

[EC 1.1.1.129 created 1972]

EC 1.1.1.130

Accepted name: 3-dehydro-L-gulonate 2-dehydrogenase
Reaction: 3-dehydro-L-gulonate + NAD(P)⁺ = (4R,5S)-4,5,6-trihydroxy-2,3-dioxohexanoate + NAD(P)H + H⁺

Other name(s): 3-keto-L-gulonate dehydrogenase; 3-ketogulonate dehydrogenase; 3-keto-L-gulonate dehydrogenase; 3-ketogulonate dehydrogenase
Systematic name: 3-dehydro-L-gulonate:NAD(P)⁺ 2-oxidoreductase
References: [4059]

[EC 1.1.1.130 created 1972]

EC 1.1.1.131

Accepted name: manuronate reductase
Reaction: D-mannonate + NAD(P)⁺ = D-mannuronate + NAD(P)H + H⁺
Other name(s): mannonate dehydrogenase; mannonate (nicotinamide adenine dinucleotide (phosphate))dehydrogenase; mannonate dehydrogenase; manuronate reductase; mannonate dehydrogenase (NAD(P)⁺); D-mannonate:nicotinamide adenine dinucleotide (phosphate oxidoreductase (D-mannuronate-forming))
Systematic name: D-mannonate:NAD(P)⁺ 6-oxidoreductase
References: [988]

[EC 1.1.1.131 created 1972 (EC 1.2.1.34 created 1972, incorporated 1983; EC 1.1.1.180 created 1983, incorporated 1984)]

EC 1.1.1.132

Accepted name: GDP-mannose 6-dehydrogenase
Reaction: GDP-D-mannose + 2 NAD⁺ + H₂O = GDP-D-mannuronate + 2 NADH + 2 H⁺
Other name(s): guanosine diphosphomannose dehydrogenase; GDP-mannose dehydrogenase; guanosine diphosphomannose dehydrogenase; guanosine diphospho-D-mannose dehydrogenase
Systematic name: GDP-D-mannose:NAD⁺ 6-oxidoreductase
Comments: Also acts on the corresponding deoxynucleoside diphosphate derivative as a substrate.
References: [3054]

[EC 1.1.1.132 created 1972]

EC 1.1.1.133

Accepted name: dTDP-4-dehydrorhamnose reductase
Reaction: dTDP-β-L-rhamnose + NADP⁺ = dTDP-4-dehydro-β-L-rhamnose + NADPH + H⁺
Other name(s): dTDP-4-keto-L-rhamnose reductase; dTDP-4-ketorhamnose reductase; TDP-4-keto-rhamnose reductase; thymidine diphospho-4-ketorhamnose reductase; dTDP-6-deoxy-L-mannose:NADP⁺ 4-oxidoreductase; dTDP-6-deoxy-β-L-mannose:NADP⁺ 4-oxidoreductase
Systematic name: dTDP-β-L-rhamnose:NADP⁺ 4-oxidoreductase
Comments: In the reverse direction, reduction on the 4-position of the hexose moiety takes place only while the substrate is bound to another enzyme that catalyses epimerization at C-3 and C-5; the complex has been referred to as dTDP-L-rhamnose synthase.
References: [2502]

[EC 1.1.1.133 created 1972]

EC 1.1.1.134

Accepted name: dTDP-6-deoxy-L-talose 4-dehydrogenase (NADP⁺)
Reaction: dTDP-6-deoxy-β-L-talose + NADP⁺ = dTDP-4-dehydro-β-L-rhamnose + NADPH + H⁺
Other name(s): thymidine diphospho-6-deoxy-L-talose dehydrogenase; TDP-6-deoxy-L-talose dehydrogenase; dTDP-6-deoxy-L-talose dehydrogenase (4-reductase); dTDP-6-deoxy-L-talose:NADP⁺ 4-oxidoreductase
Systematic name: dTDP-6-deoxy-β-L-talose:NADP⁺ 4-oxidoreductase
Comments: Oxidation on the 4-position of the hexose moiety takes place only while the substrate is bound to another enzyme that catalyses epimerization at C-3 and C-5.
References: [1167]

[EC 1.1.1.134 created 1972]

EC 1.1.1.135

Accepted name: GDP-6-deoxy-D-talose 4-dehydrogenase
Reaction: $\text{GDP-6-deoxy-}\alpha\text{-D-talose} + \text{NAD(P)}^+ = \text{GDP-4-dehydro-}\alpha\text{-D-rhamnose} + \text{NAD(P)H} + \text{H}^+$
Other name(s): guanosine diphospho-6-deoxy-D-talose dehydrogenase; GDP-6-deoxy-D-talose:NAD(P)⁺ 4-oxidoreductase
Systematic name: GDP-6-deoxy- α -D-talose:NAD(P)⁺ 4-oxidoreductase
References: [2400]

[EC 1.1.1.135 created 1972, modified 1976]

EC 1.1.1.136

Accepted name: UDP-N-acetylglucosamine 6-dehydrogenase
Reaction: $\text{UDP-N-acetyl-}\alpha\text{-D-glucosamine} + 2 \text{NAD}^+ + \text{H}_2\text{O} = \text{UDP-2-acetamido-2-deoxy-}\alpha\text{-D-glucuronate} + 2 \text{NADH} + 2 \text{H}^+$
Other name(s): uridine diphosphoacetylglucosamine dehydrogenase; UDP-acetylglucosamine dehydrogenase; UDP-2-acetamido-2-deoxy-D-glucose:NAD oxidoreductase; UDP-GlcNAc dehydrogenase; WbpA; WbpO
Systematic name: UDP-N-acetyl- α -D-glucosamine:NAD⁺ 6-oxidoreductase
Comments: This enzyme participates in the biosynthetic pathway for UDP- α -D-ManNAc3NAcA (UDP-2,3-diacetamido-2,3-dideoxy- α -D-mannuronic acid), an important precursor of B-band lipopolysaccharide.
References: [982, 2549]

[EC 1.1.1.136 created 1972, modified 2012]

EC 1.1.1.137

Accepted name: ribitol-5-phosphate 2-dehydrogenase
Reaction: $\text{D-ribitol 5-phosphate} + \text{NAD(P)}^+ = \text{D-ribulose 5-phosphate} + \text{NAD(P)H} + \text{H}^+$
Other name(s): ribitol 5-phosphate dehydrogenase
Systematic name: D-ribitol-5-phosphate:NAD(P)⁺ 2-oxidoreductase
Comments: The enzyme, characterized from the bacterium *Lactobacillus plantarum*, can use both NAD⁺ and NADP⁺ as electron acceptor [*cf.* EC 1.1.1.405, ribitol-5-phosphate 2-dehydrogenase (NADP⁺)].
References: [1218]

[EC 1.1.1.137 created 1972, modified 2017]

EC 1.1.1.138

Accepted name: mannitol 2-dehydrogenase (NADP⁺)
Reaction: $\text{D-mannitol} + \text{NADP}^+ = \text{D-fructose} + \text{NADPH} + \text{H}^+$
Other name(s): mannitol 2-dehydrogenase (NADP)
Systematic name: D-mannitol:NADP⁺ 2-oxidoreductase
References: [1747, 3686]

[EC 1.1.1.138 created 1972]

[1.1.1.139 Deleted entry. polyol dehydrogenase (NADP⁺). Now included with EC 1.1.1.21 aldehyde reductase]

[EC 1.1.1.139 created 1972, deleted 1978]

EC 1.1.1.140

Accepted name: sorbitol-6-phosphate 2-dehydrogenase
Reaction: $\text{D-sorbitol 6-phosphate} + \text{NAD}^+ = \text{D-fructose 6-phosphate} + \text{NADH} + \text{H}^+$

Other name(s): ketosephosphate reductase; ketosephosphate reductase; D-sorbitol 6-phosphate dehydrogenase; D-sorbitol-6-phosphate dehydrogenase; sorbitol-6-*P*-dehydrogenase; D-glucitol-6-phosphate dehydrogenase
Systematic name: D-sorbitol-6-phosphate:NAD⁺ 2-oxidoreductase
References: [3901, 2270]

[EC 1.1.1.140 created 1972]

EC 1.1.1.141

Accepted name: 15-hydroxyprostaglandin dehydrogenase (NAD⁺)
Reaction: (5*Z*,13*E*,15*S*)-11 α ,15-dihydroxy-9-oxoprost-5,13-dienoate + NAD⁺ = (5*Z*,13*E*)-11 α -hydroxy-9,15-dioxoprost-5,13-dienoate + NADH + H⁺
Other name(s): NAD⁺-dependent 15-hydroxyprostaglandin dehydrogenase (type I); PGDH; 11 α ,15-dihydroxy-9-oxoprost-13-enoate:NAD⁺ 15-oxidoreductase; 15-OH-PGDH; 15-hydroxyprostaglandin dehydrogenase; 15-hydroxyprostanic dehydrogenase; NAD⁺-specific 15-hydroxyprostaglandin dehydrogenase; prostaglandin dehydrogenase; 15-hydroxyprostaglandin dehydrogenase (NAD⁺); (5*Z*,13*E*)-(15*S*)-11 α ,15-dihydroxy-9-oxoprost-13-enoate:NAD⁺ 15-oxidoreductase
Systematic name: (5*Z*,13*E*,15*S*)-11 α ,15-dihydroxy-9-oxoprost-5,13-dienoate:NAD⁺ 15-oxidoreductase
Comments: Acts on prostaglandin E₂, F_{2 α} and B₁, but not on prostaglandin D₂. *cf.* EC 1.1.1.196 15-hydroxyprostaglandin-D dehydrogenase (NADP⁺) and EC 1.1.1.197 15-hydroxyprostaglandin dehydrogenase (NADP⁺).
References: [92, 383, 2175, 2177]

[EC 1.1.1.141 created 1972]

EC 1.1.1.142

Accepted name: D-pinitol dehydrogenase
Reaction: 1D-3-*O*-methyl-*chiro*-inositol + NADP⁺ = 2D-5-*O*-methyl-2,3,5/4,6-pentahydroxycyclohexanone + NADPH + H⁺
Other name(s): 5D-5-*O*-methyl-*chiro*-inositol:NADP⁺ oxidoreductase
Systematic name: 1D-3-*O*-methyl-*chiro*-inositol:NADP⁺ oxidoreductase
References: [3259]

[EC 1.1.1.142 created 1972]

EC 1.1.1.143

Accepted name: sequoyitol dehydrogenase
Reaction: 5-*O*-methyl-*myo*-inositol + NAD⁺ = 2D-5-*O*-methyl-2,3,5/4,6-pentahydroxycyclohexanone + NADH + H⁺
Other name(s): D-pinitol dehydrogenase
Systematic name: 5-*O*-methyl-*myo*-inositol:NAD⁺ oxidoreductase
References: [3259]

[EC 1.1.1.143 created 1972]

EC 1.1.1.144

Accepted name: perillyl-alcohol dehydrogenase
Reaction: perillyl alcohol + NAD⁺ = perillyl aldehyde + NADH + H⁺
Other name(s): perillyl alcohol dehydrogenase
Systematic name: perillyl-alcohol:NAD⁺ oxidoreductase
Comments: Oxidizes a number of primary alcohols with the alcohol group allylic to an endocyclic double bond and a 6-membered ring, either aromatic or hydroaromatic.
References: [182]

[EC 1.1.1.144 created 1972]

EC 1.1.1.145

Accepted name: 3 β -hydroxy- Δ^5 -steroid dehydrogenase

Reaction: a 3 β -hydroxy- Δ^5 -steroid + NAD⁺ = a 3-oxo- Δ^5 -steroid + NADH + H⁺

Other name(s): progesterone reductase; Δ^5 -3 β -hydroxysteroid dehydrogenase; 3 β -hydroxy-5-ene steroid dehydrogenase; 3 β -hydroxy steroid dehydrogenase/isomerase; 3 β -hydroxy- Δ^5 -C₂₇-steroid dehydrogenase/isomerase; 3 β -hydroxy- Δ^5 -C₂₇-steroid oxidoreductase; 3 β -hydroxy-5-ene-steroid oxidoreductase; steroid- Δ^5 -3 β -ol dehydrogenase; 3 β -HSDH; 5-ene-3- β -hydroxysteroid dehydrogenase; 3 β -hydroxy-5-ene-steroid dehydrogenase

Systematic name: 3 β -hydroxy- Δ^5 -steroid:NAD⁺ 3-oxidoreductase

Comments: This activity is found in several bifunctional enzymes that catalyse the oxidative conversion of Δ^5 -3-hydroxy steroids to a Δ^4 -3-oxo configuration. This conversion is carried out in two separate, sequential reactions; in the first reaction, which requires NAD⁺, the enzyme catalyses the dehydrogenation of the 3 β -hydroxy steroid to a 3-oxo intermediate. In the second reaction the reduced coenzyme, which remains attached to the enzyme, activates the isomerization of the Δ^5 form to a Δ^4 form (*cf.* EC 5.3.3.1, steroid Δ -isomerase). Substrates include dehydroepiandrosterone (which is converted into androst-5-ene-3,17-dione), pregnenolone (converted to progesterone) and cholest-5-en-3-one, an intermediate of cholesterol degradation.

References: [562, 2033, 2773]

[EC 1.1.1.145 created 1972]

EC 1.1.1.146

Accepted name: 11 β -hydroxysteroid dehydrogenase

Reaction: an 11 β -hydroxysteroid + NADP⁺ = an 11-oxosteroid + NADPH + H⁺

Other name(s): corticosteroid 11 β -dehydrogenase; β -hydroxysteroid dehydrogenase; 11 β -hydroxy steroid dehydrogenase; corticosteroid 11-reductase; dehydrogenase, 11 β -hydroxy steroid

Systematic name: 11 β -hydroxysteroid:NADP⁺ 11-oxidoreductase

References: [29, 459, 2114, 3001]

[EC 1.1.1.146 created 1972]

EC 1.1.1.147

Accepted name: 16 α -hydroxysteroid dehydrogenase

Reaction: a 16 α -hydroxysteroid + NAD(P)⁺ = a 16-oxosteroid + NAD(P)H + H⁺

Other name(s): 16 α -hydroxy steroid dehydrogenase

Systematic name: 16 α -hydroxysteroid:NAD(P)⁺ 16-oxidoreductase

References: [2499]

[EC 1.1.1.147 created 1972]

EC 1.1.1.148

Accepted name: estradiol 17 α -dehydrogenase

Reaction: estradiol-17 α + NAD(P)⁺ = estrone + NAD(P)H + H⁺

Other name(s): 17 α -estradiol dehydrogenase; 17 α -hydroxy steroid dehydrogenase; 17 α -hydroxy steroid oxidoreductase; 17 α -hydroxysteroid oxidoreductase; estradiol 17 α -oxidoreductase

Systematic name: 17 α -hydroxysteroid:NAD(P)⁺ 17-oxidoreductase

References: [3170]

[EC 1.1.1.148 created 1972]

EC 1.1.1.149

Accepted name: 20 α -hydroxysteroid dehydrogenase
Reaction: 17 α ,20 α -dihydroxypregn-4-en-3-one + NAD(P)⁺ = 17 α -hydroxyprogesterone + NAD(P)H + H⁺
Other name(s): 20 α -hydroxy steroid dehydrogenase; 20 α -HSD; 20 α -HSDH
Systematic name: 20 α -hydroxysteroid:NAD(P)⁺ 20-oxidoreductase
Comments: *Re*-specific with respect to NAD(P)⁺ (*cf.* EC 1.1.1.62 17 β -estradiol 17-dehydrogenase).
References: [3491, 3680]

[EC 1.1.1.149 created 1972, deleted 1983, reinstated 1986]

EC 1.1.1.150

Accepted name: 21-hydroxysteroid dehydrogenase (NAD⁺)
Reaction: pregnan-21-ol + NAD⁺ = pregnan-21-al + NADH + H⁺
Other name(s): 21-hydroxysteroid dehydrogenase (NAD)
Systematic name: 21-hydroxysteroid:NAD⁺ 21-oxidoreductase
Comments: Acts on a number of 21-hydroxycorticosteroids.
References: [2599]

[EC 1.1.1.150 created 1972]

EC 1.1.1.151

Accepted name: 21-hydroxysteroid dehydrogenase (NADP⁺)
Reaction: pregnan-21-ol + NADP⁺ = pregnan-21-al + NADPH + H⁺
Other name(s): 21-hydroxy steroid dehydrogenase; 21-hydroxy steroid (nicotinamide adenine dinucleotide phosphate) dehydrogenase; 21-hydroxy steroid dehydrogenase (nicotinamide adenine dinucleotide phosphate); NADP-21-hydroxysteroid dehydrogenase; 21-hydroxysteroid dehydrogenase (NADP)
Systematic name: 21-hydroxysteroid:NADP⁺ 21-oxidoreductase
Comments: Acts on a number of 21-hydroxycorticosteroids.
References: [2599]

[EC 1.1.1.151 created 1972]

EC 1.1.1.152

Accepted name: 3 α -hydroxy-5 β -androstane-17-one 3 α -dehydrogenase
Reaction: 3 α -hydroxy-5 β -androstane-17-one + NAD⁺ = 5 β -androstane-3,17-dione + NADH + H⁺
Other name(s): etiocholanolone 3 α -dehydrogenase; etiocholanolone 3 α -dehydrogenase; 3 α -hydroxy-5 β -steroid dehydrogenase
Systematic name: 3 α -hydroxy-5 β -steroid:NAD⁺ 3-oxidoreductase
References: [3215]

[EC 1.1.1.152 created 1972]

EC 1.1.1.153

Accepted name: sepiapterin reductase (*L-erythro*-7,8-dihydrobiopterin forming)
Reaction: (1) *L-erythro*-7,8-dihydrobiopterin + NADP⁺ = sepiapterin + NADPH + H⁺
(2) *L-erythro*-tetrahydrobiopterin + 2 NADP⁺ = 6-pyruvoyl-5,6,7,8-tetrahydropterin + 2 NADPH + 2 H⁺
Other name(s): SR
Systematic name: *L-erythro*-7,8-dihydrobiopterin:NADP⁺ oxidoreductase
Comments: This enzyme catalyses the final step in the *de novo* synthesis of tetrahydrobiopterin from GTP. The enzyme, which is found in higher animals and some fungi and bacteria, produces the *erythro* form of tetrahydrobiopterin. *cf.* EC 1.1.1.325, sepiapterin reductase (*L-threo*-7,8-dihydrobiopterin forming).
References: [1844, 2441, 4179, 1923]

[EC 1.1.1.153 created 1972, modified 2012]

EC 1.1.1.154

Accepted name: ureidoglycolate dehydrogenase
Reaction: (S)-ureidoglycolate + NAD(P)⁺ = oxalureate + NAD(P)H + H⁺
Systematic name: (S)-ureidoglycolate:NAD(P)⁺ oxidoreductase
References: [3998]

[EC 1.1.1.154 created 1976]

[1.1.1.155 Deleted entry. *homocitrate dehydrogenase. The enzyme is identical to EC 1.1.1.87, homocitrate dehydrogenase*]

[EC 1.1.1.155 created 1976, deleted 2004]

EC 1.1.1.156

Accepted name: glycerol 2-dehydrogenase (NADP⁺)
Reaction: glycerol + NADP⁺ = glycerone + NADPH + H⁺
Other name(s): dihydroxyacetone reductase; dihydroxyacetone (reduced nicotinamide adenine dinucleotide phosphate) reductase; dihydroxyacetone reductase (NADPH); DHA oxidoreductase; glycerol 2-dehydrogenase (NADP)
Systematic name: glycerol:NADP⁺ 2-oxidoreductase (glycerone-forming)
References: [254]

[EC 1.1.1.156 created 1976]

EC 1.1.1.157

Accepted name: 3-hydroxybutyryl-CoA dehydrogenase
Reaction: (S)-3-hydroxybutanoyl-CoA + NADP⁺ = 3-acetoacetyl-CoA + NADPH + H⁺
Other name(s): β-hydroxybutyryl coenzyme A dehydrogenase; L-(+)-3-hydroxybutyryl-CoA dehydrogenase; BHBD; dehydrogenase, L-3-hydroxybutyryl coenzyme A (nicotinamide adenine dinucleotide phosphate); L-(+)-3-hydroxybutyryl-CoA dehydrogenase; β-hydroxybutyryl-CoA dehydrogenase
Systematic name: (S)-3-hydroxybutanoyl-CoA:NADP⁺ oxidoreductase
References: [2352]

[EC 1.1.1.157 created 1976]

[1.1.1.158 Transferred entry. *UDP-N-acetylmuramate dehydrogenase. Now EC 1.3.1.98, UDP-N-acetylmuramate dehydrogenase*]

[EC 1.1.1.158 created 1976, modified 1983, modified 2002, deleted 2013]

EC 1.1.1.159

Accepted name: 7α-hydroxysteroid dehydrogenase
Reaction: cholate + NAD⁺ = 3α,12α-dihydroxy-7-oxo-5β-cholan-24-oate + NADH + H⁺
Other name(s): 7α-hydroxy steroid dehydrogenase; 7α-HSDH
Systematic name: 7α-hydroxysteroid:NAD⁺ 7-oxidoreductase
Comments: Catalyses the oxidation of the 7α-hydroxy group of bile acids and alcohols both in their free and conjugated forms. The *Bacteroides fragilis* and *Clostridium* enzymes can also utilize NADP⁺.
References: [1412, 2337, 2339, 2340]

[EC 1.1.1.159 created 1976, modified 1980]

EC 1.1.1.160

Accepted name: dihydrobunolol dehydrogenase
Reaction: (\pm) -5-[(*tert*-butylamino)-2'-hydroxypropoxy]-1,2,3,4-tetrahydro-1-naphthol + NADP⁺ = (\pm) -5-[(*tert*-butylamino)-2'-hydroxypropoxy]-3,4-dihydro-1(2*H*)-naphthalenone + NADPH + H⁺
Other name(s): bunolol reductase
Systematic name: (\pm) -5-[(*tert*-butylamino)-2'-hydroxypropoxy]-1,2,3,4-tetrahydro-1-naphthol:NADP⁺ oxidoreductase
Comments: Also acts, more slowly, with NAD⁺.
References: [2193]

[EC 1.1.1.160 created 1976]

[1.1.1.161 Deleted entry. *cholestanetetraol 26-dehydrogenase. The activity is part of EC 1.14.13.15, cholestanetriol 26-monoxygenase*]

[EC 1.1.1.161 created 1976, deleted 2012]

EC 1.1.1.162

Accepted name: erythrulose reductase
Reaction: D-threitol + NADP⁺ = D-erythrulose + NADPH + H⁺
Other name(s): D-erythrulose reductase; erythritol:NADP⁺ oxidoreductase
Systematic name: D-threitol:NADP⁺ oxidoreductase
Comments: NAD⁺ is also utilized, but more slowly.
References: [3964, 3962]

[EC 1.1.1.162 created 1976]

EC 1.1.1.163

Accepted name: cyclopentanol dehydrogenase
Reaction: cyclopentanol + NAD⁺ = cyclopentanone + NADH + H⁺
Systematic name: cyclopentanol:NAD⁺ oxidoreductase
Comments: 4-Methylcyclohexanol and cyclohexanol can also act as substrates.
References: [1282, 1694]

[EC 1.1.1.163 created 1976]

EC 1.1.1.164

Accepted name: hexadecanol dehydrogenase
Reaction: hexadecanol + NAD⁺ = hexadecanal + NADH + H⁺
Systematic name: hexadecanol:NAD⁺ oxidoreductase
Comments: The liver enzyme acts on long-chain alcohols from C₈ to C₁₆. The *Euglena* enzyme also oxidizes the corresponding aldehydes to fatty acids.
References: [2015, 3655]

[EC 1.1.1.164 created 1976]

EC 1.1.1.165

Accepted name: 2-alkyn-1-ol dehydrogenase
Reaction: 2-butyne-1,4-diol + NAD⁺ = 4-hydroxy-2-butyne-1,4-diol + NADH + H⁺
Systematic name: 2-butyne-1,4-diol:NAD⁺ 1-oxidoreductase
Comments: Acts on a variety of 2-alkyn-1-ols, and also on 1,4-butanediol. NADP⁺ also acts as acceptor, but more slowly.
References: [2579]

[EC 1.1.1.165 created 1976]

EC 1.1.1.166

- Accepted name:** hydroxycyclohexanecarboxylate dehydrogenase
Reaction: (1*S*,3*R*,4*S*)-3,4-dihydroxycyclohexane-1-carboxylate + NAD⁺ = (1*S*,4*S*)-4-hydroxy-3-oxocyclohexane-1-carboxylate + NADH + H⁺
Other name(s): dihydroxycyclohexanecarboxylate dehydrogenase; (-)-*t*-3,*t*-4-dihydroxycyclohexane-*c*-1-carboxylate-NAD⁺ oxidoreductase
Systematic name: (1*S*,3*R*,4*S*)-3,4-dihydroxycyclohexane-1-carboxylate:NAD⁺ 3-oxidoreductase
Comments: Acts on hydroxycyclohexanecarboxylates that have an equatorial carboxy group at C-1, an axial hydroxy group at C-3 and an equatorial hydroxy or carbonyl group at C-4, including (-)-quininate and (-)-shikimate.
References: [4195]

[EC 1.1.1.166 created 1976]

EC 1.1.1.167

- Accepted name:** hydroxymalonate dehydrogenase
Reaction: hydroxymalonate + NAD⁺ = oxomalonate + NADH + H⁺
Systematic name: hydroxymalonate:NAD⁺ oxidoreductase
References: [1782]

[EC 1.1.1.167 created 1976]

EC 1.1.1.168

- Accepted name:** 2-dehydropantolactone reductase (*Re*-specific)
Reaction: (*R*)-pantolactone + NADP⁺ = 2-dehydropantolactone + NADPH + H⁺
Other name(s): 2-oxopantoyl lactone reductase; ketopantoyl lactone reductase; 2-ketopantoyl lactone reductase; 2-dehydropantoyl-lactone reductase (*A*-specific); (*R*)-pantolactone:NADP⁺ oxidoreductase (*A*-specific); 2-dehydropantolactone reductase (*A*-specific)
Systematic name: (*R*)-pantolactone:NADP⁺ oxidoreductase (*Re*-specific)
Comments: The yeast enzyme differs from that from *Escherichia coli* [EC 1.1.1.214 2-dehydropantolactone reductase (*Si*-specific)], which is specific for the *Si*-face of NADP⁺, and in receptor requirements from EC 1.1.99.26 3-hydroxycyclohexanone dehydrogenase.
References: [1932, 4214]

[EC 1.1.1.168 created 1976, modified 1986, modified 1999]

EC 1.1.1.169

- Accepted name:** 2-dehydropantoate 2-reductase
Reaction: (*R*)-pantoate + NADP⁺ = 2-dehydropantoate + NADPH + H⁺
Other name(s): 2-oxopantoate reductase; 2-ketopantoate reductase; 2-ketopantoic acid reductase; ketopantoate reductase; ketopantoic acid reductase
Systematic name: (*R*)-pantoate:NADP⁺ 2-oxidoreductase
References: [1932]

[EC 1.1.1.169 created 1976]

EC 1.1.1.170

- Accepted name:** 3β-hydroxysteroid-4α-carboxylate 3-dehydrogenase (decarboxylating)
Reaction: a 3β-hydroxysteroid-4α-carboxylate + NAD(P)⁺ = a 3-oxosteroid + CO₂ + NAD(P)H
Other name(s): 3β-hydroxy-4β-methylcholestenecarboxylate 3-dehydrogenase (decarboxylating); 3β-hydroxy-4β-methylcholestenoate dehydrogenase; sterol 4α-carboxylic decarboxylase; sterol-4α-carboxylate 3-dehydrogenase (decarboxylating) (ambiguous); ERG26 (gene name); NSDHL (gene name)
Systematic name: 3β-hydroxysteroid-4α-carboxylate:NAD(P)⁺ 3-oxidoreductase (decarboxylating)

Comments: The enzyme catalyses the decarboxylation of the C-4 carbon and the dehydrogenation of a 3 β hydroxyl at the C-3 carbon of 3 β -hydroxysteroid-4 α -carboxylates. It is involved in zymosterol and cholesterol biosynthesis.

References: [381, 3105, 1132, 477]

[EC 1.1.1.170 created 1978, modified 2002, modified 2012]

[1.1.1.171 *Transferred entry. methylenetetrahydrofolate reductase (NADPH). Now EC 1.5.1.20, methylenetetrahydrofolate reductase [NAD(P)H]*]

[EC 1.1.1.171 created 1978, deleted 1984]

EC 1.1.1.172

Accepted name: 2-oxoadipate reductase
Reaction: 2-hydroxyadipate + NAD⁺ = 2-oxoadipate + NADH + H⁺
Other name(s): 2-ketoadipate reductase; α -ketoadipate reductase; 2-ketoadipate reductase
Systematic name: 2-hydroxyadipate:NAD⁺ 2-oxidoreductase
References: [3705]

[EC 1.1.1.172 created 1978]

EC 1.1.1.173

Accepted name: L-rhamnose 1-dehydrogenase
Reaction: L-rhamnofuranose + NAD⁺ = L-rhamno-1,4-lactone + NADH + H⁺
Systematic name: L-rhamnofuranose:NAD⁺ 1-oxidoreductase
References: [3188, 3189]

[EC 1.1.1.173 created 1978]

EC 1.1.1.174

Accepted name: cyclohexane-1,2-diol dehydrogenase
Reaction: *trans*-cyclohexane-1,2-diol + NAD⁺ = 2-hydroxycyclohexan-1-one + NADH + H⁺
Systematic name: *trans*-cyclohexane-1,2-diol:NAD⁺ 1-oxidoreductase
Comments: Also oxidizes, more slowly, the *cis* isomer and 2-hydroxycyclohexanone.
References: [752]

[EC 1.1.1.174 created 1978]

EC 1.1.1.175

Accepted name: D-xylose 1-dehydrogenase
Reaction: D-xylose + NAD⁺ = D-xylonolactone + NADH + H⁺
Other name(s): NAD-D-xylose dehydrogenase; D-xylose dehydrogenase; (NAD)-linked D-xylose dehydrogenase
Systematic name: D-xylose:NAD⁺ 1-oxidoreductase
References: [4320]

[EC 1.1.1.175 created 1978]

EC 1.1.1.176

Accepted name: 12 α -hydroxysteroid dehydrogenase
Reaction: cholate + NADP⁺ = 3 α ,7 α -dihydroxy-12-oxo-5 β -cholan-24-oate + NADPH + H⁺
Other name(s): 12 α -hydroxy steroid dehydrogenase; NAD⁺-dependent 12 α -hydroxysteroid dehydrogenase; NADP⁺-12 α -hydroxysteroid dehydrogenase
Systematic name: 12 α -hydroxysteroid:NADP⁺ 12-oxidoreductase

Comments: Catalyses the oxidation of the 12 α -hydroxy group of bile acids, both in their free and conjugated form. Also acts on bile alcohols.

References: [2336, 2372]

[EC 1.1.1.176 created 1978]

EC 1.1.1.177

Accepted name: glycerol-3-phosphate 1-dehydrogenase (NADP⁺)

Reaction: *sn*-glycerol 3-phosphate + NADP⁺ = D-glyceraldehyde 3-phosphate + NADPH + H⁺

Other name(s): glycerol phosphate (nicotinamide adenine dinucleotide phosphate) dehydrogenase; L-glycerol 3-phosphate:NADP⁺ oxidoreductase; glycerin-3-phosphate dehydrogenase; NADPH-dependent glycerin-3-phosphate dehydrogenase; NADP-specific glycerol 3-phosphate 1-dehydrogenase

Systematic name: *sn*-glycerol-3-phosphate:NADP⁺ 1-oxidoreductase

References: [1225, 4249]

[EC 1.1.1.177 created 1980, modified 1980]

EC 1.1.1.178

Accepted name: 3-hydroxy-2-methylbutyryl-CoA dehydrogenase

Reaction: (2*S*,3*S*)-3-hydroxy-2-methylbutanoyl-CoA + NAD⁺ = 2-methylacetoacetyl-CoA + NADH + H⁺

Other name(s): 2-methyl-3-hydroxybutyryl coenzyme A dehydrogenase; 2-methyl-3-hydroxybutyryl coenzyme A dehydrogenase; 2-methyl-3-hydroxy-butryl CoA dehydrogenase

Systematic name: (2*S*,3*S*)-3-hydroxy-2-methylbutanoyl-CoA:NAD⁺ oxidoreductase

Comments: Also acts, more slowly, on (2*S*,3*S*)-2-hydroxy-3-methylpentanoyl-CoA.

References: [651]

[EC 1.1.1.178 created 1981]

EC 1.1.1.179

Accepted name: D-xylose 1-dehydrogenase (NADP⁺)

Reaction: D-xylose + NADP⁺ = D-xylo-1,5-lactone + NADPH + H⁺

Other name(s): D-xylose (nicotinamide adenine dinucleotide phosphate) dehydrogenase; D-xylose-NADP dehydrogenase; D-xylose:NADP⁺ oxidoreductase; D-xylose 1-dehydrogenase (NADP)

Systematic name: D-xylose:NADP⁺ 1-oxidoreductase

Comments: Also acts, more slowly, on L-arabinose and D-ribose.

References: [4231, 4232]

[EC 1.1.1.179 created 1982]

[1.1.1.180 Deleted entry. mannonate dehydrogenase (NAD(P)⁺). Now included with EC 1.1.1.131 mannuronate reductase]

[EC 1.1.1.180 created 1983, deleted 1984]

EC 1.1.1.181

Accepted name: cholest-5-ene-3 β ,7 α -diol 3 β -dehydrogenase

Reaction: cholest-5-ene-3 β ,7 α -diol + NAD⁺ = 7 α -hydroxycholest-4-en-3-one + NADH + H⁺

Other name(s): 3 β -hydroxy- Δ^5 -C₂₇-steroid oxidoreductase

Systematic name: cholest-5-ene-3 β ,7 α -diol:NAD⁺ 3-oxidoreductase

Comments: Highly specific for 3 β -hydroxy-C₂₇-steroids with Δ^5 -double bond.

References: [4210]

[EC 1.1.1.181 created 1983]

[1.1.1.182 Deleted entry. fenchol dehydrogenase. Now included with EC 1.1.1.198 (+)-borneol dehydrogenase, EC 1.1.1.227

(-)-borneol dehydrogenase and EC 1.1.1.228 (+)-sabinol dehydrogenase]

[EC 1.1.1.182 created 1983, deleted 1990]

EC 1.1.1.183

Accepted name: geraniol dehydrogenase (NADP⁺)
Reaction: geraniol + NADP⁺ = geranial + NADPH + H⁺
Systematic name: geraniol:NADP⁺ oxidoreductase
Comments: Also acts, more slowly on farnesol but not on nerol. The enzyme produces a mixture known as citral, which includes geranial and neral. It is still not known whether neral is produced directly by the enzyme, or by isomerization of geranial.
References: [3045, 3437, 3288]

[EC 1.1.1.183 created 1983]

EC 1.1.1.184

Accepted name: carbonyl reductase (NADPH)
Reaction: R-CHOH-R' + NADP⁺ = R-CO-R' + NADPH + H⁺
Other name(s): aldehyde reductase 1; prostaglandin 9-ketoreductase; xenobiotic ketone reductase; NADPH-dependent carbonyl reductase; ALR₃; carbonyl reductase; nonspecific NADPH-dependent carbonyl reductase; carbonyl reductase (NADPH₂)
Systematic name: secondary-alcohol:NADP⁺ oxidoreductase
Comments: Acts on a wide range of carbonyl compounds, including quinones, aromatic aldehydes, ketoaldehydes, daunorubicin and prostaglandins E and F, reducing them to the corresponding alcohol. *Si*-specific with respect to NADPH [*cf.* EC 1.1.1.2 alcohol dehydrogenase (NADP⁺)].
References: [36, 2258, 4177]

[EC 1.1.1.184 created 1983]

EC 1.1.1.185

Accepted name: L-glycol dehydrogenase
Reaction: an L-glycol + NAD(P)⁺ = a 2-hydroxycarbonyl compound + NAD(P)H + H⁺
Other name(s): glycol (nicotinamide adenine dinucleotide (phosphate)) dehydrogenase; L-(+)-glycol:NAD(P) oxidoreductase; L-glycol:NAD(P) dehydrogenase
Systematic name: L-glycol:NAD(P)⁺ oxidoreductase
Comments: The 2-hydroxycarbonyl compound formed can be further oxidized to a vicinal dicarbonyl compound. In the reverse direction, vicinal diketones, glyceraldehyde, glyoxal, methylglyoxal, 2-oxo-hydroxyketones and 2-ketoacid esters can be reduced.
References: [271]

[EC 1.1.1.185 created 1984]

EC 1.1.1.186

Accepted name: dTDP-galactose 6-dehydrogenase
Reaction: dTDP-D-galactose + 2 NADP⁺ + H₂O = dTDP-D-galacturonate + 2 NADPH + 2 H⁺
Other name(s): thymidine-diphosphate-galactose dehydrogenase
Systematic name: dTDP-D-galactose:NADP⁺ 6-oxidoreductase
References: [1828]

[EC 1.1.1.186 created 1984, modified 2002]

EC 1.1.1.187

Accepted name: GDP-4-dehydro-D-rhamnose reductase

Reaction: (1) $\text{GDP-}\alpha\text{-D-rhamnose} + \text{NAD(P)}^+ = \text{GDP-4-dehydro-}\alpha\text{-D-rhamnose} + \text{NAD(P)H} + \text{H}^+$
(2) $\text{GDP-6-deoxy-}\alpha\text{-D-talose} + \text{NAD(P)}^+ = \text{GDP-4-dehydro-}\alpha\text{-D-rhamnose} + \text{NAD(P)H} + \text{H}^+$
Other name(s): GDP-4-keto-6-deoxy-D-mannose reductase; GDP-4-keto-D-rhamnose reductase; guanosine diphosphate-4-keto-D-rhamnose reductase; GDP-6-deoxy-D-mannose:NAD(P)⁺ 4-oxidoreductase; GDP-6-deoxy- α -D-mannose:NAD(P)⁺ 4-oxidoreductase
Systematic name: GDP-4-dehydro- α -D-rhamnose:NAD(P)⁺ 4-oxidoreductase
Comments: The enzyme, which operates in the opposite direction to that shown, forms a mixture of GDP- α -D-rhamnose and its C-4 epimer, GDP-6-deoxy- α -D-talose. *cf.* EC 1.1.1.281, GDP-4-dehydro-6-deoxy-D-mannose reductase and EC 1.1.1.135, GDP-6-deoxy-D-talose 4-dehydrogenase.
References: [196, 4226]

[EC 1.1.1.187 created 1984]

EC 1.1.1.188

Accepted name: prostaglandin-F synthase
Reaction: $(5Z,13E)\text{-}(15S)\text{-}9\alpha,11\alpha,15\text{-trihydroxyprosta-5,13-dienoate} + \text{NADP}^+ = (5Z,13E)\text{-}(15S)\text{-}9\alpha,15\text{-dihydroxy-11-oxoprosta-5,13-dienoate} + \text{NADPH} + \text{H}^+$
Other name(s): prostaglandin-D₂ 11-reductase; reductase, 15-hydroxy-11-oxoprostaglandin; PGD₂ 11-ketoreductase; PGF_{2 α} synthetase; prostaglandin 11-ketoreductase; prostaglandin D₂-ketoreductase; prostaglandin F synthase; prostaglandin F synthetase; synthetase, prostaglandin F_{2 α} ; PGF synthetase; NADPH-dependent prostaglandin D₂ 11-keto reductase; prostaglandin 11-keto reductase
Systematic name: $(5Z,13E)\text{-}(15S)\text{-}9\alpha,11\alpha,15\text{-trihydroxyprosta-5,13-dienoate:NADP}^+$ 11-oxidoreductase
Comments: Reduces prostaglandin D₂ and prostaglandin H₂ to prostaglandin F₂; prostaglandin D₂ is not an intermediate in the reduction of prostaglandin H₂. Also catalyses the reduction of a number of carbonyl compounds, such as 9,10-phenanthroquinone and 4-nitroacetophenone.
References: [3162, 4142, 4144, 4245, 4246]

[EC 1.1.1.188 created 1984, modified 1989, modified 1990]

EC 1.1.1.189

Accepted name: prostaglandin-E₂ 9-reductase
Reaction: $(5Z,13E)\text{-}(15S)\text{-}9\alpha,11\alpha,15\text{-trihydroxyprosta-5,13-dienoate} + \text{NADP}^+ = (5Z,13E)\text{-}(15S)\text{-}11\alpha,15\text{-dihydroxy-9-oxoprosta-5,13-dienoate} + \text{NADPH} + \text{H}^+$
Other name(s): PGE₂-9-OR; reductase, 15-hydroxy-9-oxoprostaglandin; 9-keto-prostaglandin E₂ reductase; 9-ketoprostaglandin reductase; PGE-9-ketoreductase; PGE₂ 9-oxoreductase; PGE₂-9-ketoreductase; prostaglandin 9-ketoreductase; prostaglandin E 9-ketoreductase; prostaglandin E₂-9-oxoreductase
Systematic name: $(5Z,13E)\text{-}(15S)\text{-}9\alpha,11\alpha,15\text{-trihydroxyprosta-5,13-dienoate:NADP}^+$ 9-oxidoreductase
Comments: Reduces prostaglandin E₂ to prostaglandin F_{2 α} . A number of other 9-oxo- and 15-oxo-prostaglandin derivatives can also be reduced to the corresponding hydroxy compounds. May be identical with EC 1.1.1.197 15-hydroxyprostaglandin dehydrogenase (NADP⁺).
References: [2176, 3369, 3777, 4149]

[EC 1.1.1.189 created 1984, modified 1989]

EC 1.1.1.190

Accepted name: indole-3-acetaldehyde reductase (NADH)
Reaction: $(\text{indol-3-yl})\text{ethanol} + \text{NAD}^+ = (\text{indol-3-yl})\text{acetaldehyde} + \text{NADH} + \text{H}^+$
Other name(s): indoleacetaldehyde reductase; indole-3-acetaldehyde reductase (NADH); indole-3-ethanol:NAD⁺ oxidoreductase
Systematic name: $(\text{indol-3-yl})\text{ethanol:NAD}^+$ oxidoreductase
References: [418]

[EC 1.1.1.190 created 1984]

EC 1.1.1.191

Accepted name: indole-3-acetaldehyde reductase (NADPH)
Reaction: (indol-3-yl)ethanol + NADP⁺ = (indol-3-yl)acetaldehyde + NADPH + H⁺
Other name(s): indoleacetaldehyde (reduced nicotinamide adenine dinucleotide phosphate) reductase; indole-3-acetaldehyde reductase (NADPH); indole-3-ethanol:NADP⁺ oxidoreductase
Systematic name: (indol-3-yl)ethanol:NADP⁺ oxidoreductase
References: [418]

[EC 1.1.1.191 created 1984]

EC 1.1.1.192

Accepted name: long-chain-alcohol dehydrogenase
Reaction: a long-chain alcohol + 2 NAD⁺ + H₂O = a long-chain carboxylate + 2 NADH + 2 H⁺
Other name(s): long-chain alcohol dehydrogenase; fatty alcohol oxidoreductase
Systematic name: long-chain-alcohol:NAD⁺ oxidoreductase
Comments: Hexadecanol is a good substrate.
References: [2180]

[EC 1.1.1.192 created 1984]

EC 1.1.1.193

Accepted name: 5-amino-6-(5-phosphoribosylamino)uracil reductase
Reaction: 5-amino-6-(5-phospho-D-ribitylamino)uracil + NADP⁺ = 5-amino-6-(5-phospho-D-ribosylamino)uracil + NADPH + H⁺
Other name(s): aminodioxyposphoribosylaminopyrimidine reductase
Systematic name: 5-amino-6-(5-phospho-D-ribitylamino)uracil:NADP⁺ 1'-oxidoreductase
References: [452]

[EC 1.1.1.193 created 1984, modified 2011]

EC 1.1.1.194

Accepted name: coniferyl-alcohol dehydrogenase
Reaction: coniferyl alcohol + NADP⁺ = coniferyl aldehyde + NADPH + H⁺
Other name(s): CAD (ambiguous)
Systematic name: coniferyl-alcohol:NADP⁺ oxidoreductase
Comments: Specific for coniferyl alcohol; does not act on cinnamyl alcohol, 4-coumaryl alcohol or sinapyl alcohol.
References: [2388, 4273]

[EC 1.1.1.194 created 1984]

EC 1.1.1.195

Accepted name: cinnamyl-alcohol dehydrogenase
Reaction: cinnamyl alcohol + NADP⁺ = cinnamaldehyde + NADPH + H⁺
Other name(s): cinnamyl alcohol dehydrogenase; CAD (ambiguous)
Systematic name: cinnamyl-alcohol:NADP⁺ oxidoreductase
Comments: Acts on coniferyl alcohol, sinapyl alcohol, 4-coumaryl alcohol and cinnamyl alcohol (*cf.* EC 1.1.1.194 coniferyl-alcohol dehydrogenase).
References: [3314, 4273, 4274]

[EC 1.1.1.195 created 1984]

EC 1.1.1.196

- Accepted name:** 15-hydroxyprostaglandin-D dehydrogenase (NADP⁺)
Reaction: (5Z,13E)-(15S)-9 α ,15-dihydroxy-11-oxoprost-5,13-dienoate + NADP⁺ = (5Z,13E)-9 α -hydroxy-11,15-dioxoprost-5,13-dienoate + NADPH + H⁺
Other name(s): prostaglandin-D 15-dehydrogenase (NADP); dehydrogenase, prostaglandin D₂; NADP-PGD₂ dehydrogenase; dehydrogenase, 15-hydroxyprostaglandin (nicotinamide adenine dinucleotide phosphate); 15-hydroxy PGD₂ dehydrogenase; 15-hydroxyprostaglandin dehydrogenase (NADP); NADP-dependent 15-hydroxyprostaglandin dehydrogenase; prostaglandin D₂ dehydrogenase; NADP-linked 15-hydroxyprostaglandin dehydrogenase; NADP-specific 15-hydroxyprostaglandin dehydrogenase; NADP-linked prostaglandin D₂ dehydrogenase; 15-hydroxyprostaglandin-D dehydrogenase (NADP)
Systematic name: (5Z,13E)-(15S)-9 α ,15-dihydroxy-11-oxoprost-5,13-dienoate:NADP⁺ 15-oxidoreductase
Comments: Specific for prostaglandins D [*cf.* EC 1.1.1.141 15-hydroxyprostaglandin dehydrogenase (NAD⁺) and EC 1.1.1.197 15-hydroxyprostaglandin dehydrogenase (NADP⁺)].
References: [4143]

[EC 1.1.1.196 created 1984, modified 1990]

EC 1.1.1.197

- Accepted name:** 15-hydroxyprostaglandin dehydrogenase (NADP⁺)
Reaction: (13E)-(15S)-11 α ,15-dihydroxy-9-oxoprost-13-enoate + NADP⁺ = (13E)-11 α -hydroxy-9,15-dioxoprost-13-enoate + NADPH + H⁺
Other name(s): NADP-dependent 15-hydroxyprostaglandin dehydrogenase; NADP-linked 15-hydroxyprostaglandin dehydrogenase; NADP-specific 15-hydroxyprostaglandin dehydrogenase; type II 15-hydroxyprostaglandin dehydrogenase; 15-hydroxyprostaglandin dehydrogenase (NADP)
Systematic name: (13E)-(15S)-11 α ,15-dihydroxy-9-oxoprost-13-enoate:NADP⁺ 15-oxidoreductase
Comments: Acts on prostaglandins E₂, F_{2 α} and B₁, but not on prostaglandin D₂ [*cf.* EC 1.1.1.141 15-hydroxyprostaglandin dehydrogenase (NAD⁺) and EC 1.1.1.196 15-hydroxyprostaglandin-D dehydrogenase (NADP⁺)]. May be identical with EC 1.1.1.189 prostaglandin-E₂ 9-reductase.
References: [2175, 2177]

[EC 1.1.1.197 created 1984]

EC 1.1.1.198

- Accepted name:** (+)-borneol dehydrogenase
Reaction: (+)-borneol + NAD⁺ = (+)-camphor + NADH + H⁺
Other name(s): bicyclic monoterpenol dehydrogenase
Systematic name: (+)-borneol:NAD⁺ oxidoreductase
Comments: NADP⁺ can also act, but more slowly.
References: [696, 777]

[EC 1.1.1.198 created 1984, modified 1990 (EC 1.1.1.182 created 1983, part incorporated 1990)]

EC 1.1.1.199

- Accepted name:** (S)-usnate reductase
Reaction: (6R)-2-acetyl-6-(3-acetyl-2,4,6-trihydroxy-5-methylphenyl)-3-hydroxy-6-methyl-2,4-cyclohexadien-1-one + NAD⁺ = (S)-usnate + NADH + H⁺
Other name(s): L-usnic acid dehydrogenase
Systematic name: reduced-(S)-usnate:NAD⁺ oxidoreductase (ether-bond-forming)
References: [966]

[EC 1.1.1.199 created 1984]

EC 1.1.1.200

Accepted name: aldose-6-phosphate reductase (NADPH)
Reaction: D-sorbitol 6-phosphate + NADP⁺ = D-glucose 6-phosphate + NADPH + H⁺
Other name(s): aldose 6-phosphate reductase; NADP-dependent aldose 6-phosphate reductase; A6PR; aldose-6-*P* reductase; aldose-6-phosphate reductase; alditol 6-phosphate:NADP 1-oxidoreductase; aldose-6-phosphate reductase (NADPH₂)
Systematic name: D-aldose-6-phosphate:NADP⁺ 1-oxidoreductase
Comments: In the reverse reaction, acts also on D-galactose 6-phosphate and, more slowly, on D-mannose 6-phosphate and 2-deoxy-D-glucose 6-phosphate.
References: [2758]

[EC 1.1.1.200 created 1984]

EC 1.1.1.201

Accepted name: 7β-hydroxysteroid dehydrogenase (NADP⁺)
Reaction: a 7β-hydroxysteroid + NADP⁺ = a 7-oxosteroid + NADPH + H⁺
Other name(s): NADP-dependent 7β-hydroxysteroid dehydrogenase; 7β-hydroxysteroid dehydrogenase (NADP)
Systematic name: 7β-hydroxysteroid:NADP⁺ 7-oxidoreductase
Comments: Catalyses the oxidation of the 7β-hydroxy group of bile acids such as ursodeoxycholate.
References: [1515, 2337, 2338]

[EC 1.1.1.201 created 1984]

EC 1.1.1.202

Accepted name: 1,3-propanediol dehydrogenase
Reaction: propane-1,3-diol + NAD⁺ = 3-hydroxypropanal + NADH + H⁺
Other name(s): 3-hydroxypropionaldehyde reductase; 1,3-PD:NAD⁺ oxidoreductase; 1,3-propanediol:NAD⁺ oxidoreductase; 1,3-propanediol dehydrogenase
Systematic name: propane-1,3-diol:NAD⁺ 1-oxidoreductase
References: [2, 1030]

[EC 1.1.1.202 created 1984]

EC 1.1.1.203

Accepted name: uronate dehydrogenase
Reaction: (1) β-D-galacturonate + NAD⁺ = D-galactaro-1,5-lactone + NADH + H⁺
(2) β-D-glucuronate + NAD⁺ = D-glucaro-1,5-lactone + NADH + H⁺
Other name(s): uronate:NAD-oxidoreductase; uronic acid dehydrogenase
Systematic name: uronate:NAD⁺ 1-oxidoreductase
Comments: Requires Mg²⁺. The enzyme, characterized from the bacterium *Agrobacterium fabrum*, participates in oxidative degradation pathways for galacturonate and glucuronate. The enzyme can only accept the β anomeric form of the substrate [2943]. The 1,5-lactone product is rather stable at cytosolic pH and does not hydrolyse spontaneously at a substantial rate.
References: [1906, 331, 79, 2943]

[EC 1.1.1.203 created 1972 as EC 1.2.1.35, transferred 1984 to EC 1.1.1.203, modified 2014]

[1.1.1.204 Transferred entry. xanthine dehydrogenase. Now EC 1.1.1.1.4, xanthine dehydrogenase. The enzyme was incorrectly classified as acting on a CH-OH group]

[EC 1.1.1.204 created 1972 as EC 1.2.1.37, transferred 1984 to EC 1.1.1.204, modified 1989, deleted 2004]

EC 1.1.1.205

Accepted name: IMP dehydrogenase
Reaction: IMP + NAD⁺ + H₂O = XMP + NADH + H⁺

Other name(s): inosine-5'-phosphate dehydrogenase; inosinic acid dehydrogenase; inosinate dehydrogenase; inosine 5'-monophosphate dehydrogenase; inosine monophosphate dehydrogenase; IMP oxidoreductase; inosine monophosphate oxidoreductase
Systematic name: IMP:NAD⁺ oxidoreductase
Comments: The enzyme acts on the hydroxy group of the hydrated derivative of the substrate.
References: [2359, 3949]

[EC 1.1.1.205 created 1961 as EC 1.2.1.14, transferred 1984 to EC 1.1.1.205]

EC 1.1.1.206

Accepted name: tropinone reductase I
Reaction: tropine + NADP⁺ = tropinone + NADPH + H⁺
Other name(s): tropine dehydrogenase; tropinone reductase (ambiguous); TR-I
Systematic name: tropine:NADP⁺ 3 α -oxidoreductase
Comments: Also oxidizes other tropane-3 α -ols, but not the corresponding β -derivatives [1994]. This enzyme along with EC 1.1.1.236, tropinone reductase II, represents a branch point in tropane alkaloid metabolism [867]. Tropine (the product of EC 1.1.1.206) is incorporated into hyoscyamine and scopolamine whereas pseudotropine (the product of EC 1.1.1.236) is the first specific metabolite on the pathway to the calystegines [867]. Both enzymes are always found together in any given tropane-alkaloid-producing species, have a common substrate, tropinone, and are strictly stereospecific [2701].
References: [1994, 674, 2701, 867]

[EC 1.1.1.206 created 1984, modified 2007]

EC 1.1.1.207

Accepted name: (-)-menthol dehydrogenase
Reaction: (-)-menthol + NADP⁺ = (-)-menthone + NADPH + H⁺
Other name(s): monoterpenoid dehydrogenase
Systematic name: (-)-menthol:NADP⁺ oxidoreductase
Comments: Not identical with EC 1.1.1.208 (+)-neomenthol dehydrogenase. Acts also on a number of other cyclohexanols and cyclohexenols.
References: [1956]

[EC 1.1.1.207 created 1984]

EC 1.1.1.208

Accepted name: (+)-neomenthol dehydrogenase
Reaction: (+)-neomenthol + NADP⁺ = (-)-menthone + NADPH + H⁺
Other name(s): monoterpenoid dehydrogenase
Systematic name: (+)-neomenthol:NADP⁺ oxidoreductase
Comments: Not identical with EC 1.1.1.207 (-)-menthol dehydrogenase. Acts also on a number of other cyclohexanols and cyclohexenols.
References: [1956]

[EC 1.1.1.208 created 1984]

EC 1.1.1.209

Accepted name: 3(or 17) α -hydroxysteroid dehydrogenase
Reaction: androsterone + NAD(P)⁺ = 5 α -androstane-3,17-dione + NAD(P)H + H⁺
Other name(s): 3(17) α -hydroxysteroid dehydrogenase
Systematic name: 3(or 17) α -hydroxysteroid:NAD(P)⁺ oxidoreductase
Comments: Acts on the 3 α -hydroxy group of androgens of the 5 α -androstane series; and also, more slowly, on the 17 α -hydroxy group of both androgenic and estrogenic substrates (*cf.* EC 1.1.1.51 3(or 17) β -hydroxysteroid dehydrogenase).

References: [2149, 2150]

[EC 1.1.1.209 created 1986]

EC 1.1.1.210

Accepted name: 3 β (or 20 α)-hydroxysteroid dehydrogenase
Reaction: 5 α -androstan-3 β ,17 β -diol + NADP⁺ = 17 β -hydroxy-5 α -androstan-3-one + NADPH + H⁺
Other name(s): progesterone reductase; dehydrogenase, 3 β ,20 α -hydroxy steroid; 3 β ,20 α -hydroxysteroid oxidoreductase
Systematic name: 3 β (or 20 α)-hydroxysteroid:NADP⁺ oxidoreductase
Comments: Also acts on 20 α -hydroxysteroids.
References: [3461]

[EC 1.1.1.210 created 1986]

EC 1.1.1.211

Accepted name: long-chain-3-hydroxyacyl-CoA dehydrogenase
Reaction: a long-chain (*S*)-3-hydroxyacyl-CoA + NAD⁺ = a long-chain 3-oxoacyl-CoA + NADH + H⁺
Other name(s): β -hydroxyacyl-CoA dehydrogenase; long-chain 3-hydroxyacyl coenzyme A dehydrogenase; 3-hydroxyacyl-CoA dehydrogenase; LCHAD
Systematic name: long-chain-(*S*)-3-hydroxyacyl-CoA:NAD⁺ oxidoreductase
Comments: This enzyme was purified from the mitochondrial inner membrane. The enzyme has a preference for long-chain substrates, and activity with a C₁₆ substrate was 6- to 15-fold higher than with a C₄ substrate (*cf.* EC 1.1.1.35 3-hydroxyacyl-CoA dehydrogenase).
References: [936]

[EC 1.1.1.211 created 1986]

EC 1.1.1.212

Accepted name: 3-oxoacyl-[acyl-carrier-protein] reductase (NADH)
Reaction: a (3*R*)-3-hydroxyacyl-[acyl-carrier protein] + NAD⁺ = a 3-oxoacyl-[acyl-carrier protein] + NADH + H⁺
Other name(s): 3-oxoacyl-[acyl carrier protein] (reduced nicotinamide adenine dinucleotide) reductase; 3-oxoacyl-[acyl-carrier-protein] reductase (NADH); (3*R*)-3-hydroxyacyl-[acyl-carrier-protein]:NAD⁺ oxidoreductase
Systematic name: (3*R*)-3-hydroxyacyl-[acyl-carrier protein]:NAD⁺ oxidoreductase
Comments: Forms part of the fatty acid synthase system in plants. Can be separated from EC 1.1.1.100, 3-oxoacyl-[acyl-carrier-protein] reductase.
References: [521]

[EC 1.1.1.212 created 1986]

EC 1.1.1.213

Accepted name: 3 α -hydroxysteroid 3-dehydrogenase (*Re*-specific)
Reaction: a 3 α -hydroxysteroid + NAD(P)⁺ = a 3-oxosteroid + NAD(P)H + H⁺
Other name(s): 3 α -hydroxysteroid dehydrogenase; 3 α -hydroxysteroid:NAD(P)⁺ 3-oxidoreductase (A-specific); 3 α -hydroxysteroid 3-dehydrogenase (A-specific)
Systematic name: 3 α -hydroxysteroid:NAD(P)⁺ 3-oxidoreductase (*Re*-specific)
Comments: The enzyme acts on multiple 3 α -hydroxysteroids. *Re*-specific with respect to NAD⁺ or NADP⁺ [*cf.* EC 1.1.1.50, 3 α -hydroxysteroid 3-dehydrogenase (*Si*-specific)]. Enzymes whose stereo-specificity with respect to NAD⁺ or NADP⁺ is not known are described by EC 1.1.1.357, 3 α -hydroxysteroid 3-dehydrogenase.
References: [304, 3905]

[EC 1.1.1.213 created 1986, modified 2012]

EC 1.1.1.214

Accepted name: 2-dehydropantolactone reductase (*Si*-specific)
Reaction: (*R*)-pantolactone + NADP⁺ = 2-dehydropantolactone + NADPH + H⁺
Other name(s): 2-oxopantoyl lactone reductase; 2-ketopantoyl lactone reductase; ketopantoyl lactone reductase; 2-dehydropantoyl-lactone reductase (B-specific); (*R*)-pantolactone:NADP⁺ oxidoreductase (B-specific); 2-dehydropantolactone reductase (B-specific)
Systematic name: (*R*)-pantolactone:NADP⁺ oxidoreductase (*Si*-specific)
Comments: The *Escherichia coli* enzyme differs from that from yeast [EC 1.1.1.168 2-dehydropantolactone reductase (*Re*-specific)], which is specific for the *Re*-face of NADP⁺, and in receptor requirements from EC 1.1.99.26 3-hydroxycyclohexanone dehydrogenase.
References: [4214]

[EC 1.1.1.214 created 1986, modified 1999, modified 2013]

EC 1.1.1.215

Accepted name: gluconate 2-dehydrogenase
Reaction: D-gluconate + NADP⁺ = 2-dehydro-D-gluconate + NADPH + H⁺
Other name(s): 2-keto-D-gluconate reductase; 2-ketogluconate reductase
Systematic name: D-gluconate:NADP⁺ oxidoreductase
Comments: Also acts on L-idonate, D-galactonate and D-xylonate.
References: [14, 600]

[EC 1.1.1.215 created 1989]

EC 1.1.1.216

Accepted name: farnesol dehydrogenase (NADP⁺)
Reaction: (*2E,6E*)-farnesol + NADP⁺ = (*2E,6E*)-farnesal + NADPH + H⁺
Other name(s): NADP⁺-farnesol dehydrogenase; farnesol (nicotinamide adenine dinucleotide phosphate) dehydrogenase
Systematic name: (*2E,6E*)-farnesol:NADP⁺ 1-oxidoreductase
Comments: Also acts, more slowly, on (*2Z,6E*)-farnesol, geraniol, citronerol and nerol.
References: [1652]

[EC 1.1.1.216 created 1989]

EC 1.1.1.217

Accepted name: benzyl-2-methyl-hydroxybutyrate dehydrogenase
Reaction: benzyl (*2R,3S*)-2-methyl-3-hydroxybutanoate + NADP⁺ = benzyl 2-methyl-3-oxobutanoate + NADPH + H⁺
Other name(s): benzyl 2-methyl-3-hydroxybutyrate dehydrogenase
Systematic name: benzyl-(*2R,3S*)-2-methyl-3-hydroxybutanoate:NADP⁺ 3-oxidoreductase
Comments: Also acts on benzyl (*2S,3S*)-2-methyl-3-hydroxybutanoate; otherwise highly specific.
References: [1122]

[EC 1.1.1.217 created 1989]

EC 1.1.1.218

Accepted name: morphine 6-dehydrogenase
Reaction: morphine + NAD(P)⁺ = morphinone + NAD(P)H + H⁺
Other name(s): naloxone reductase; reductase, naloxone

Systematic name: morphine:NAD(P)⁺ 6-oxidoreductase
Comments: Also acts on some other alkaloids, including codeine, normorphine and ethylmorphine, but only very slowly on 7,8-saturated derivatives such as dihydromorphine and dihydrocodeine. In the reverse direction, also reduces naloxone to the 6 α -hydroxy analogue. Activated by 2-mercaptoethanol.
References: [4324, 4325]

[EC 1.1.1.218 created 1989, modified 1990]

EC 1.1.1.219

Accepted name: dihydroflavonol 4-reductase
Reaction: a (2*R*,3*S*,4*S*)-leucoanthocyanidin + NADP⁺ = a (2*R*,3*R*)-dihydroflavonol + NADPH + H⁺
Other name(s): dihydrokaempferol 4-reductase; dihydromyricetin reductase; NADPH-dihydromyricetin reductase; dihydroquercetin reductase; DFR (gene name); *cis*-3,4-leucopelargonidin:NADP⁺ 4-oxidoreductase; dihydroflavanol 4-reductase (incorrect)
Systematic name: (2*R*,3*S*,4*S*)-leucoanthocyanidin:NADP⁺ 4-oxidoreductase
Comments: This plant enzyme, involved in the biosynthesis of anthocyanidins, is known to act on (+)-dihydrokaempferol, (+)-taxifolin, and (+)-dihydromyricetin, although some enzymes may act only on a subset of these compounds. Each dihydroflavonol is reduced to the corresponding *cis*-flavan-3,4-diol. NAD⁺ can act instead of NADP⁺, but more slowly.
References: [1469, 3617, 1019, 2224]

[EC 1.1.1.219 created 1989, modified 2016]

EC 1.1.1.220

Accepted name: 6-pyruvoyltetrahydropterin 2'-reductase
Reaction: 6-lactoyl-5,6,7,8-tetrahydropterin + NADP⁺ = 6-pyruvoyltetrahydropterin + NADPH + H⁺
Other name(s): 6-pyruvoyltetrahydropterin reductase; 6PPH4(2'-oxo) reductase; 6-pyruvoyl tetrahydropterin (2'-oxo)reductase; 6-pyruvoyl-tetrahydropterin 2'-reductase; pyruvoyl-tetrahydropterin reductase
Systematic name: 6-lactoyl-5,6,7,8-tetrahydropterin:NADP⁺ 2'-oxidoreductase
Comments: Not identical with EC 1.1.1.153 sepiapterin reductase.
References: [2550]

[EC 1.1.1.220 created 1989]

EC 1.1.1.221

Accepted name: vomifoliol dehydrogenase
Reaction: (6*S*,9*R*)-6-hydroxy-3-oxo- α -ionol + NAD⁺ = (6*S*)-6-hydroxy-3-oxo- α -ionone + NADH + H⁺
Other name(s): vomifoliol 4'-dehydrogenase; vomifoliol:NAD⁺ 4'-oxidoreductase
Systematic name: (6*S*,9*R*)-6-hydroxy-3-oxo- α -ionol:NAD⁺ oxidoreductase
Comments: Oxidizes vomifoliol to dehydrovomifoliol; involved in the metabolism of abscisic acid in *Corynebacterium* sp.
References: [1408]

[EC 1.1.1.221 created 1989]

[1.1.1.222 *Transferred entry. (R)-4-hydroxyphenyllactate dehydrogenase. Now included with EC 1.1.1.110, aromatic 2-oxoacid reductase*]

[EC 1.1.1.222 created 1989, deleted 2018]

EC 1.1.1.223

Accepted name: isopiperitenol dehydrogenase
Reaction: (-)-*trans*-isopiperitenol + NAD⁺ = (-)-isopiperitenone + NADH + H⁺
Systematic name: (-)-*trans*-isopiperitenol:NAD⁺ oxidoreductase

Comments: Acts on (-)-*trans*-isopiperitenol, (+)-*trans*-piperitenol and (+)-*trans*-pulegol. Involved in the biosynthesis of menthol and related monoterpenes in peppermint (*Mentha piperita*) leaves.
References: [1957]

[EC 1.1.1.223 created 1989]

EC 1.1.1.224

Accepted name: mannose-6-phosphate 6-reductase
Reaction: D-mannitol 1-phosphate + NADP⁺ = D-mannose 6-phosphate + NADPH + H⁺
Other name(s): NADPH-dependent mannose 6-phosphate reductase; mannose-6-phosphate reductase; 6-phosphomannose reductase; NADP-dependent mannose-6-P:mannitol-1-*P* oxidoreductase; NADPH-dependent M6P reductase; NADPH-mannose-6-*P* reductase
Systematic name: D-mannitol-1-phosphate:NADP⁺ 6-oxidoreductase
Comments: Involved in the biosynthesis of mannitol in celery (*Apium graveolens*) leaves.
References: [3260]

[EC 1.1.1.224 created 1989]

EC 1.1.1.225

Accepted name: chlordecone reductase
Reaction: chlordecone alcohol + NADP⁺ = chlordecone + NADPH + H⁺
Other name(s): CDR
Systematic name: chlordecone-alcohol:NADP⁺ 2-oxidoreductase
Comments: Chlordecone is an organochlorine pesticide.
References: [2597]

[EC 1.1.1.225 created 1989]

EC 1.1.1.226

Accepted name: 4-hydroxycyclohexanecarboxylate dehydrogenase
Reaction: *trans*-4-hydroxycyclohexanecarboxylate + NAD⁺ = 4-oxocyclohexanecarboxylate + NADH + H⁺
Other name(s): *trans*-4-hydroxycyclohexanecarboxylate dehydrogenase
Systematic name: *trans*-4-hydroxycyclohexanecarboxylate:NAD⁺ 4-oxidoreductase
Comments: The enzyme from *Corynebacterium cyclohexanicum* is highly specific for the *trans*-4-hydroxy derivative.
References: [2833]

[EC 1.1.1.226 created 1990]

EC 1.1.1.227

Accepted name: (-)-borneol dehydrogenase
Reaction: (-)-borneol + NAD⁺ = (-)-camphor + NADH + H⁺
Systematic name: (-)-borneol:NAD⁺ oxidoreductase
Comments: NADP⁺ can also act, but more slowly.
References: [777]

[EC 1.1.1.227 created 1990 (EC 1.1.1.182 created 1983, part incorporated 1990)]

EC 1.1.1.228

Accepted name: (+)-sabinol dehydrogenase
Reaction: (+)-*cis*-sabinol + NAD⁺ = (+)-sabinone + NADH + H⁺
Other name(s): (+)-*cis*-sabinol dehydrogenase

Systematic name: (+)-*cis*-sabinol:NAD⁺ oxidoreductase
Comments: NADP⁺ can also act, but more slowly. Involved in the biosynthesis of (+)-3-thujone and (-)-3-isothujone.
References: [777]

[EC 1.1.1.228 created 1990 (EC 1.1.1.182 created 1983, part incorporated 1990)]

EC 1.1.1.229

Accepted name: diethyl 2-methyl-3-oxosuccinate reductase
Reaction: diethyl (2*R*,3*R*)-2-methyl-3-hydroxysuccinate + NADP⁺ = diethyl 2-methyl-3-oxosuccinate + NADPH + H⁺
Systematic name: diethyl-(2*R*,3*R*)-2-methyl-3-hydroxysuccinate:NADP⁺ 3-oxidoreductase
Comments: Also acts on diethyl (2*S*,3*R*)-2-methyl-3-hydroxysuccinate; and on the corresponding dimethyl esters.
References: [1123]

[EC 1.1.1.229 created 1990]

EC 1.1.1.230

Accepted name: 3 α -hydroxyglycyrrhetinate dehydrogenase
Reaction: 3 α -hydroxyglycyrrhetinate + NADP⁺ = 3-oxoglycyrrhetinate + NADPH + H⁺
Systematic name: 3 α -hydroxyglycyrrhetinate:NADP⁺ 3-oxidoreductase
Comments: Highly specific to 3 α -hydroxy derivatives of glycyrrhetinate and its analogues. Not identical to EC 1.1.1.50 3 α -hydroxysteroid dehydrogenase (*Si*-specific).
References: [43]

[EC 1.1.1.230 created 1990]

EC 1.1.1.231

Accepted name: 15-hydroxyprostaglandin-I dehydrogenase (NADP⁺)
Reaction: (5*Z*,13*E*)-(15*S*)-6,9 α -epoxy-11 α ,15-dihydroxyprosta-5,13-dienoate + NADP⁺ = (5*Z*,13*E*)-6,9 α -epoxy-11 α -hydroxy-15-oxoprosta-5,13-dienoate + NADPH + H⁺
Other name(s): prostacyclin dehydrogenase; PG I₂ dehydrogenase; prostacyclin dehydrogenase; NADP-linked 15-hydroxyprostaglandin (prostacyclin) dehydrogenase; NADP⁺-dependent PGI₂-specific 15-hydroxyprostaglandin dehydrogenase; 15-hydroxyprostaglandin-I dehydrogenase (NADP)
Systematic name: (5*Z*,13*E*)-(15*S*)-6,9 α -epoxy-11 α ,15-dihydroxyprosta-5,13-dienoate:NADP⁺ 15-oxidoreductase
Comments: Specific for prostaglandin I₂.
References: [2031]

[EC 1.1.1.231 created 1990]

EC 1.1.1.232

Accepted name: 15-hydroxyicosatetraenoate dehydrogenase
Reaction: (15*S*)-15-hydroxy-5,8,11-*cis*-13-*trans*-icosatetraenoate + NAD(P)⁺ = 15-oxo-5,8,11-*cis*-13-*trans*-icosatetraenoate + NAD(P)H + H⁺
Other name(s): 15-hydroxyeicosatetraenoate dehydrogenase
Systematic name: (15*S*)-15-hydroxy-5,8,11-*cis*-13-*trans*-icosatetraenoate:NAD(P)⁺ 15-oxidoreductase
References: [3572]

[EC 1.1.1.232 created 1992]

EC 1.1.1.233

Accepted name: *N*-acylmannosamine 1-dehydrogenase

Reaction: $N\text{-acyl-D-mannosamine} + \text{NAD}^+ = N\text{-acyl-D-mannosaminolactone} + \text{NADH} + \text{H}^+$
Other name(s): *N*-acylmannosamine dehydrogenase; *N*-acetyl-D-mannosamine dehydrogenase; *N*-acyl-D-mannosamine dehydrogenase; *N*-acylmannosamine dehydrogenase
Systematic name: *N*-acyl-D-mannosamine:NAD⁺ 1-oxidoreductase
Comments: Acts on acetyl-D-mannosamine and glycolyl-D-mannosamine. Highly specific.
References: [1570]

[EC 1.1.1.233 created 1992]

EC 1.1.1.234

Accepted name: flavanone 4-reductase
Reaction: $(2S)\text{-flavan-4-ol} + \text{NADP}^+ = (2S)\text{-flavanone} + \text{NADPH} + \text{H}^+$
Systematic name: $(2S)\text{-flavan-4-ol:NADP}^+$ 4-oxidoreductase
Comments: Involved in the biosynthesis of 3-deoxyanthocyanidins from flavanones such as naringenin or eriodictyol.
References: [3644]

[EC 1.1.1.234 created 1992]

EC 1.1.1.235

Accepted name: 8-oxocoformycin reductase
Reaction: $\text{coformycin} + \text{NADP}^+ = 8\text{-oxocoformycin} + \text{NADPH} + \text{H}^+$
Other name(s): 8-ketodeoxycorformycin reductase
Systematic name: coformycin:NADP⁺ 8-oxidoreductase
Comments: *Si*-specific with respect to NADPH. Also reduces 8-oxodeoxy-coformycin to the nucleoside antibiotic deoxycorformycin.
References: [1383]

[EC 1.1.1.235 created 1992]

EC 1.1.1.236

Accepted name: tropinone reductase II
Reaction: $\text{pseudotropine} + \text{NADP}^+ = \text{tropinone} + \text{NADPH} + \text{H}^+$
Other name(s): tropinone (ψ -tropine-forming) reductase; pseudotropine forming tropinone reductase; tropinone reductase (ambiguous); TR-II
Systematic name: pseudotropine:NADP⁺ 3-oxidoreductase
Comments: This enzyme along with EC 1.1.1.206, tropine dehydrogenase, represents a branch point in tropane alkaloid metabolism [2701]. Tropine (the product of EC 1.1.1.206) is incorporated into hyoscyamine and scopolamine whereas pseudotropine (the product of EC 1.1.1.236) is the first specific metabolite on the pathway to the calystegines [2701]. Both enzymes are always found together in any given tropane-alkaloid-producing species, have a common substrate, tropinone, and are strictly stereospecific [674].
References: [868, 674, 2701, 867]

[EC 1.1.1.236 created 1992, modified 2007]

EC 1.1.1.237

Accepted name: hydroxyphenylpyruvate reductase
Reaction: (1) $(R)\text{-3-(4-hydroxyphenyl)lactate} + \text{NAD(P)}^+ = 3\text{-(4-hydroxyphenyl)pyruvate} + \text{NAD(P)H} + \text{H}^+$
(2) $(R)\text{-3-(3,4-dihydroxyphenyl)lactate} + \text{NAD(P)}^+ = 3\text{-(3,4-dihydroxyphenyl)pyruvate} + \text{NAD(P)H} + \text{H}^+$
Other name(s): HPPR

Systematic name: (*R*)-3-(4-hydroxyphenyl)lactate:NAD(P)⁺ oxidoreductase
Comments: The enzyme participates in the biosynthesis of rosmarinic acid. It belongs to the family of D-isomer-specific 2-hydroxyacid dehydrogenases, and prefers NADPH to NADH.
References: [2987, 1913, 1924, 4105]

[EC 1.1.1.237 created 1992, modified 2018]

EC 1.1.1.238

Accepted name: 12 β -hydroxysteroid dehydrogenase
Reaction: 3 α ,7 α ,12 β -trihydroxy-5 β -cholan-24-oate + NADP⁺ = 3 α ,7 α -dihydroxy-12-oxo-5 β -cholan-24-oate + NADPH + H⁺
Other name(s): 12 β -hydroxy steroid (nicotinamide adenine dinucleotide phosphate) dehydrogenase
Systematic name: 12 β -hydroxysteroid:NADP⁺ 12-oxidoreductase
Comments: Acts on a number of bile acids, both in their free and conjugated forms.
References: [914]

[EC 1.1.1.238 created 1992]

EC 1.1.1.239

Accepted name: 3 α (17 β)-hydroxysteroid dehydrogenase (NAD⁺)
Reaction: testosterone + NAD⁺ = androstenedione + NADH + H⁺
Other name(s): 3 α ,17 β -hydroxy steroid dehydrogenase; 3 α (17 β)-HSD; 17-ketoreductase (ambiguous); 17 β -HSD (ambiguous); HSD17B6 (gene name); HSD17B8 (gene name)
Systematic name: 3 α (or 17 β)-hydroxysteroid:NAD⁺ oxidoreductase
Comments: Also acts on other 17 β -hydroxysteroids and on the 3 α -hydroxy group of pregnanes and bile acids. Different from EC 1.1.1.50 3 α -hydroxysteroid dehydrogenase (*Si*-specific) or EC 1.1.1.213 3 α -hydroxysteroid dehydrogenase (*Re*-specific).
References: [3761, 4046, 946, 2849]

[EC 1.1.1.239 created 1992, modified 2012 (EC 1.1.1.63 created 1965, incorporated 2012)]

EC 1.1.1.240

Accepted name: *N*-acetylhexosamine 1-dehydrogenase
Reaction: *N*-acetyl- α -D-glucosamine + NAD⁺ = *N*-acetyl-D-glucosamine + NADH + H⁺
Other name(s): *N*-acetylhexosamine dehydrogenase; *N*-acetyl-D-hexosamine dehydrogenase
Systematic name: *N*-acetyl-D-hexosamine:NAD⁺ 1-oxidoreductase
Comments: Also acts on *N*-acetylgalactosamine and, more slowly, on *N*-acetylmannosamine. Anomeric specificity was tested with *N*-acetyl-D-glucosamine, and it was shown that the enzyme is specific for the α anomer.
References: [1571]

[EC 1.1.1.240 created 1992]

EC 1.1.1.241

Accepted name: 6-*endo*-hydroxycineole dehydrogenase
Reaction: 6-*endo*-hydroxycineole + NAD⁺ = 6-oxocineole + NADH + H⁺
Systematic name: 6-*endo*-hydroxycineole:NAD⁺ 6-oxidoreductase
References: [4217]

[EC 1.1.1.241 created 1992]

[1.1.1.242 Transferred entry. zeatin reductase. Now EC 1.3.1.69, zeatin reductase]

[EC 1.1.1.242 created 1992, deleted 2001]

EC 1.1.1.243

Accepted name: carveol dehydrogenase
Reaction: (-)-*trans*-carveol + NADP⁺ = (-)-carvone + NADPH + H⁺
Other name(s): (-)-*trans*-carveol dehydrogenase
Systematic name: (-)-*trans*-carveol:NADP⁺ oxidoreductase
References: [1186]

[EC 1.1.1.243 created 1992]

EC 1.1.1.244

Accepted name: methanol dehydrogenase
Reaction: methanol + NAD⁺ = formaldehyde + NADH + H⁺
Systematic name: methanol:NAD⁺ oxidoreductase
References: [119]

[EC 1.1.1.244 created 1992]

EC 1.1.1.245

Accepted name: cyclohexanol dehydrogenase
Reaction: cyclohexanol + NAD⁺ = cyclohexanone + NADH + H⁺
Systematic name: cyclohexanol:NAD⁺ oxidoreductase
Comments: Also oxidizes some other alicyclic alcohols and diols.
References: [741, 857, 3932]

[EC 1.1.1.245 created 1992]

[1.1.1.246 *Transferred entry. pterocarpin synthase. This activity is now known to be catalysed by two enzymes, vestitone reductase (EC 1.1.1.348) and medicarpin synthase (EC 4.2.1.139).*]

[EC 1.1.1.246 created 1992, deleted 2013]

EC 1.1.1.247

Accepted name: codeinone reductase (NADPH)
Reaction: codeine + NADP⁺ = codeinone + NADPH + H⁺
Systematic name: codeine:NADP⁺ oxidoreductase
Comments: Catalyses the reversible reduction of codeinone to codeine, which is a direct precursor of morphine in the opium poppy plant, *Papaver somniferum*.
References: [2198, 2197]

[EC 1.1.1.247 created 1999, modified 2001]

EC 1.1.1.248

Accepted name: salutaridine reductase (NADPH)
Reaction: salutaridinol + NADP⁺ = salutaridine + NADPH + H⁺
Systematic name: salutaridinol:NADP⁺ 7-oxidoreductase
Comments: Catalyses the reversible reduction of salutaridine to salutaridinol, which is a direct precursor of morphinan alkaloids in the poppy plant.
References: [1182]

[EC 1.1.1.248 created 1999, modified 2001]

[1.1.1.249 *Deleted entry. Provisional entry deleted. Revised and reinstated as EC 2.5.1.46 deoxyhypusine synthase*]

[EC 1.1.1.249 provisional version created 1999, deleted 1999 (reinstated 2001 as EC 2.5.1.46)]

EC 1.1.1.250

Accepted name: D-arabinitol 2-dehydrogenase
Reaction: D-arabinitol + NAD⁺ = D-ribulose + NADH + H⁺
Other name(s): D-arabinitol 2-dehydrogenase (ribulose-forming)
Systematic name: D-arabinitol:NAD⁺ 2-oxidoreductase (D-ribulose-forming)
References: [4244, 3094]

[EC 1.1.1.250 created 1999]

EC 1.1.1.251

Accepted name: galactitol-1-phosphate 5-dehydrogenase
Reaction: galactitol 1-phosphate + NAD⁺ = D-tagatose 6-phosphate + NADH + H⁺
Other name(s): *gatD* (gene name)
Systematic name: galactitol-1-phosphate:NAD⁺ oxidoreductase
Comments: The enzyme from the bacterium *Escherichia coli* is involved in a galactitol degradation pathway. It contains two zinc atoms per subunit.
References: [4240, 2806, 257]

[EC 1.1.1.251 created 1999]

EC 1.1.1.252

Accepted name: tetrahydroxynaphthalene reductase
Reaction: scytalone + NADP⁺ = 1,3,6,8-tetrahydroxynaphthalene + NADPH + H⁺
Systematic name: scytalone:NADP⁺ Δ⁵-oxidoreductase
Comments: Reduces 1,3,6,8-tetrahydroxynaphthalene to scytalone and also reduces 1,3,8-trihydroxynaphthalene to vermeline. Involved with EC 4.2.1.94 scytalone dehydratase in the biosynthesis of melanin in pathogenic fungi.
References: [4187, 4041, 3876]

[EC 1.1.1.252 created 1992 as EC 1.3.1.50, transferred 1999 to EC 1.1.1.252]

[1.1.1.253] Transferred entry. *pteridine reductase*. Now EC 1.5.1.33, *pteridine reductase*

[EC 1.1.1.253 created 1999, deleted 2003]

EC 1.1.1.254

Accepted name: (S)-carnitine 3-dehydrogenase
Reaction: (S)-carnitine + NAD⁺ = 3-dehydrocarnitine + NADH + H⁺
Systematic name: (S)-carnitine:NAD⁺ oxidoreductase
Comments: Specific for the (S)-enantiomer of carnitine, i.e., the enantiomer of the substrate of EC 1.1.1.108 carnitine 3-dehydrogenase
References: [3447]

[EC 1.1.1.254 created 1999]

EC 1.1.1.255

Accepted name: mannitol dehydrogenase
Reaction: D-mannitol + NAD⁺ = D-mannose + NADH + H⁺
Other name(s): MTD; NAD-dependent mannitol dehydrogenase
Systematic name: mannitol:NAD⁺ 1-oxidoreductase
Comments: The enzyme from *Apium graveolens* (celery) oxidizes alditols with a minimum requirement of 2R chirality at the carbon adjacent to the primary carbon undergoing the oxidation. The enzyme is specific for NAD⁺ and does not use NADP⁺.
References: [3665, 3666, 4223, 3664]

[EC 1.1.1.255 created 2000]

EC 1.1.1.256

Accepted name: fluoren-9-ol dehydrogenase
Reaction: fluoren-9-ol + NAD(P)⁺ = fluoren-9-one + NAD(P)H + H⁺
Systematic name: fluoren-9-ol:NAD(P)⁺ oxidoreductase
Comments: Involved in the pathway for fluorene metabolism in *Arthrobacter* sp.
References: [516, 1285]

[EC 1.1.1.256 created 2000]

EC 1.1.1.257

Accepted name: 4-(hydroxymethyl)benzenesulfonate dehydrogenase
Reaction: 4-(hydroxymethyl)benzenesulfonate + NAD⁺ = 4-formylbenzenesulfonate + NADH + H⁺
Systematic name: 4-(hydroxymethyl)benzenesulfonate:NAD⁺ oxidoreductase
Comments: Involved in the toluene-4-sulfonate degradation pathway in *Comamonas testosteroni*.
References: [1789]

[EC 1.1.1.257 created 2000]

EC 1.1.1.258

Accepted name: 6-hydroxyhexanoate dehydrogenase
Reaction: 6-hydroxyhexanoate + NAD⁺ = 6-oxohexanoate + NADH + H⁺
Systematic name: 6-hydroxyhexanoate:NAD⁺ oxidoreductase
Comments: Involved in the cyclohexanol degradation pathway in *Acinetobacter* NCIB 9871.
References: [857, 1450]

[EC 1.1.1.258 created 2000]

EC 1.1.1.259

Accepted name: 3-hydroxypimeloyl-CoA dehydrogenase
Reaction: 3-hydroxypimeloyl-CoA + NAD⁺ = 3-oxopimeloyl-CoA + NADH + H⁺
Systematic name: 3-hydroxypimeloyl-CoA:NAD⁺ oxidoreductase
Comments: Involved in the anaerobic pathway of benzoate degradation in bacteria.
References: [1405]

[EC 1.1.1.259 created 2000]

EC 1.1.1.260

Accepted name: sulcatone reductase
Reaction: sulcatol + NAD⁺ = sulcatone + NADH + H⁺
Systematic name: sulcatol:NAD⁺ oxidoreductase
Comments: Studies on the effects of growth-stage and nutrient supply on the stereochemistry of sulcatone reduction in *Clostridia pasteurianum*, *C. tyrobutyricum* and *Lactobacillus brevis* suggest that there may be at least two sulcatone reductases with different stereospecificities.
References: [250, 3888, 3889]

[EC 1.1.1.260 created 2000, modified 2001]

EC 1.1.1.261

Accepted name: *sn*-glycerol-1-phosphate dehydrogenase
Reaction: *sn*-glycerol 1-phosphate + NAD(P)⁺ = glycerone phosphate + NAD(P)H + H⁺

Other name(s): glycerol-1-phosphate dehydrogenase [NAD(P)⁺]; *sn*-glycerol-1-phosphate:NAD⁺ oxidoreductase; G-1-*P* dehydrogenase; Gro1PDH; AraM

Systematic name: *sn*-glycerol-1-phosphate:NAD(P)⁺ 2-oxidoreductase

Comments: This enzyme is found primarily as a Zn²⁺-dependent form in archaea but a Ni²⁺-dependent form has been found in Gram-positive bacteria [1311]. The Zn²⁺-dependent metalloenzyme is responsible for the formation of archaea-specific *sn*-glycerol-1-phosphate, the first step in the biosynthesis of polar lipids in archaea. It is the enantiomer of *sn*-glycerol 3-phosphate, the form of glycerophosphate found in bacteria and eukaryotes. The other enzymes involved in the biosynthesis of polar lipids in archaea are EC 2.5.1.41 (phosphoglycerol geranylgeranyltransferase) and EC 2.5.1.42 (geranylgeranylglycerol-phosphate geranylgeranyltransferase), which together alkylate the hydroxy groups of glycerol 1-phosphate to give unsaturated archaetidic acid, which is acted upon by EC 2.7.7.67 (CDP-archaeol synthase) to form CDP-unsaturated archaeol. The final step in the pathway involves the addition of L-serine, with concomitant removal of CMP, leading to the production of unsaturated archaetidylserine [2621]. Activity of the enzyme is stimulated by K⁺ [2793].

References: [2792, 2793, 2000, 2621, 1360, 1311]

[EC 1.1.1.261 created 2000, modified 2009]

EC 1.1.1.262

Accepted name: 4-hydroxythreonine-4-phosphate dehydrogenase

Reaction: 4-phosphooxy-L-threonine + NAD⁺ = 3-amino-2-oxopropyl phosphate + CO₂ + NADH + H⁺

Other name(s): NAD⁺-dependent threonine 4-phosphate dehydrogenase; L-threonine 4-phosphate dehydrogenase; 4-(phosphohydroxy)-L-threonine dehydrogenase; PdxA; 4-(phosphonoxy)-L-threonine:NAD⁺ oxidoreductase; 4-phosphooxy-L-threonine:NAD⁺ oxidoreductase

Systematic name: 4-phosphooxy-L-threonine:NAD⁺ 3-oxidoreductase (decarboxylating)

Comments: The enzyme is part of the biosynthesis pathway of the coenzyme pyridoxal 5'-phosphate found in anaerobic bacteria.

References: [492, 2109, 3545, 193]

[EC 1.1.1.262 created 2000, modified 2006]

EC 1.1.1.263

Accepted name: 1,5-anhydro-D-fructose reductase

Reaction: 1,5-anhydro-D-glucitol + NADP⁺ = 1,5-anhydro-D-fructose + NADPH + H⁺

Systematic name: 1,5-anhydro-D-glucitol:NADP⁺ oxidoreductase

Comments: Also reduces pyridine-3-aldehyde and 2,3-butanedione. Acetaldehyde, 2-dehydroglucose (glucosone) and glucuronate are poor substrates, but there is no detectable action on glucose, mannose and fructose.

References: [3295]

[EC 1.1.1.263 created 2000]

EC 1.1.1.264

Accepted name: L-idonate 5-dehydrogenase

Reaction: L-idonate + NAD(P)⁺ = 5-dehydro-D-gluconate + NAD(P)H + H⁺

Systematic name: L-idonate:NAD(P)⁺ oxidoreductase

Comments: The enzyme from the bacterium *Escherichia coli* is specific for 5-dehydro-D-gluconate. *cf.* EC 1.1.1.366, L-idonate 5-dehydrogenase (NAD⁺).

References: [223]

[EC 1.1.1.264 created 2000, modified 2013]

EC 1.1.1.265

Accepted name: 3-methylbutanal reductase
Reaction: 3-methylbutanol + NAD(P)⁺ = 3-methylbutanal + NAD(P)H + H⁺
Systematic name: 3-methylbutanol:NAD(P)⁺ oxidoreductase
Comments: The enzyme purified from *Saccharomyces cerevisiae* catalyses the reduction of a number of straight-chain and branched aldehydes, as well as some aromatic aldehydes.
References: [4007, 2755]

[EC 1.1.1.265 created 2000]

EC 1.1.1.266

Accepted name: dTDP-4-dehydro-6-deoxyglucose reductase
Reaction: dTDP- α -D-fucopyranose + NAD(P)⁺ = dTDP-4-dehydro-6-deoxy- α -D-glucose + NAD(P)H + H⁺
Other name(s): dTDP-4-keto-6-deoxyglucose reductase; dTDP-D-fucose:NADP⁺ oxidoreductase; Fcf1; dTDP-6-deoxy-D-xylo-hex-4-ulopyranose reductase
Systematic name: dTDP- α -D-fucopyranose:NAD(P)⁺ oxidoreductase
Comments: The enzymes from the Gram-negative bacteria *Aggregatibacter actinomycetemcomitans* and *Escherichia coli* O52 are involved in activation of fucose for incorporation into capsular polysaccharide O-antigens [4382, 4114]. The enzyme from the Gram-positive bacterium *Anoxybacillus tepidamans* (*Geobacillus tepidamans*) is involved in activation of fucose for incorporation into the organism's S-layer [4428]. The enzyme from *Escherichia coli* O52 has a higher catalytic efficiency with NADH than with NADPH [4114].
References: [4382, 4428, 4114]

[EC 1.1.1.266 created 2001, modified 2013]

EC 1.1.1.267

Accepted name: 1-deoxy-D-xylulose-5-phosphate reductoisomerase
Reaction: 2-C-methyl-D-erythritol 4-phosphate + NADP⁺ = 1-deoxy-D-xylulose 5-phosphate + NADPH + H⁺
Other name(s): DXP-reductoisomerase; 1-deoxy-D-xylulose-5-phosphate isomeroreductase; 2-C-methyl-D-erythritol 4-phosphate (MEP) synthase
Systematic name: 2-C-methyl-D-erythritol-4-phosphate:NADP⁺ oxidoreductase (isomerizing)
Comments: The enzyme requires Mn²⁺, Co²⁺ or Mg²⁺ for activity, with the first being most effective. The enzyme from several eubacteria, including *Escherichia coli*, forms part of an alternative nonmevalonate pathway for terpenoid biosynthesis (for diagram, click here). The mechanism has been shown to be a retroaldol/aldol reaction [2662].
References: [3780, 2662]

[EC 1.1.1.267 created 2001]

EC 1.1.1.268

Accepted name: 2-(R)-hydroxypropyl-CoM dehydrogenase
Reaction: 2-(R)-hydroxypropyl-CoM + NAD⁺ = 2-oxopropyl-CoM + NADH + H⁺
Other name(s): 2-(2-(R)-hydroxypropylthio)ethanesulfonate dehydrogenase
Systematic name: 2-[2-(R)-hydroxypropylthio]ethanesulfonate:NAD⁺ oxidoreductase
Comments: The enzyme is highly specific for (R)-2-hydroxyalkyl thioethers of CoM, in contrast to EC 1.1.1.269, 2-(S)-hydroxypropyl-CoM dehydrogenase, which is highly specific for the (S)-enantiomer. This enzyme forms component III of a four-component enzyme system comprising EC 4.4.1.23 (2-hydroxypropyl-CoM lyase; component I), EC 1.8.1.5 [2-oxopropyl-CoM reductase (carboxylating); component II], EC 1.1.1.268 [2-(R)-hydroxypropyl-CoM dehydrogenase; component III] and EC 1.1.1.269 [2-(S)-hydroxypropyl-CoM dehydrogenase; component IV] that is involved in epoxyalkane carboxylation in *Xanthobacter* sp. strain Py2.
References: [62]

[EC 1.1.1.268 created 2001]

EC 1.1.1.269

- Accepted name:** 2-(*S*)-hydroxypropyl-CoM dehydrogenase
Reaction: (2*S*)-2-hydroxypropyl-CoM + NAD⁺ = 2-oxopropyl-CoM + NADH + H⁺
Other name(s): 2-(2-(*S*)-hydroxypropylthio)ethanesulfonate dehydrogenase; 2-[2-(*S*)-hydroxypropylthio]ethanesulfonate:NAD⁺ oxidoreductase
Systematic name: 2-[(2*S*)-2-hydroxypropyl]sulfanylethanesulfonate:NAD⁺ oxidoreductase
Comments: The enzyme is highly specific for (2*S*)-2-hydroxyalkyl thioethers of CoM, in contrast to EC 1.1.1.268, 2-(*R*)-hydroxypropyl-CoM dehydrogenase, which is highly specific for the (*R*)-enantiomer. This enzyme forms component IV of a four-component enzyme system EC 4.4.1.23 (2-hydroxypropyl-CoM lyase; component I), EC 1.8.1.5 [2-oxopropyl-CoM reductase (carboxylating); component II], EC 1.1.1.268 [2-(*R*)-hydroxypropyl-CoM dehydrogenase; component III] and EC 1.1.1.269 [2-(*S*)-hydroxypropyl-CoM dehydrogenase; component IV].html";click here that is involved in epoxyalkane carboxylation in *Xanthobacter* sp. strain Py2.
References: [62]

[EC 1.1.1.269 created 2001]

EC 1.1.1.270

- Accepted name:** 3β-hydroxysteroid 3-dehydrogenase
Reaction: a 3β-hydroxysteroid + NADP⁺ = a 3-oxosteroid + NADPH + H⁺
Other name(s): 3-keto-steroid reductase; 3-KSR; HSD17B7 (gene name); ERG27 (gene name)
Systematic name: 3β-hydroxysteroid:NADP⁺ 3-oxidoreductase
Comments: The enzyme acts on multiple 3β-hydroxysteroids. Participates in the biosynthesis of zemosterol and cholesterol, where it catalyses the reaction in the opposite direction to that shown. The mammalian enzyme is bifunctional and also catalyses EC 1.1.1.62, 17β-estradiol 17-dehydrogenase [2398].
References: [3763, 297, 1133, 2398]

[EC 1.1.1.270 created 2002, modified 2012]

EC 1.1.1.271

- Accepted name:** GDP-L-fucose synthase
Reaction: GDP-β-L-fucose + NADP⁺ = GDP-4-dehydro-α-D-rhamnose + NADPH + H⁺
Other name(s): GDP-4-keto-6-deoxy-D-mannose-3,5-epimerase-4-reductase; GDP-L-fucose:NADP⁺ 4-oxidoreductase (3,5-epimerizing)
Systematic name: GDP-β-L-fucose:NADP⁺ 4-oxidoreductase (3,5-epimerizing)
Comments: Both human and *Escherichia coli* enzymes can use NADH in place of NADPH to a slight extent.
References: [540, 2467, 2505, 3576]

[EC 1.1.1.271 created 2002, modified 2003]

EC 1.1.1.272

- Accepted name:** D-2-hydroxyacid dehydrogenase (NADP⁺)
Reaction: an (*R*)-2-hydroxycarboxylate + NADP⁺ = a 2-oxocarboxylate + NADPH + H⁺
Other name(s): *ddh* (gene name)
Systematic name: (*R*)-2-hydroxycarboxylate:NADP⁺ oxidoreductase
Comments: This enzyme, characterized from the halophilic archaeon *Haloferax mediterranei* and the mold *Aspergillus oryzae*, catalyses a stereospecific reduction of 2-oxocarboxylic acids into the corresponding D-2-hydroxycarboxylic acids. The enzyme prefers substrates with a main chain of 5 carbons (such as 4-methyl-2-oxopentanoate) to those with a shorter chain, and can use NADH with much lower efficiency. cf. EC 1.1.1.345, (*d*)-2-hydroxyacid dehydrogenase (NAD⁺).
References: [851, 3500]

[EC 1.1.1.272 created 2002, modified 2013]

EC 1.1.1.273

Accepted name: vellosimine dehydrogenase
Reaction: 10-deoxysarpagine + NADP⁺ = vellosimine + NADPH + H⁺
Systematic name: 10-deoxysarpagine:NADP⁺ oxidoreductase
Comments: Also acts on related alkaloids with an endo-aldehyde group as vellosimine (same stereochemistry at C-16) but only slight activity with exo-aldehydes. Detected in many cell suspension cultures of plants from the family Apocynaceae.
References: [2997]

[EC 1.1.1.273 created 2002]

EC 1.1.1.274

Accepted name: 2,5-didehydrogluconate reductase (2-dehydro-D-gluconate-forming)
Reaction: 2-dehydro-D-gluconate + NADP⁺ = 2,5-didehydro-D-gluconate + NADPH + H⁺
Other name(s): 2,5-diketo-D-gluconate reductase (ambiguous)
Systematic name: 2-dehydro-D-gluconate:NADP⁺ 2-oxidoreductase (2-dehydro-D-gluconate-forming)
Comments: The enzyme is involved in the catabolism of 2,5-didehydrogluconate. *cf.* EC 1.1.1.346, 2,5-didehydrogluconate reductase (2-dehydro-L-gulonate-forming).
References: [3583]

[EC 1.1.1.274 created 2002, modified 2013]

EC 1.1.1.275

Accepted name: (+)-*trans*-carveol dehydrogenase
Reaction: (+)-*trans*-carveol + NAD⁺ = (+)-(*S*)-carvone + NADH + H⁺
Other name(s): carveol dehydrogenase
Systematic name: (+)-*trans*-carveol:NAD⁺ oxidoreductase
Comments: NADP⁺ cannot replace NAD⁺. Forms part of the monoterpenoid biosynthesis pathway in *Carum carvi* (caraway) seeds.
References: [368]

[EC 1.1.1.275 created 2003]

EC 1.1.1.276

Accepted name: serine 3-dehydrogenase (NADP⁺)
Reaction: L-serine + NADP⁺ = 2-aminoacetaldehyde + CO₂ + NADPH + H⁺ (overall reaction)
(1a) L-serine + NADP⁺ = 2-aminomalonaldehyde + NADPH + H⁺
(1b) 2-aminomalonaldehyde = 2-aminoacetaldehyde + CO₂ (spontaneous)
Other name(s): serine 3-dehydrogenase
Systematic name: L-serine:NADP⁺ 3-oxidoreductase
Comments: NAD⁺ cannot replace NADP⁺ [*cf.* EC 1.1.1.387, serine 3-dehydrogenase (NAD⁺)].
References: [1096, 616]

[EC 1.1.1.276 created 2003, modified 2015]

EC 1.1.1.277

Accepted name: 3β-hydroxy-5β-steroid dehydrogenase
Reaction: 3β-hydroxy-5β-pregnane-20-one + NADP⁺ = 5β-pregnan-3,20-dione + NADPH + H⁺
Other name(s): 3β-hydroxysteroid 5β-oxidoreductase; 3β-hydroxysteroid 5β-progesterone oxidoreductase
Systematic name: 3β-hydroxy-5β-steroid:NADP⁺ 3-oxidoreductase
References: [3696, 3432, 2260]

[EC 1.1.1.277 created 2003]

EC 1.1.1.278

Accepted name: 3 β -hydroxy-5 α -steroid dehydrogenase
Reaction: 3 β -hydroxy-5 α -pregnane-20-one + NADP⁺ = 5 α -pregnan-3,20-dione + NADPH + H⁺
Systematic name: 3 β -hydroxy-5 α -steroid:NADP⁺ 3-oxidoreductase
References: [2260, 4135]

[EC 1.1.1.278 created 2003]

EC 1.1.1.279

Accepted name: (*R*)-3-hydroxyacid-ester dehydrogenase
Reaction: ethyl (*R*)-3-hydroxyhexanoate + NADP⁺ = ethyl 3-oxohexanoate + NADPH + H⁺
Other name(s): 3-oxo ester (*R*)-reductase
Systematic name: ethyl-(*R*)-3-hydroxyhexanoate:NADP⁺ 3-oxidoreductase
Comments: Also acts on ethyl (*R*)-3-oxobutanoate and some other (*R*)-3-hydroxy acid esters. The (*R*)- symbol is allotted on the assumption that no substituents change the order of priority from O-3 > C-2 > C-4. A subunit of yeast fatty acid synthase EC 2.3.1.86, fatty-acyl-CoA synthase system. *cf.* EC 1.1.1.280, (*S*)-3-hydroxyacid ester dehydrogenase.
References: [1459]

[EC 1.1.1.279 created 1990 as EC 1.2.1.55, transferred 2003 to EC 1.1.1.279, modified 2018]

EC 1.1.1.280

Accepted name: (*S*)-3-hydroxyacid-ester dehydrogenase
Reaction: ethyl (*S*)-3-hydroxyhexanoate + NADP⁺ = ethyl 3-oxohexanoate + NADPH + H⁺
Other name(s): 3-oxo ester (*S*)-reductase
Systematic name: ethyl-(*S*)-3-hydroxyhexanoate:NADP⁺ 3-oxidoreductase
Comments: Also acts on 4-oxo- and 5-oxo-fatty acids and their esters. *cf.* EC 1.1.1.279 (*R*)-3-hydroxyacid-ester dehydrogenase.
References: [1459]

[EC 1.1.1.280 created 1990 as EC 1.2.1.56, transferred 2003 to EC 1.1.1.280]

EC 1.1.1.281

Accepted name: GDP-4-dehydro-6-deoxy-D-mannose reductase
Reaction: GDP- α -D-rhamnose + NAD(P)⁺ = GDP-4-dehydro- α -D-rhamnose + NAD(P)H + H⁺
Other name(s): GDP-4-keto-6-deoxy-D-mannose reductase [ambiguous]; GDP-6-deoxy-D-*lyxo*-4-hexulose reductase; Rmd; GDP-6-deoxy-D-mannose:NAD(P)⁺ 4-oxidoreductase (D-rhamnose-forming); GDP-6-deoxy- α -D-mannose:NAD(P)⁺ 4-oxidoreductase (D-rhamnose-forming)
Systematic name: GDP- α -D-rhamnose:NAD(P)⁺ 4-oxidoreductase
Comments: This enzyme differs from EC 1.1.1.187, GDP-4-dehydro-D-rhamnose reductase, in that the only product formed is GDP- α -D-rhamnose. D-Rhamnose is a constituent of lipopolysaccharides of Gram-negative plant and human pathogenic bacteria.
References: [1972, 2377]

[EC 1.1.1.281 created 2004]

EC 1.1.1.282

Accepted name: quinate/shikimate dehydrogenase
Reaction: (1) L-quininate + NAD(P)⁺ = 3-dehydroquininate + NAD(P)H + H⁺
(2) shikimate + NAD(P)⁺ = 3-dehydroshikimate + NAD(P)H + H⁺

Other name(s): YdiB
Systematic name: L-quininate:NAD(P)⁺ 3-oxidoreductase
Comments: This is the second shikimate dehydrogenase enzyme found in *Escherichia coli* and differs from EC 1.1.1.25, shikimate dehydrogenase, in that it can use both quininate and shikimate as substrate and either NAD⁺ or NADP⁺ as acceptor.
References: [2527, 256]

[EC 1.1.1.282 created 2004]

EC 1.1.1.283

Accepted name: methylglyoxal reductase (NADPH)
Reaction: (S)-lactaldehyde + NADP⁺ = 2-oxopropanal + NADPH + H⁺
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 enantiopure products. Among the substrates are methylglyoxal (which is reduced to (S)-lactaldehyde) [2669, 566], 3-methylbutanal [1426], hexane-2,5-dione [2652] and 3-chloro-1-phenylpropan-1-one [611]. The enzyme differs from EC 1.1.1.78, methylglyoxal reductase (NADH), which is found in mammals, by its coenzyme requirement, reaction direction, and enantiomeric preference.
References: [2669, 566, 1426, 2652, 611, 393]

[EC 1.1.1.283 created 2005, modified 2013]

EC 1.1.1.284

Accepted name: S-(hydroxymethyl)glutathione dehydrogenase
Reaction: S-(hydroxymethyl)glutathione + NAD(P)⁺ = S-formylglutathione + NAD(P)H + H⁺
Other name(s): NAD-linked formaldehyde dehydrogenase (incorrect); formaldehyde dehydrogenase (incorrect); formic dehydrogenase (incorrect); class III alcohol dehydrogenase; ADH3; χ -ADH; FDH (incorrect); formaldehyde dehydrogenase (glutathione) (incorrect); GS-FDH (incorrect); glutathione-dependent formaldehyde dehydrogenase (incorrect); NAD-dependent formaldehyde dehydrogenase; GD-FALDH; NAD- and glutathione-dependent formaldehyde dehydrogenase
Systematic name: S-(hydroxymethyl)glutathione:NAD⁺ oxidoreductase
Comments: The substrate, S-(hydroxymethyl)glutathione, forms spontaneously from glutathione and formaldehyde; its rate of formation is increased in some bacteria by the presence of EC 4.4.1.22, S-(hydroxymethyl)glutathione synthase. This enzyme forms part of the pathway that detoxifies formaldehyde, since the product is hydrolysed by EC 3.1.2.12, S-formylglutathione hydrolase. The human enzyme belongs to the family of zinc-dependent alcohol dehydrogenases. Also specifically reduces S-nitrosylglutathione.
References: [1712, 3233, 2280, 3309, 4009, 3127, 197]

[EC 1.1.1.284 created 2005 (EC 1.2.1.1 created 1961, modified 1982, modified 2002, part transferred 2005 to EC 1.1.1.284)]

EC 1.1.1.285

Accepted name: 3''-deamino-3''-oxonicotianamine reductase
Reaction: 2'-deoxymugineic acid + NAD(P)⁺ = 3''-deamino-3''-oxonicotianamine + NAD(P)H + H⁺
Systematic name: 2'-deoxymugineic acid:NAD(P)⁺ 3''-oxidoreductase
References: [3519]

[EC 1.1.1.285 created 2005]

EC 1.1.1.286

Accepted name: isocitrate—homoisocitrate dehydrogenase
Reaction: (1) isocitrate + NAD⁺ = 2-oxoglutarate + CO₂ + NADH
(2) (1*R*,2*S*)-1-hydroxybutane-1,2,4-tricarboxylate + NAD⁺ = 2-oxoadipate + CO₂ + NADH + H⁺
Other name(s): homoisocitrate—isocitrate dehydrogenase; PH1722
Systematic name: isocitrate(homoisocitrate):NAD⁺ oxidoreductase (decarboxylating)
Comments: Requires Mn²⁺ and K⁺ or NH₄⁺ for activity. Unlike EC 1.1.1.41, isocitrate dehydrogenase (NAD⁺) and EC 1.1.1.87, homoisocitrate dehydrogenase, this enzyme, from *Pyrococcus horikoshii*, can use both isocitrate and homoisocitrate as substrates. The enzyme may play a role in both the lysine and glutamate biosynthesis pathways.
References: [2575]

[EC 1.1.1.286 created 2005]

EC 1.1.1.287

Accepted name: D-arabinitol dehydrogenase (NADP⁺)
Reaction: (1) D-arabinitol + NADP⁺ = D-xylulose + NADPH + H⁺
(2) D-arabinitol + NADP⁺ = D-ribulose + NADPH + H⁺
Other name(s): NADP⁺-dependent D-arabitol dehydrogenase; ARD1p; D-arabitol dehydrogenase 1
Systematic name: D-arabinitol:NADP⁺ oxidoreductase
Comments: The enzyme from the rust fungus *Uromyces fabae* can use D-arabinitol and D-mannitol as substrates in the forward direction and D-xylulose, D-ribulose and, to a lesser extent, D-fructose as substrates in the reverse direction. This enzyme carries out the reactions of both EC 1.1.1.11, D-arabinitol 4-dehydrogenase and EC 1.1.1.250, D-arabinitol 2-dehydrogenase, but unlike them, uses NADP⁺ rather than NAD⁺ as cofactor. D-Arabinitol is capable of quenching reactive oxygen species involved in defense reactions of the host plant.
References: [2268]

[EC 1.1.1.287 created 2005]

EC 1.1.1.288

Accepted name: xanthoxin dehydrogenase
Reaction: xanthoxin + NAD⁺ = abscisic aldehyde + NADH + H⁺
Other name(s): xanthoxin oxidase; ABA2
Systematic name: xanthoxin:NAD⁺ oxidoreductase
Comments: Requires a molybdenum cofactor for activity. NADP⁺ cannot replace NAD⁺ and short-chain alcohols such as ethanol, isopropanol, butanol and cyclohexanol cannot replace xanthoxin as substrate [1240]. Involved in the abscisic-acid biosynthesis pathway in plants, along with EC 1.2.3.14 (abscisic-aldehyde oxidase), EC 1.13.11.51 (9-*cis*-epoxycarotenoid dioxygenase) and EC 1.14.13.93 [(+)-abscisic acid 8'-hydroxylase]. Abscisic acid is a sesquiterpenoid plant hormone that is involved in the control of a wide range of essential physiological processes, including seed development, germination and responses to stress [1240].
References: [3535, 3411, 1240]

[EC 1.1.1.288 created 2005]

EC 1.1.1.289

Accepted name: sorbose reductase
Reaction: D-glucitol + NADP⁺ = L-sorbose + NADPH + H⁺
Other name(s): Sou1p
Systematic name: D-glucitol:NADP⁺ oxidoreductase
Comments: The reaction occurs predominantly in the reverse direction. This enzyme can also convert D-fructose into D-mannitol, but more slowly. Belongs in the short-chain dehydrogenase family.
References: [1274, 1275, 3713, 3513]

[EC 1.1.1.289 created 2006]

EC 1.1.1.290

- Accepted name:** 4-phosphoerythronate dehydrogenase
Reaction: 4-phospho-D-erythronate + NAD⁺ = (3*R*)-3-hydroxy-2-oxo-4-phosphooxybutanoate + NADH + H⁺
Other name(s): PdxB; PdxB 4PE dehydrogenase; 4-*O*-phosphoerythronate dehydrogenase; 4PE dehydrogenase; erythronate-4-phosphate dehydrogenase
Systematic name: 4-phospho-D-erythronate:NAD⁺ 2-oxidoreductase
Comments: This enzyme catalyses a step in a bacterial pathway for the biosynthesis of pyridoxal 5'-phosphate. The enzyme contains a tightly-bound NAD(H) cofactor that is not re-oxidized by free NAD⁺. In order to re-oxidize the cofactor and restore enzyme activity, the enzyme catalyses the reduction of a 2-oxo acid (such as 2-oxoglutarate, oxaloacetate, or pyruvate) to the respective (*R*)-hydroxy acid [3252]. *cf.* EC 1.1.1.399, 2-oxoglutarate reductase.
References: [2115, 2969, 4459, 1258, 3390, 3252]

[EC 1.1.1.290 created 2006, modified 2016]

EC 1.1.1.291

- Accepted name:** 2-hydroxymethylglutarate dehydrogenase
Reaction: (*S*)-2-hydroxymethylglutarate + NAD⁺ = 2-formylglutarate + NADH + H⁺
Other name(s): HgD
Systematic name: (*S*)-2-hydroxymethylglutarate:NAD⁺ oxidoreductase
Comments: NADP⁺ cannot replace NAD⁺. Forms part of the nicotinate-fermentation catabolism pathway in *Eubacterium barkeri*. Other enzymes involved in this pathway are EC 1.17.1.5 (nicotinate dehydrogenase), EC 1.3.7.1 (6-hydroxynicotinate reductase), EC 3.5.2.18 (enamidase), EC 5.4.99.4 (2-methyleneglutarate mutase), EC 5.3.3.6 (methylitaconate Δ -isomerase), EC 4.2.1.85 (dimethylmaleate hydratase) and EC 4.1.3.32 (2,3-dimethylmalate lyase).
References: [61]

[EC 1.1.1.291 created 2006]

EC 1.1.1.292

- Accepted name:** 1,5-anhydro-D-fructose reductase (1,5-anhydro-D-mannitol-forming)
Reaction: 1,5-anhydro-D-mannitol + NADP⁺ = 1,5-anhydro-D-fructose + NADPH + H⁺
Other name(s): 1,5-anhydro-D-fructose reductase (ambiguous); AFR
Systematic name: 1,5-anhydro-D-mannitol:NADP⁺ oxidoreductase
Comments: This enzyme is present in some but not all *Rhizobium* species and belongs in the GFO/IDH/MocA protein family [732]. This enzyme differs from hepatic 1,5-anhydro-D-fructose reductase, which yields 1,5-anhydro-D-glucitol as the product (see EC 1.1.1.263). In *Sinorhizobium morelense*, the product of the reaction, 1,5-anhydro-D-mannitol, can be further metabolized to D-mannose [2070]. The enzyme also reduces 1,5-anhydro-D-erythro-hexo-2,3-diulose and 2-ketoaldoses (called osones), such as D-glucosone (D-*arabino*-hexos-2-ulose) and 6-deoxy-D-glucosone. It does not reduce common aldoses and ketoses, or non-sugar aldehydes and ketones [2070].
References: [2070, 732]

[EC 1.1.1.292 created 2007]

[1.1.1.293 Deleted entry. tropinone reductase I. This enzyme was already in the Enzyme List as EC 1.1.1.206, tropine dehydrogenase so EC 1.1.1.293 has been withdrawn at the public-review stage]

[EC 1.1.1.293 created 2007, withdrawn while undergoing public review]

EC 1.1.1.294

- Accepted name:** chlorophyll(ide) *b* reductase

Reaction: $7^1\text{-hydroxychlorophyllide } a + \text{NAD(P)}^+ = \text{chlorophyllide } b + \text{NAD(P)H} + \text{H}^+$
Other name(s): chlorophyll *b* reductase; Chl *b* reductase
Systematic name: $7^1\text{-hydroxychlorophyllide-}a\text{:NAD(P)}^+$ oxidoreductase
Comments: This enzyme carries out the first step in the conversion of chlorophyll *b* to chlorophyll *a*. It is involved in chlorophyll degradation, which occurs during leaf senescence [1575] and it also forms part of the chlorophyll cycle, which interconverts chlorophyll *a* and *b* in response to changing light conditions [1681, 3250].
References: [3362, 3363, 1575, 1681, 3250]

[EC 1.1.1.294 created 2007]

EC 1.1.1.295

Accepted name: momilactone-A synthase
Reaction: $3\beta\text{-hydroxy-}9\beta\text{-pimara-7,15-diene-19,6}\beta\text{-olide} + \text{NAD(P)}^+ = \text{momilactone A} + \text{NAD(P)H} + \text{H}^+$
Other name(s): momilactone A synthase; OsMAS
Systematic name: $3\beta\text{-hydroxy-}9\beta\text{-pimara-7,15-diene-19,6}\beta\text{-olide:NAD(P)}^+$ oxidoreductase
Comments: The rice phytoalexin momilactone A is a diterpenoid secondary metabolite that is involved in the defense mechanism of the plant. Momilactone A is produced in response to attack by a pathogen through the perception of elicitor signal molecules such as chitin oligosaccharide, or after exposure to UV irradiation. The enzyme, which catalyses the last step in the biosynthesis of momilactone A, can use both NAD^+ and NADP^+ but activity is higher with NAD^+ [136].
References: [136, 3508]

[EC 1.1.1.295 created 2008]

EC 1.1.1.296

Accepted name: dihydrocarveol dehydrogenase
Reaction: $\text{menth-8-en-2-ol} + \text{NAD}^+ = \text{menth-8-en-2-one} + \text{NADH} + \text{H}^+$
Other name(s): carveol dehydrogenase (ambiguous)
Systematic name: $\text{menth-8-en-2-ol:NAD}^+$ oxidoreductase
Comments: This enzyme from the Gram-positive bacterium *Rhodococcus erythropolis* DCL14 forms part of the carveol and dihydrocarveol degradation pathway. The enzyme accepts all eight stereoisomers of menth-8-en-2-ol as substrate, although some isomers are converted faster than others. The preferred substrates are (+)-neoisodihydrocarveol, (+)-isodihydrocarveol, (+)-dihydrocarveol and (–)-isodihydrocarveol.
References: [3999]

[EC 1.1.1.296 created 2008]

EC 1.1.1.297

Accepted name: limonene-1,2-diol dehydrogenase
Reaction: $\text{menth-8-ene-1,2-diol} + \text{NAD}^+ = 1\text{-hydroxymenth-8-en-2-one} + \text{NADH} + \text{H}^+$ (general reaction)
(1) $(1S,2S,4R)\text{-menth-8-ene-1,2-diol} + \text{NAD}^+ = (1S,4R)\text{-1-hydroxymenth-8-en-2-one} + \text{NADH} + \text{H}^+$
(2) $(1R,2R,4S)\text{-menth-8-ene-1,2-diol} + \text{NAD}^+ = (1R,4S)\text{-1-hydroxymenth-8-en-2-one} + \text{NADH} + \text{H}^+$
Other name(s): NAD^+ -dependent limonene-1,2-diol dehydrogenase
Systematic name: $\text{menth-8-ene-1,2-diol:NAD}^+$ oxidoreductase
Comments: While the enzyme from the Gram-positive bacterium *Rhodococcus erythropolis* DCL14 can use both (1*S*,2*S*,4*R*)- and (1*R*,2*R*,4*S*)-menth-8-ene-1,2-diol as substrate, activity is higher with (1*S*,2*S*,4*R*)-menth-8-ene-1,2-diol as substrate.
References: [4000]

[EC 1.1.1.297 created 2008]

EC 1.1.1.298

- Accepted name:** 3-hydroxypropionate dehydrogenase (NADP⁺)
Reaction: 3-hydroxypropanoate + NADP⁺ = malonate semialdehyde + NADPH + H⁺
Other name(s): 3-hydroxypropanoate dehydrogenase (NADP⁺); 3-hydroxypropionate:NADP⁺ oxidoreductase
Systematic name: 3-hydroxypropanoate:NADP⁺ oxidoreductase
Comments: Catalyses the reduction of malonate semialdehyde to 3-hydroxypropanoate, a key step in the 3-hydroxypropanoate and the 3-hydroxypropanoate/4-hydroxybutanoate cycles, autotrophic CO₂ fixation pathways found in some green non-sulfur phototrophic bacteria and archaea, respectively [3671, 265]. The enzyme from *Chloroflexus aurantiacus* is bifunctional, and also catalyses the up-stream reaction in the pathway, EC 1.2.1.75 [1604]. Different from EC 1.1.1.59 [3-hydroxypropionate dehydrogenase (NAD⁺)] by cofactor preference.
References: [3671, 265, 1604]

[EC 1.1.1.298 created 2009]

EC 1.1.1.299

- Accepted name:** malate dehydrogenase [NAD(P)⁺]
Reaction: (S)-malate + NAD(P)⁺ = oxaloacetate + NAD(P)H + H⁺
Other name(s): MdH II, NAD(P)⁺-dependent malate dehydrogenase
Systematic name: (S)-malate:NAD(P)⁺ oxidoreductase
Comments: This enzyme, which was characterized from the methanogenic archaeon *Methanobacterium thermoautotrophicum*, catalyses only the reduction of oxaloacetate, and can use NAD⁺ and NADP⁺ with similar specific activity [3874]. Different from EC 1.1.1.37 (malate dehydrogenase (NAD⁺)), EC 1.1.1.82 (malate dehydrogenase (NADP⁺)) and EC 1.1.5.4 (malate dehydrogenase (quinone)).
References: [3874]

[EC 1.1.1.299 created 2009]

EC 1.1.1.300

- Accepted name:** NADP-retinol dehydrogenase
Reaction: retinol + NADP⁺ = retinal + NADPH + H⁺
Other name(s): *all-trans* retinal reductase (ambiguous); *all-trans*-retinol dehydrogenase; NADP(H)-dependent retinol dehydrogenase/reductase; RDH11; RDH12; RDH13; RDH14; retinol dehydrogenase 12; retinol dehydrogenase 14; retinol dehydrogenase [NADP⁺]; RalR1; PSDR1
Systematic name: retinol:NADP⁺ oxidoreductase
Comments: Greater catalytic efficiency in the reductive direction. This observation, and the enzyme's localization at the entrance to the mitochondrial matrix, suggest that it may function to protect mitochondria against oxidative stress associated with the highly reactive retinal produced from dietary β-carotene by EC 1.13.11.63 (β-carotene 15,15'-dioxygenase) [252]. *K_m*-values for NADP⁺ and NADPH are at least 800-fold lower than those for NAD⁺ and NADH [253, 1867]. This enzyme differs from EC 1.1.1.105, retinol dehydrogenase, which prefers NAD⁺ and NADH.
References: [253, 252, 1335, 1867]

[EC 1.1.1.300 created 2009]

EC 1.1.1.301

- Accepted name:** D-arabitol-phosphate dehydrogenase
Reaction: D-arabinitol 1-phosphate + NAD⁺ = D-xylulose 5-phosphate + NADH + H⁺
Other name(s): APDH; D-arabitol 1-phosphate dehydrogenase; D-arabitol 5-phosphate dehydrogenase; D-arabinitol 1-phosphate dehydrogenase; D-arabinitol 5-phosphate dehydrogenase
Systematic name: D-arabinitol-phosphate:NAD⁺ oxidoreductase
Comments: This enzyme participates in arabinitol catabolism. The enzyme also converts D-arabinitol 5-phosphate to D-ribulose 5-phosphate at a lower rate [3048].
References: [3048]

[EC 1.1.1.301 created 2010]

EC 1.1.1.302

- Accepted name:** 2,5-diamino-6-(ribosylamino)-4(3*H*)-pyrimidinone 5'-phosphate reductase
Reaction: 2,5-diamino-6-(5-phospho-D-ribitylamino)pyrimidin-4(3*H*)-one + NAD(P)⁺ = 2,5-diamino-6-(5-phospho-D-ribosylamino)pyrimidin-4(3*H*)-one + NAD(P)H + H⁺
Other name(s): 2,5-diamino-6-ribosylamino-4(3*H*)-pyrimidinone 5'-phosphate reductase; MjaRED; MJ0671 (gene name)
Systematic name: 2,5-diamino-6-(5-phospho-D-ribosylamino)pyrimidin-4(3*H*)-one:NAD(P)⁺ oxidoreductase
Comments: The reaction proceeds in the opposite direction. A step in riboflavin biosynthesis, NADPH and NADH function equally well as reductant. Differs from EC 1.1.1.193 [5-amino-6-(5-phosphoribosylamino)uracil reductase] since it does not catalyse the reduction of 5-amino-6-ribosylaminopyrimidine-2,4(1*H*,3*H*)-dione 5'-phosphate [1262].
References: [1262, 555]

[EC 1.1.1.302 created 2010, modified 2011]

EC 1.1.1.303

- Accepted name:** diacetyl reductase [(*R*)-acetoin forming]
Reaction: (*R*)-acetoin + NAD⁺ = diacetyl + NADH + H⁺
Other name(s): (*R*)-acetoin dehydrogenase
Systematic name: (*R*)-acetoin:NAD⁺ oxidoreductase
Comments: The reaction is catalysed in the reverse direction. This activity is usually associated with butanediol dehydrogenase activity (EC 1.1.1.4 or EC 1.1.1.76). While the butanediol dehydrogenase activity is reversible, diacetyl reductase activity is irreversible. This enzyme has been reported in the yeast *Saccharomyces cerevisiae* [1460, 1239]. Different from EC 1.1.1.304, diacetyl reductase [(*S*)-acetoin forming].
References: [1460, 1239]

[EC 1.1.1.303 created 2010 (EC 1.1.1.5 created 1961, modified 1976, part incorporated 2010)]

EC 1.1.1.304

- Accepted name:** diacetyl reductase [(*S*)-acetoin forming]
Reaction: (*S*)-acetoin + NAD⁺ = diacetyl + NADH + H⁺
Other name(s): (*S*)-acetoin dehydrogenase
Systematic name: (*S*)-acetoin:NAD⁺ oxidoreductase
Comments: The reaction is catalysed in the reverse direction. This activity is usually associated with butanediol dehydrogenase activity (EC 1.1.1.4 or EC 1.1.1.76). While the butanediol dehydrogenase activity is reversible, diacetyl reductase activity is irreversible. This enzyme has been reported in the bacteria *Geobacillus stearothermophilus*, *Enterobacter aerogenes* and *Klebsiella pneumoniae* [1207, 501, 3967]. Different from EC 1.1.1.303, diacetyl reductase [(*R*)-acetoin forming].
References: [1207, 501, 3967]

[EC 1.1.1.304 created 2010 (EC 1.1.1.5 created 1961, modified 1976, part incorporated 2010)]

EC 1.1.1.305

- Accepted name:** UDP-glucuronic acid dehydrogenase (UDP-4-keto-hexauronic acid decarboxylating)
Reaction: UDP- α -D-glucuronate + NAD⁺ = UDP- β -L-threo-pentapyranos-4-ulose + CO₂ + NADH + H⁺
Other name(s): UDP-GlcUA decarboxylase; ArnADH; UDP-glucuronate:NAD⁺ oxidoreductase (decarboxylating)
Systematic name: UDP- α -D-glucuronate:NAD⁺ oxidoreductase (decarboxylating)
Comments: The activity is part of a bifunctional enzyme also performing the reaction of EC 2.1.2.13 (UDP-4-amino-4-deoxy-L-arabinose formyltransferase).
References: [390, 1164, 4219, 1165, 4329]

[EC 1.1.1.305 created 2010]

EC 1.1.1.306

- Accepted name:** *S*-(hydroxymethyl)mycothiol dehydrogenase
Reaction: *S*-(hydroxymethyl)mycothiol + NAD⁺ = *S*-formylmycothiol + NADH + H⁺
Other name(s): NAD/factor-dependent formaldehyde dehydrogenase; mycothiol-dependent formaldehyde dehydrogenase
Systematic name: *S*-(hydroxymethyl)mycothiol:NAD⁺ oxidoreductase
Comments: *S*-hydroxymethylmycothiol is believed to form spontaneously from formaldehyde and mycothiol. This enzyme oxidizes the product of this spontaneous reaction to *S*-formylmycothiol, in a reaction that is analogous to EC 1.1.1.284, *S*-(hydroxymethyl)glutathione dehydrogenase.
References: [2560, 2819, 4052, 3136]

[EC 1.1.1.306 created 2010 as EC 1.2.1.66, transferred 2010 to EC 1.1.1.306]

EC 1.1.1.307

- Accepted name:** D-xylose reductase
Reaction: xylitol + NAD(P)⁺ = D-xylose + NAD(P)H + H⁺
Other name(s): XylR; XyrA; msXR; dsXR; monospecific xylose reductase; dual specific xylose reductase; NAD(P)H-dependent xylose reductase; xylose reductase
Systematic name: xylitol:NAD(P)⁺ oxidoreductase
Comments: Xylose reductase catalyses the initial reaction in the xylose utilization pathway, the NAD(P)H dependent reduction of xylose to xylitol.
References: [2766, 2783, 1621, 572, 4031, 999, 2170, 4252]

[EC 1.1.1.307 created 2010]

EC 1.1.1.308

- Accepted name:** sulfopropanediol 3-dehydrogenase
Reaction: (*R*)-2,3-dihydroxypropane-1-sulfonate + 2 NAD⁺ + H₂O = (*R*)-3-sulfolactate + 2 NADH + 2 H⁺
Other name(s): DHPS 3-dehydrogenase (sulfolactate forming); 2,3-dihydroxypropane-1-sulfonate 3-dehydrogenase (sulfolactate forming); dihydroxypropanesulfonate 3-dehydrogenase; *hpsN* (gene name)
Systematic name: (*R*)-2,3-dihydroxypropane-1-sulfonate:NAD⁺ 3-oxidoreductase
Comments: The enzyme is involved in degradation of (*R*)-2,3-dihydroxypropanesulfonate.
References: [2474]

[EC 1.1.1.308 created 2011]

EC 1.1.1.309

- Accepted name:** phosphonoacetaldehyde reductase (NADH)
Reaction: 2-hydroxyethylphosphonate + NAD⁺ = phosphonoacetaldehyde + NADH + H⁺
Other name(s): PhpC
Systematic name: 2-hydroxyethylphosphonate:NAD⁺ oxidoreductase
Comments: The enzyme from *Streptomyces viridochromogenes* catalyses a step in the biosynthesis of phosphinothricin tripeptide, the reduction of phosphonoacetaldehyde to 2-hydroxyethylphosphonate. The preferred cofactor is NADH, lower activity with NADPH [325].
References: [325]

[EC 1.1.1.309 created 2011]

EC 1.1.1.310

- Accepted name:** (*S*)-sulfolactate dehydrogenase

Reaction: (2*S*)-3-sulfolactate + NAD⁺ = 3-sulfopyruvate + NADH + H⁺
Other name(s): (2*S*)-3-sulfolactate dehydrogenase; SlcC
Systematic name: (2*S*)-sulfolactate:NAD⁺ oxidoreductase
Comments: This enzyme, isolated from the bacterium *Chromohalobacter salexigens* DSM 3043, acts only on the (*S*)-enantiomer of 3-sulfolactate. Combined with EC 1.1.1.338, (2*R*)-3-sulfolactate dehydrogenase (NADP⁺), it provides a racemase system that converts (2*S*)-3-sulfolactate to (2*R*)-3-sulfolactate, which is degraded further by EC 4.4.1.24, (2*R*)-sulfolactate sulfo-lyase. The enzyme is specific for NAD⁺.
References: [794]

[EC 1.1.1.310 created 2011, modified 2013]

EC 1.1.1.311

Accepted name: (*S*)-1-phenylethanol dehydrogenase
Reaction: (*S*)-1-phenylethanol + NAD⁺ = acetophenone + NADH + H⁺
Other name(s): PED
Systematic name: (*S*)-1-phenylethanol:NAD⁺ oxidoreductase
Comments: The enzyme is involved in degradation of ethylbenzene.
References: [1975, 1532]

[EC 1.1.1.311 created 2011]

EC 1.1.1.312

Accepted name: 2-hydroxy-4-carboxymuconate semialdehyde hemiacetal dehydrogenase
Reaction: 4-carboxy-2-hydroxymuconate semialdehyde hemiacetal + NADP⁺ = 2-oxo-2*H*-pyran-4,6-dicarboxylate + NADPH + H⁺
Other name(s): 2-hydroxy-4-carboxymuconate 6-semialdehyde dehydrogenase; 4-carboxy-2-hydroxy-*cis,cis*-muconate-6-semialdehyde:NADP⁺ oxidoreductase; α-hydroxy-γ-carboxymuconic ε-semialdehyde dehydrogenase; 4-carboxy-2-hydroxymuconate-6-semialdehyde dehydrogenase; LigC; ProD
Systematic name: 4-carboxy-2-hydroxymuconate semialdehyde hemiacetal:NADP⁺ 2-oxidoreductase
Comments: The enzyme does not act on unsubstituted aliphatic or aromatic aldehydes or glucose; NAD⁺ can replace NADP⁺, but with lower affinity. The enzyme was initially believed to act on 4-carboxy-2-hydroxy-*cis,cis*-muconate 6-semialdehyde and produce 4-carboxy-2-hydroxy-*cis,cis*-muconate [2423]. However, later studies showed that the substrate is the hemiacetal form [2422], and the product is 2-oxo-2*H*-pyran-4,6-dicarboxylate [2421, 2426].
References: [2423, 2421, 2422, 2426]

[EC 1.1.1.312 created 1978 as EC 1.2.1.45, transferred 2011 to EC 1.1.1.312]

EC 1.1.1.313

Accepted name: sulfoacetaldehyde reductase
Reaction: isethionate + NADP⁺ = 2-sulfoacetaldehyde + NADPH + H⁺
Other name(s): *isfD* (gene name)
Systematic name: isethionate:NADP⁺ oxidoreductase
Comments: Catalyses the reaction only in the opposite direction. Involved in taurine degradation. The bacterium *Chromohalobacter salexigens* strain DSM 3043 possesses two enzymes that catalyse this reaction, a constitutive enzyme (encoded by *isfD2*) and an inducible enzyme (encoded by *isfD*). The latter is induced by taurine, and is responsible for most of the activity observed in taurine-grown cells.
References: [2055]

[EC 1.1.1.313 created 2011]

[1.1.1.314 Deleted entry. *germacrene A alcohol dehydrogenase*. Now known to be catalyzed by EC 1.14.14.95, *germacrene A hydroxylase*]

[EC 1.1.1.314 created 2011, deleted 2018]

EC 1.1.1.315

Accepted name: 11-*cis*-retinol dehydrogenase
Reaction: 11-*cis*-retinol—[retinal-binding-protein] + NAD⁺ = 11-*cis*-retinal—[retinol-binding-protein] + NADH + H⁺
Other name(s): RDH5 (gene name)
Systematic name: 11-*cis*-retinol:NAD⁺ oxidoreductase
Comments: This enzyme, abundant in the retinal pigment epithelium, catalyses the reduction of 11-*cis*-retinol to 11-*cis*-retinal [3533] while the substrate is bound to the retinal-binding protein [4268]. This is a crucial step in the regeneration of 11-*cis*-retinal, the chromophore of rhodopsin. The enzyme can also accept other *cis* forms of retinol [4106].
References: [3533, 4106, 2247, 4268]

[EC 1.1.1.315 created 2011]

EC 1.1.1.316

Accepted name: L-galactose 1-dehydrogenase
Reaction: L-galactose + NAD⁺ = L-galactono-1,4-lactone + NADH + H⁺
Other name(s): L-GalDH; L-galactose dehydrogenase
Systematic name: L-galactose:NAD⁺ 1-oxidoreductase
Comments: The enzyme catalyses a step in the ascorbate biosynthesis in higher plants (Smirnoff-Wheeler pathway). The activity with NADP⁺ is less than 10% of the activity with NAD⁺.
References: [2529, 1163, 4186, 2845]

[EC 1.1.1.316 created 2011]

EC 1.1.1.317

Accepted name: perakine reductase
Reaction: raucaffrinoline + NADP⁺ = perakine + NADPH + H⁺
Systematic name: raucaffrinoline:NADP⁺ oxidoreductase
Comments: The biosynthesis of raucaffrinoline from perakine is a side route of the ajmaline biosynthesis pathway. The enzyme is a member of the aldo-keto reductase enzyme superfamily from higher plants.
References: [3732, 3236]

[EC 1.1.1.317 created 2011]

EC 1.1.1.318

Accepted name: eugenol synthase
Reaction: eugenol + a carboxylate + NADP⁺ = a coniferyl ester + NADPH + H⁺
Other name(s): LtCES1; EGS1; EGS2
Systematic name: eugenol:NADP⁺ oxidoreductase (coniferyl ester reducing)
Comments: The enzyme acts in the opposite direction. The enzymes from the plants *Ocimum basilicum* (sweet basil) [1991, 2301], *Clarkia breweri* and *Petunia hybrida* [1992] only accept coniferyl acetate and form eugenol. The enzyme from *Pimpinella anisum* (anise) forms anol (from 4-coumaryl acetate) *in vivo*, although the recombinant enzyme can form eugenol from coniferyl acetate [1990]. The enzyme from *Larrea tridentata* (creosote bush) also forms chavicol from a coumaryl ester and can use NADH [100].
References: [1991, 100, 2301, 1992, 1990]

[EC 1.1.1.318 created 2012]

EC 1.1.1.319

Accepted name: isoeugenol synthase
Reaction: isoeugenol + acetate + NADP⁺ = coniferyl acetate + NADPH + H⁺
Other name(s): IGS1; *t*-anol/isoeugenol synthase 1
Systematic name: eugenol:NADP⁺ oxidoreductase (coniferyl acetate reducing)
Comments: The enzyme acts in the opposite direction. In *Ocimum basilicum* (sweet basil), *Clarkia breweri* and *Petunia hybrida* only isoeugenol is formed [1991, 1992]. However in *Pimpinella anisum* (anise) only anol is formed *in vivo*, although the cloned enzyme does produce isoeugenol [1990].
References: [1991, 1992, 1990]

[EC 1.1.1.319 created 2012]

EC 1.1.1.320

Accepted name: benzil reductase [(*S*)-benzoin forming]
Reaction: (*S*)-benzoin + NADP⁺ = benzil + NADPH + H⁺
Other name(s): YueD
Systematic name: (*S*)-benzoin:NADP⁺ oxidoreductase
Comments: The enzyme also reduces 1-phenylpropane-1,2-dione. The enzyme from *Bacillus cereus* in addition reduces 1,4-naphthoquinone and 1-(4-methylphenyl)-2-phenylethane-1,2-dione with high efficiency [2425].
References: [2424, 2425]

[EC 1.1.1.320 created 2012]

EC 1.1.1.321

Accepted name: benzil reductase [(*R*)-benzoin forming]
Reaction: (*R*)-benzoin + NADP⁺ = benzil + NADPH + H⁺
Systematic name: (*R*)-benzoin:NADP⁺ oxidoreductase
Comments: The enzyme from the bacterium *Xanthomonas oryzae* is able to reduce enantioselectively only one of the two carbonyl groups of benzil to give optically active (*R*)-benzoin.
References: [2024]

[EC 1.1.1.321 created 2012]

EC 1.1.1.322

Accepted name: (–)-*endo*-fenchol dehydrogenase
Reaction: (–)-*endo*-fenchol + NAD(P)⁺ = (+)-fenchone + NAD(P)H + H⁺
Other name(s): *l-endo*-fenchol dehydrogenase; FDH
Systematic name: (–)-*endo*-fenchol:NAD(P)⁺ oxidoreductase
Comments: Isolated from the plant *Foeniculum vulgare* (fennel). NADH is slightly preferred to NADPH.
References: [695]

[EC 1.1.1.322 created 2012]

EC 1.1.1.323

Accepted name: (+)-thujan-3-ol dehydrogenase
Reaction: (+)-thujan-3-ol + NAD(P)⁺ = (+)-thujan-3-one + NAD(P)H + H⁺
Other name(s): *d*-3-thujanol dehydrogenase; TDH
Systematic name: (+)-thujan-3-ol:NAD(P)⁺ oxidoreductase
Comments: Isolated from the plant *Tanacetum vulgare* (tansy). NADH is preferred to NADPH.
References: [695]

[EC 1.1.1.323 created 2012]

EC 1.1.1.324

- Accepted name:** 8-hydroxygeraniol dehydrogenase
Reaction: (6E)-8-hydroxygeraniol + 2 NADP⁺ = (6E)-8-oxogeraniol + 2 NADPH + 2 H⁺ (overall reaction)
(1a) (6E)-8-hydroxygeraniol + NADP⁺ = (6E)-8-hydroxygeraniol + NADPH + H⁺
(1b) (6E)-8-hydroxygeraniol + NADP⁺ = (6E)-8-oxogeraniol + NADPH + H⁺
(1c) (6E)-8-hydroxygeraniol + NADP⁺ = (6E)-8-oxogeraniol + NADPH + H⁺
(1d) (6E)-8-oxogeraniol + NADP⁺ = (6E)-8-oxogeraniol + NADPH + H⁺
Other name(s): 8-hydroxygeraniol oxidoreductase; CYP76B10; G10H; CrG10H; SmG10H; acyclic monoterpene primary alcohol:NADP⁺ oxidoreductase
Systematic name: (6E)-8-hydroxygeraniol:NADP⁺ oxidoreductase
Comments: Contains Zn²⁺. The enzyme catalyses the oxidation of (6E)-8-hydroxygeraniol to (6E)-8-oxogeraniol via either (6E)-8-hydroxygeraniol or (6E)-8-oxogeraniol. Also acts on geraniol, nerol and citronellol. May be identical to EC 1.1.1.183 geraniol dehydrogenase. The recommended numbering of geraniol gives 8-hydroxygeraniol as the substrate rather than 10-hydroxygeraniol as used by references 1 and 2. See prenol nomenclature Pr-1.
References: [1630, 1347]

[EC 1.1.1.324 created 2012]

EC 1.1.1.325

- Accepted name:** sepiapterin reductase (*L-threo*-7,8-dihydrobiopterin forming)
Reaction: (1) *L-threo*-7,8-dihydrobiopterin + NADP⁺ = sepiapterin + NADPH + H⁺
(2) *L-threo*-tetrahydrobiopterin + 2 NADP⁺ = 6-pyruvoyl-5,6,7,8-tetrahydropterin + 2 NADPH + 2 H⁺
Systematic name: *L-threo*-7,8-dihydrobiopterin:NADP⁺ oxidoreductase
Comments: This enzyme, isolated from the bacterium *Chlorobium tepidum*, catalyses the final step in the *de novo* synthesis of tetrahydrobiopterin from GTP. *cf.* EC 1.1.1.153, sepiapterin reductase (*L-erythro*-7,8-dihydrobiopterin forming).
References: [605, 3744]

[EC 1.1.1.325 created 2012]

EC 1.1.1.326

- Accepted name:** zerumbone synthase
Reaction: 10-hydroxy- α -humulene + NAD⁺ = zerumbone + NADH + H⁺
Other name(s): ZSD1
Systematic name: 10-hydroxy- α -humulene:NAD⁺ oxidoreductase
Comments: The enzyme was cloned from shampoo ginger, *Zingiber zerumbet*.
References: [2863]

[EC 1.1.1.326 created 2012]

EC 1.1.1.327

- Accepted name:** 5-*exo*-hydroxycamphor dehydrogenase
Reaction: 5-*exo*-hydroxycamphor + NAD⁺ = bornane-2,5-dione + NADH + H⁺
Other name(s): F-dehydrogenase; FdeH
Systematic name: 5-*exo*-hydroxycamphor:NAD⁺ oxidoreductase
Comments: Contains Zn²⁺. Isolated from *Pseudomonas putida*, and involved in degradation of (+)-camphor.
References: [3176, 1998, 110]

[EC 1.1.1.327 created 2012]

EC 1.1.1.328

- Accepted name:** nicotine blue oxidoreductase

Reaction: 3,3'-bipyridine-2,2',5,5',6,6'-hexol + NAD(P)⁺ = (E)-2,2',5,5'-tetrahydroxy-6H,6'H-[3,3'-bipyridinylidene]-6,6'-dione + NAD(P)H + H⁺

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

Systematic name: 3,3'-bipyridine-2,2',5,5',6,6'-hexol:NADP⁺ 11-oxidoreductase

Comments: The enzyme, characterized from the nicotine degrading bacterium *Arthrobacter nicotinovorans*, catalyses the reduction of "nicotine blue" to its hydroquinone form (the opposite direction from that shown). Nicotine blue is the name given to the compound formed by the autocatalytic condensation of two molecules of 2,3,6-trihydroxypyridine, an intermediate in the nicotine degradation pathway. The main role of the enzyme may be to prevent the intracellular formation of nicotine blue semiquinone radicals, which by redox cycling would lead to the formation of toxic reactive oxygen species. The enzyme possesses a slight preference for NADH over NADPH.

References: [2535]

[EC 1.1.1.328 created 2012]

EC 1.1.1.329

Accepted name: 2-deoxy-*scyllo*-inosamine dehydrogenase

Reaction: 2-deoxy-*scyllo*-inosamine + NAD(P)⁺ = 3-amino-2,3-dideoxy-*scyllo*-inosose + NAD(P)H + H⁺

Other name(s): *neoA* (gene name); *kanK* (gene name, ambiguous); *kanE* (gene name, ambiguous)

Systematic name: 2-deoxy-*scyllo*-inosamine:NAD(P)⁺ 1-oxidoreductase

Comments: Requires zinc. Involved in the biosynthetic pathways of several clinically important aminocyclitol antibiotics, including kanamycin, neomycin and ribostamycin. *cf.* EC 1.1.99.38, 2-deoxy-*scyllo*-inosamine dehydrogenase (AdoMet-dependent).

References: [2068, 2763]

[EC 1.1.1.329 created 2012]

EC 1.1.1.330

Accepted name: very-long-chain 3-oxoacyl-CoA reductase

Reaction: a very-long-chain (3*R*)-3-hydroxyacyl-CoA + NADP⁺ = a very-long-chain 3-oxoacyl-CoA + NADPH + H⁺

Other name(s): very-long-chain 3-ketoacyl-CoA reductase; very-long-chain β-ketoacyl-CoA reductase; KCR (gene name); IFA38 (gene name)

Systematic name: (3*R*)-3-hydroxyacyl-CoA:NADP⁺ oxidoreductase

Comments: The second component of the elongase, a microsomal protein complex responsible for extending palmitoyl-CoA and stearoyl-CoA (and modified forms thereof) to very-long-chain acyl CoAs. The enzyme is active with substrates with chain length of C₁₆ to C₃₄, depending on the species. *cf.* EC 2.3.1.199, very-long-chain 3-oxoacyl-CoA synthase, EC 4.2.1.134, very-long-chain (3*R*)-3-hydroxyacyl-[acyl-carrier protein] dehydratase, and EC 1.3.1.93, very-long-chain enoyl-CoA reductase.

References: [231, 1358, 232]

[EC 1.1.1.330 created 2012]

EC 1.1.1.331

Accepted name: secoisolariciresinol dehydrogenase

Reaction: (–)-secoisolariciresinol + 2 NAD⁺ = (–)-matairesinol + 2 NADH + 2 H⁺

Systematic name: (–)-secoisolariciresinol:NAD⁺ oxidoreductase

Comments: Isolated from the plants *Forsythia intermedia* [4275] and *Podophyllum peltatum* [4275, 4394, 2590]. An intermediate lactol is detected *in vitro*.

References: [4275, 4394, 2590]

[EC 1.1.1.331 created 2012]

EC 1.1.1.332

Accepted name: chanoclavine-I dehydrogenase
Reaction: chanoclavine-I + NAD⁺ = chanoclavine-I aldehyde + NADH + H⁺
Other name(s): *easD* (gene name); *fgaDH* (gene name)
Systematic name: chanoclavine-I:NAD⁺ oxidoreductase
Comments: The enzyme catalyses a step in the pathway of ergot alkaloid biosynthesis in certain fungi.
References: [4096, 4095]

[EC 1.1.1.332 created 2012]

EC 1.1.1.333

Accepted name: decaprenylphospho-β-D-erythro-pentofuranosid-2-ulose 2-reductase
Reaction: *trans,octacis*-decaprenylphospho-β-D-arabinofuranose + NAD⁺ = *trans,octacis*-decaprenylphospho-β-D-erythro-pentofuranosid-2-ulose + NADH + H⁺
Other name(s): decaprenylphospho-β-D-ribofuranose 2'-epimerase; Rv3791; DprE2
Systematic name: *trans,octacis*-decaprenylphospho-β-D-arabinofuranose:NAD⁺ 2-oxidoreductase
Comments: The reaction is catalysed in the reverse direction. The enzyme, isolated from the bacterium *Mycobacterium smegmatis*, is involved, along with EC 1.1.98.3, decaprenylphospho-β-D-ribofuranose 2-oxidase, in the epimerization of *trans,octacis*-decaprenylphospho-β-D-ribofuranose to *trans,octacis*-decaprenylphospho-β-D-arabinoofuranose, the arabinosyl donor for the biosynthesis of mycobacterial cell wall arabinan polymers.
References: [3925]

[EC 1.1.1.333 created 2012]

EC 1.1.1.334

Accepted name: methylecgonone reductase
Reaction: ecgonine methyl ester + NADP⁺ = ecgonone methyl ester + NADPH + H⁺
Other name(s): MecgoR (gene name)
Systematic name: ecgonine methyl ester:NADP⁺ oxidoreductase
Comments: The enzyme from the plant *Erythroxylum coca* catalyses the penultimate step in the biosynthesis of cocaine. *In vivo* the reaction proceeds in the opposite direction. With NADH instead of NADPH the reaction rate is reduced to 14%. The enzyme also reduces tropinone, nortropinone and 6-hydroxytropinone but with lower reaction rates.
References: [1746]

[EC 1.1.1.334 created 2012]

EC 1.1.1.335

Accepted name: UDP-*N*-acetyl-2-amino-2-deoxyglucuronate dehydrogenase
Reaction: UDP-*N*-acetyl-2-amino-2-deoxy-α-D-glucuronate + NAD⁺ = UDP-2-acetamido-2-deoxy-α-D-ribohex-3-uluronate + NADH + H⁺
Other name(s): WlbA; WbpB
Systematic name: UDP-*N*-acetyl-2-amino-2-deoxy-α-D-glucuronate:NAD⁺ 3-oxidoreductase
Comments: This enzyme participates in the biosynthetic pathway for UDP-α-D-ManNAc3NAcA (UDP-2,3-diacetamido-2,3-dideoxy-α-D-mannuronic acid), an important precursor of B-band lipopolysaccharide. The enzymes from *Pseudomonas aeruginosa* serotype O5 and *Thermus thermophilus* form a complex with the the enzyme catalysing the next step the pathway (EC 2.6.1.98, UDP-2-acetamido-2-deoxy-ribohexuluronate aminotransferase). The enzyme also possesses an EC 1.1.99.2 (L-2-hydroxyglutarate dehydrogenase) activity, and utilizes the 2-oxoglutarate produced by EC 2.6.1.98 to regenerate the tightly bound NAD⁺. The enzymes from *Bordetella pertussis* and *Chromobacterium violaceum* do not bind NAD⁺ as tightly and do not require 2-oxoglutarate to function.
References: [4184, 2140, 3865, 3866]

[EC 1.1.1.335 created 2012]

EC 1.1.1.336

Accepted name: UDP-*N*-acetyl-D-mannosamine dehydrogenase
Reaction: UDP-*N*-acetyl- α -D-mannosamine + 2 NAD⁺ + H₂O = UDP-*N*-acetyl- α -D-mannosaminuronate + 2 NADH + 2 H⁺
Other name(s): UDP-ManNAc 6-dehydrogenase; *wecC* (gene name)
Systematic name: UDP-*N*-acetyl- α -D-mannosamine:NAD⁺ 6-oxidoreductase
Comments: Part of the pathway for acetamido sugar biosynthesis in bacteria and archaea. The enzyme has no activity with NADP⁺.
References: [2728]

[EC 1.1.1.336 created 2012]

EC 1.1.1.337

Accepted name: L-2-hydroxycarboxylate dehydrogenase (NAD⁺)
Reaction: a (2*S*)-2-hydroxycarboxylate + NAD⁺ = a 2-oxocarboxylate + NADH + H⁺
Other name(s): (*R*)-sulfolactate:NAD⁺ oxidoreductase; L-sulfolactate dehydrogenase; (*R*)-sulfolactate dehydrogenase; L-2-hydroxyacid dehydrogenase (NAD⁺); ComC
Systematic name: (2*S*)-2-hydroxycarboxylate:NAD⁺ oxidoreductase
Comments: The enzyme from the archaeon *Methanocaldococcus jannaschii* acts on multiple (*S*)-2-hydroxycarboxylates including (2*R*)-3-sulfolactate, (*S*)-malate, (*S*)-lactate, and (*S*)-2-hydroxyglutarate [1256]. Note that (2*R*)-3-sulfolactate has the same stereo configuration as (2*S*)-2-hydroxycarboxylates.
References: [1261, 1260, 1256, 3159]

[EC 1.1.1.337 created 2012]

EC 1.1.1.338

Accepted name: (2*R*)-3-sulfolactate dehydrogenase (NADP⁺)
Reaction: (2*R*)-3-sulfolactate + NADP⁺ = 3-sulfo-pyruvate + NADPH + H⁺
Other name(s): (*R*)-sulfolactate:NADP⁺ oxidoreductase; L-sulfolactate dehydrogenase; (*R*)-sulfolactate dehydrogenase; ComC
Systematic name: (2*R*)-3-sulfolactate:NADP⁺ oxidoreductase
Comments: The enzyme from the bacterium *Chromohalobacter salexigens* can only utilize NADP⁺. It functions both biosynthetically in coenzyme M biosynthesis and degradatively, in the degradation of sulfolactate. It can not use (*S*)-malate and (*S*)-lactate.
References: [794]

[EC 1.1.1.338 created 2012]

EC 1.1.1.339

Accepted name: dTDP-6-deoxy-L-talose 4-dehydrogenase (NAD⁺)
Reaction: dTDP-6-deoxy- β -L-talose + NAD⁺ = dTDP-4-dehydro- β -L-rhamnose + NADH + H⁺
Other name(s): *tll* (gene name)
Systematic name: dTDP-6-deoxy- β -L-talose:NAD⁺ 4-oxidoreductase
Comments: The enzyme has been characterized from the bacterium *Aggregatibacter actinomycetemcomitans*, in which it participates in the biosynthesis of the serotype c-specific polysaccharide antigen. Shows no activity with NADP⁺.
References: [2717]

[EC 1.1.1.339 created 2012]

EC 1.1.1.340

Accepted name: 1-deoxy-11 β -hydroxypentalenate dehydrogenase
Reaction: 1-deoxy-11 β -hydroxypentalenate + NAD⁺ = 1-deoxy-11-oxopentalenate + NADH + H⁺
Other name(s): 1-deoxy-11 β -hydroxypentalenic acid dehydrogenase; *ptlF* (gene name); *penF* (gene name)
Systematic name: 1-deoxy-11 β -hydroxypentalenate:NAD⁺ oxidoreductase
Comments: Isolated from the bacterium *Streptomyces avermitilis* and present in many other *Streptomyces* species. Part of the pathway for pentalenolactone biosynthesis.
References: [4390]

[EC 1.1.1.340 created 2012]

EC 1.1.1.341

Accepted name: CDP-abequose synthase
Reaction: CDP- α -D-abequose + NADP⁺ = CDP-4-dehydro-3,6-dideoxy- α -D-glucose + NADPH + H⁺
Other name(s): *rfbJ* (gene name)
Systematic name: CDP- α -D-abequose:NADP⁺ 4-oxidoreductase
Comments: Isolated from *Yersinia pseudotuberculosis* [1891, 3880] and *Salmonella enterica* [1891, 4271].
References: [1891, 4271, 3880]

[EC 1.1.1.341 created 2012]

EC 1.1.1.342

Accepted name: CDP-paratose synthase
Reaction: CDP- α -D-paratose + NADP⁺ = CDP-4-dehydro-3,6-dideoxy- α -D-glucose + NADPH + H⁺
Other name(s): *rfbS* (gene name)
Systematic name: CDP- α -D-paratose:NADP⁺ 4-oxidoreductase
Comments: The enzyme is involved in synthesis of paratose and tyvelose, unusual 3,6-dideoxyhexose sugars that form part of the O-antigen in the lipopolysaccharides of several enteric bacteria. Isolated from *Salmonella enterica* subsp. *enterica* serovar Typhi (*Salmonella typhi*).
References: [4035, 1349]

[EC 1.1.1.342 created 2012]

EC 1.1.1.343

Accepted name: phosphogluconate dehydrogenase (NAD⁺-dependent, decarboxylating)
Reaction: 6-phospho-D-gluconate + NAD⁺ = D-ribulose 5-phosphate + CO₂ + NADH + H⁺
Other name(s): 6-PGDH (ambiguous); *gntZ* (gene name); GNDI
Systematic name: 6-phospho-D-gluconate:NAD⁺ 2-oxidoreductase (decarboxylating)
Comments: Highly specific for NAD⁺. The enzyme catalyses both the oxidation and decarboxylation of 6-phospho-D-gluconate. In the bacterium *Methylobacillus flagellatus* the enzyme participates in a formaldehyde oxidation pathway [597]. cf. EC 1.1.1.44, phosphogluconate dehydrogenase (NADP⁺-dependent, decarboxylating).
References: [1939, 2846, 4423, 597]

[EC 1.1.1.343 created 2013]

EC 1.1.1.344

Accepted name: dTDP-6-deoxy-L-talose 4-dehydrogenase [NAD(P)⁺]
Reaction: dTDP-6-deoxy- β -L-talose + NAD(P)⁺ = dTDP-4-dehydro- β -L-rhamnose + NAD(P)H + H⁺
Other name(s): *tal* (gene name)
Systematic name: dTDP-6-deoxy- β -L-talose:NAD(P)⁺ 4-oxidoreductase
Comments: The enzyme works equally well with NAD⁺ and NADP⁺.
References: [1814]

[EC 1.1.1.344 created 2013]

EC 1.1.1.345

- Accepted name:** D-2-hydroxyacid dehydrogenase (NAD⁺)
Reaction: an (R)-2-hydroxycarboxylate + NAD⁺ = a 2-oxocarboxylate + NADH + H⁺
Other name(s): LdhA; HdhD; D-2-hydroxyisocaproate dehydrogenase; R-HicDH; D-HicDH; (R)-2-hydroxy-4-methylpentanoate:NAD⁺ oxidoreductase; (R)-2-hydroxyisocaproate dehydrogenase; D-mandelate dehydrogenase (ambiguous)
Systematic name: (R)-2-hydroxycarboxylate:NAD⁺ oxidoreductase
Comments: The enzymes, characterized from bacteria (*Peptoclostridium difficile*, *Enterococcus faecalis* and from lactic acid bacteria) prefer substrates with a main chain of 5 carbons (such as 4-methyl-2-oxopentanoate) to those with a shorter chain. It also utilizes phenylpyruvate. The enzyme from the halophilic archaeon *Haloferax mediterranei* prefers substrates with a main chain of 3-4 carbons (pyruvate and 2-oxobutanoate). *cf.* EC 1.1.1.272, (D)-2-hydroxyacid dehydrogenase (NADP⁺).
References: [796, 344, 1908, 4076, 533, 2571]

[EC 1.1.1.345 created 2013]

EC 1.1.1.346

- Accepted name:** 2,5-didehydrogluconate reductase (2-dehydro-L-gulonate-forming)
Reaction: 2-dehydro-L-gulonate + NADP⁺ = 2,5-didehydro-D-gluconate + NADPH + H⁺
Other name(s): 2,5-diketo-D-gluconate-reductase (ambiguous); YqhE reductase; *dkgA* (gene name); *dkgB* (gene name)
Systematic name: 2-dehydro-D-gluconate:NADP⁺ 2-oxidoreductase (2-dehydro-L-gulonate-forming)
Comments: The enzyme is involved in ketogluconate metabolism, and catalyses the reaction *in vivo* in the reverse direction to that shown [3584]. It is used in the commercial microbial production of ascorbate. *cf.* EC 1.1.1.274, 2,5-didehydrogluconate reductase (2-dehydro-D-gluconate-forming).
References: [3584, 2543, 4412, 2396, 1901]

[EC 1.1.1.346 created 2013]

EC 1.1.1.347

- Accepted name:** geraniol dehydrogenase (NAD⁺)
Reaction: geraniol + NAD⁺ = geranial + NADH + H⁺
Other name(s): GeDH; *geoA* (gene name)
Systematic name: geraniol:NAD⁺ oxidoreductase
Comments: The enzyme from the bacterium *Castellaniella defragrans* is most active *in vitro* with perillyl alcohol [2312]. The enzyme from the prune mite *Carpoglyphus lactis* also acts (more slowly) on farnesol but not on nerol [2809].
References: [2809, 2312]

[EC 1.1.1.347 created 2013]

EC 1.1.1.348

- Accepted name:** (3R)-2'-hydroxyisoflavanone reductase
Reaction: a (4R)-4,2'-dihydroxyisoflavan + NADP⁺ = a (3R)-2'-hydroxyisoflavanone + NADPH + H⁺
Other name(s): vestitone reductase; pterocarpin synthase (incorrect); pterocarpan synthase (incorrect)
Systematic name: (3R)-2'-hydroxyisoflavanone:NADP⁺ 4-oxidoreductase
Comments: This plant enzyme participates in the biosynthesis of the pterocarpan phytoalexins medicarpin, maackiain, and several forms of glyceollin. The enzyme has a strict stereo specificity for the 3R-isoflavanones.
References: [323, 1315, 1316, 1317, 3460]

[EC 1.1.1.348 created 1992 as EC 1.1.1.246, part transferred 2013 to EC 1.1.1.348]

EC 1.1.1.349

Accepted name: norsolorinic acid ketoreductase
Reaction: (1'*S*)-averantin + NADP⁺ = norsolorinic acid + NADPH + H⁺
Other name(s): *aflD* (gene name); nor-1 (gene name)
Systematic name: (1'*S*)-averantin:NADP⁺ oxidoreductase
Comments: Involved in the synthesis of aflatoxins in the fungus *Aspergillus parasiticus*.
References: [4295, 4474]

[EC 1.1.1.349 created 2013]

EC 1.1.1.350

Accepted name: ureidoglycolate dehydrogenase (NAD⁺)
Reaction: (S)-ureidoglycolate + NAD⁺ = *N*-carbamoyl-2-oxoglycine + NADH + H⁺
Systematic name: (S)-ureidoglycolate:NAD⁺ oxidoreductase
Comments: Involved in catabolism of purines. The enzyme from the bacterium *Escherichia coli* is specific for NAD⁺ [1916]. *cf.* EC 1.1.1.154, ureidoglycolate dehydrogenase [NAD(P)⁺].
References: [711, 1916]

[EC 1.1.1.350 created 2013]

EC 1.1.1.351

Accepted name: phosphogluconate dehydrogenase [NAD(P)⁺-dependent, decarboxylating]
Reaction: 6-phospho-D-gluconate + NAD(P)⁺ = D-ribulose 5-phosphate + CO₂ + NAD(P)H + H⁺
Systematic name: 6-phospho-D-gluconate:NAD(P)⁺ 2-oxidoreductase (decarboxylating)
Comments: The enzyme participates in the oxidative branch of the pentose phosphate pathway, whose main purpose is to produce reducing power and pentose for biosynthetic reactions. Unlike EC 1.1.1.44, phosphogluconate dehydrogenase (NADP⁺-dependent, decarboxylating), it is not specific for NADP⁺ and can accept both cofactors with similar efficiency. *cf.* EC 1.1.1.343, phosphogluconate dehydrogenase [NAD⁺-dependent, decarboxylating].
References: [255, 3667, 2218]

[EC 1.1.1.351 created 2013]

EC 1.1.1.352

Accepted name: 5'-hydroxyaverantin dehydrogenase
Reaction: (1) (1'*S*,5'*S*)-hydroxyaverantin + NAD⁺ = 5'-oxoaverantin + NADH + H⁺
(2) (1'*S*,5'*R*)-hydroxyaverantin + NAD⁺ = 5'-oxoaverantin + NADH + H⁺
Other name(s): HAVN dehydrogenase; *adhA* (gene name)
Systematic name: (1'*S*,5'*S*)-hydroxyaverantin:NAD⁺ oxidoreductase
Comments: Isolated from the aflatoxin-producing mold *Aspergillus parasiticus* [3296]. Involved in aflatoxin biosynthesis. 5'-Oxoaverantin will spontaneously form averufin by intramolecular ketalisation. *cf.* EC 4.2.1.142, 5'-oxoaverantin cyclase.
References: [538, 3296]

[EC 1.1.1.352 created 2013]

EC 1.1.1.353

Accepted name: versiconal hemiacetal acetate reductase
Reaction: (1) versicolorone + NADP⁺ = 1'-hydroxyversicolorone + NADPH + H⁺
(2) versiconol acetate + NADP⁺ = versiconal hemiacetal acetate + NADPH + H⁺

(3) versiconol + NADP⁺ = versiconal + NADPH + H⁺

Other name(s): VHA reductase; VHA reductase I; VHA reductase II; *vrdA* (gene name)
Systematic name: versiconol-acetate:NADP⁺ oxidoreductase
Comments: Isolated from the mold *Aspergillus parasiticus*. Involved in a metabolic grid that leads to aflatoxin biosynthesis.
References: [2455, 3493]

[EC 1.1.1.353 created 2013]

EC 1.1.1.354

Accepted name: farnesol dehydrogenase (NAD⁺)
Reaction: (2*E*,6*E*)-farnesol + NAD⁺ = (2*E*,6*E*)-farnesal + NADH + H⁺
Other name(s): NAD⁺-farnesol dehydrogenase
Systematic name: (2*E*,6*E*)-farnesol:NAD⁺ 1-oxidoreductase
Comments: The enzyme from the prune mite *Carpoglyphus lactis* also acts on geraniol with greater activity [*cf.* EC 1.1.1.347, geraniol dehydrogenase (NAD⁺)]. Unlike EC 1.1.1.216, farnesol dehydrogenase (NADP⁺), this enzyme cannot use NADP⁺ as cofactor.
References: [2809]

[EC 1.1.1.354 created 2013]

EC 1.1.1.355

Accepted name: 2'-dehydrokanamycin reductase
Reaction: kanamycin A + NADP⁺ = 2'-dehydrokanamycin A + NADPH + H⁺
Other name(s): *kanK* (gene name, ambiguous)
Systematic name: kanamycin A:NADP⁺ oxidoreductase
Comments: Found in the bacterium *Streptomyces kanamyceticus* where it is involved in the conversion of kanamycin B to kanamycin A.
References: [3704]

[EC 1.1.1.355 created 2013]

EC 1.1.1.356

Accepted name: GDP-L-colitose synthase
Reaction: GDP-β-L-colitose + NAD(P)⁺ = GDP-4-dehydro-3,6-dideoxy-α-D-mannose + NAD(P)H + H⁺
Other name(s): ColC
Systematic name: GDP-β-L-colitose:NAD(P)⁺ 4-oxidoreductase (5-epimerizing)
Comments: The enzyme is involved in biosynthesis of L-colitose, a 3,6-dideoxyhexose found in the O-antigen of Gram-negative lipopolysaccharides, where it catalyses the reaction in the reverse direction. The enzyme also performs the NAD(P)H-dependent epimerisation at C-5 of the sugar. The enzyme from *Yersinia pseudotuberculosis* is *Si*-specific with respect to NAD(P)H [49].
References: [49]

[EC 1.1.1.356 created 2013]

EC 1.1.1.357

Accepted name: 3α-hydroxysteroid 3-dehydrogenase
Reaction: a 3α-hydroxysteroid + NAD(P)⁺ = a 3-oxosteroid + NAD(P)H + H⁺
Other name(s): 3α-hydroxysteroid dehydrogenase; AKR1C4 (gene name); AKR1C2 (gene name); *hsdA* (gene name)
Systematic name: 3α-hydroxysteroid:NAD(P)⁺ 3-oxidoreductase

Comments: The enzyme acts on multiple 3 α -hydroxysteroids, such as androsterone and 5 α -dihydrotestosterone. The mammalian enzymes are involved in inactivation of steroid hormones, while the bacterial enzymes are involved in steroid degradation. This entry stands for enzymes whose stereo-specificity with respect to NAD⁺ or NADP⁺ is not known. [*cf.* EC 1.1.1.50, 3 α -hydroxysteroid 3-dehydrogenase (*Si*-specific) and EC 1.1.1.213, 3 α -hydroxysteroid 3-dehydrogenase (*Re*-specific)].

References: [811, 1896, 2893, 2585, 2691]

[EC 1.1.1.357 created 2013]

EC 1.1.1.358

Accepted name: 2-dehydropantolactone reductase
Reaction: (*R*)-pantolactone + NADP⁺ = 2-dehydropantolactone + NADPH + H⁺
Other name(s): 2-oxopantoyl lactone reductase; 2-ketopantoyl lactone reductase; ketopantoyl lactone reductase; 2-dehydropantoyl-lactone reductase
Systematic name: (*R*)-pantolactone:NADP⁺ oxidoreductase
Comments: The enzyme participates in an alternative pathway for biosynthesis of (*R*)-pantothenate (vitamin B₅). This entry covers enzymes whose stereo specificity for NADP⁺ is not known. *cf.* EC 1.1.1.168 2-dehydropantolactone reductase (*Re*-specific) and EC 1.1.1.214, 2-dehydropantolactone reductase (*Si*-specific).
References: [1416]

[EC 1.1.1.358 created 2013]

EC 1.1.1.359

Accepted name: aldose 1-dehydrogenase [NAD(P)⁺]
Reaction: an aldopyranose + NAD(P)⁺ = an aldono-1,5-lactone + NAD(P)H + H⁺
Systematic name: an aldopyranose:NAD(P)⁺ 1-oxidoreductase
Comments: The enzyme from the archaeon *Sulfolobus solfataricus* shows broad specificity towards aldoses (D-glucose, D-galactose, D-xylose, L-arabinose, 6-deoxy-D-glucose, D-fucose) and can utilize NAD⁺ and NADP⁺ with similar catalytic efficiency. It is involved in aldose catabolism via the branched variant of the Entner-Doudoroff pathway.
References: [1196, 3557, 2121, 3856, 2540, 1336]

[EC 1.1.1.359 created 2013]

EC 1.1.1.360

Accepted name: glucose/galactose 1-dehydrogenase
Reaction: (1) D-glucopyranose + NADP⁺ = D-glucono-1,5-lactone + NADPH + H⁺
(2) D-galactopyranose + NADP⁺ = D-galactono-1,5-lactone + NADPH + H⁺
Other name(s): GdhA; dual-specific glucose/galactose dehydrogenase; glucose (galactose) dehydrogenase; glucose/galactose dehydrogenase
Systematic name: D-glucose/D-galactose 1-dehydrogenase (NADPH)
Comments: A zinc protein. The enzyme from the archaeon *Picrophilus torridus* is involved in glucose and galactose catabolism via the nonphosphorylative variant of the Entner-Doudoroff pathway. It shows 20-fold higher activity with NADP⁺ compared to NAD⁺. The oxidation of D-glucose and D-galactose is catalysed at a comparable rate (*cf.* EC 1.1.1.119, glucose 1-dehydrogenase (NADP⁺) and EC 1.1.1.120, galactose 1-dehydrogenase (NADP⁺)).
References: [91, 2540]

[EC 1.1.1.360 created 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⁺
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: [4037]

[EC 1.1.1.361 created 2013]

EC 1.1.1.362

Accepted name: aklaviketone reductase
Reaction: aklavinone + NADP⁺ = aklaviketone + NADPH + H⁺
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: [818]

[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⁺) and EC 1.1.1.388, glucose-6-phosphate dehydrogenase (NAD⁺).
References: [2872, 2181, 669, 3102]

[EC 1.1.1.363 created 2013, modified 2015]

EC 1.1.1.364

Accepted name: dTDP-4-dehydro-6-deoxy- α -D-gulose 4-ketoreductase
Reaction: dTDP-6-deoxy- α -D-allose + NAD(P)⁺ = dTDP-4-dehydro-6-deoxy- α -D-gulose + NAD(P)H + H⁺
Other name(s): dTDP-4-dehydro-6-deoxygulose reductase; *tylD* (gene name); *gerKI* (gene name); *chmD* (gene name); *mydI* (gene name)
Systematic name: dTDP-6-deoxy- α -D-allose:NAD(P)⁺ oxidoreductase
Comments: The enzyme forms an activated deoxy- α -D-allose, which is converted to mycinose after attachment to the aglycones of several macrolide antibiotics, including tylosin, chalcomycin, dihydrochalcomycin, and mycinamicin II.
References: [211, 99, 3882, 2066]

[EC 1.1.1.364 created 2013]

EC 1.1.1.365

Accepted name: D-galacturonate reductase
Reaction: L-galactonate + NADP⁺ = D-galacturonate + NADPH + H⁺
Other name(s): GalUR; *gar1* (gene name)
Systematic name: L-galactonate:NADP⁺ oxidoreductase

Comments: The enzyme from plants is involved in ascorbic acid (vitamin C) biosynthesis [1663, 32]. The enzyme from the fungus *Trichoderma reesei* (*Hypocrea jecorina*) is involved in a eukaryotic degradation pathway of D-galacturonate. It is also active with D-glucuronate and glyceraldehyde [2085]. Neither enzyme shows any activity with NADH.

References: [1663, 32, 2085, 2411]

[EC 1.1.1.365 created 2013]

EC 1.1.1.366

Accepted name: L-idonate 5-dehydrogenase (NAD⁺)

Reaction: L-idonate + NAD⁺ = 5-dehydro-D-gluconate + NADH + H⁺

Systematic name: L-idonate:NAD⁺ oxidoreductase

Comments: Involved in the catabolism of ascorbate (vitamin C) to tartrate. No activity is observed with NADP⁺ (cf. EC 1.1.1.264, L-idonate 5-dehydrogenase).

References: [772]

[EC 1.1.1.366 created 2013]

EC 1.1.1.367

Accepted name: UDP-2-acetamido-2,6-β-L-*arabino*-hexul-4-ose reductase

Reaction: UDP-2-acetamido-2,6-dideoxy-β-L-talose + NAD(P)⁺ = UDP-2-acetamido-2,6-β-L-*arabino*-hexul-4-ose + NAD(P)H + H⁺

Other name(s): WbjC; Cap5F

Systematic name: UDP-2-acetamido-2,6-dideoxy-L-talose:NADP⁺ oxidoreductase

Comments: Part of the biosynthesis of UDP-*N*-acetyl-L-fucosamine. Isolated from the bacteria *Pseudomonas aeruginosa* and *Staphylococcus aureus*.

References: [1973, 2660, 2570]

[EC 1.1.1.367 created 2014]

EC 1.1.1.368

Accepted name: 6-hydroxycyclohex-1-ene-1-carbonyl-CoA dehydrogenase

Reaction: 6-hydroxycyclohex-1-ene-1-carbonyl-CoA + NAD⁺ = 6-oxocyclohex-1-ene-1-carbonyl-CoA + NADH + H⁺

Systematic name: 6-hydroxycyclohex-1-ene-1-carbonyl-CoA:NAD⁺ 6-oxidoreductase

Comments: The enzyme participates in the central benzoyl-CoA degradation pathway of some anaerobic bacteria such as *Thauera aromatica*.

References: [2112]

[EC 1.1.1.368 created 2014]

EC 1.1.1.369

Accepted name: D-*chiro*-inositol 1-dehydrogenase

Reaction: 1D-*chiro*-inositol + NAD⁺ = 2D-2,3,5/4,6-pentahydroxycyclohexanone + NADH + H⁺

Other name(s): DCI 1-dehydrogenase; IolG

Systematic name: 1D-*chiro*-inositol:NAD⁺ 1-oxidoreductase

Comments: The enzyme, found in the bacterium *Bacillus subtilis*, also catalyses the reaction of EC 1.1.1.18, inositol 2-dehydrogenase, and can also use D-glucose and D-xylose. It shows trace activity with D-ribose and D-fructose [3118]. It is part of a *myo*-inositol/D-*chiro*-inositol degradation pathway leading to acetyl-CoA.

References: [3118, 4376]

[EC 1.1.1.369 created 2014]

EC 1.1.1.370

- Accepted name:** *scyllo*-inositol 2-dehydrogenase (NAD⁺)
Reaction: *scyllo*-inositol + NAD⁺ = 2,4,6/3,5-pentahydroxycyclohexanone + NADH + H⁺
Other name(s): *iolX* (gene name)
Systematic name: *scyllo*-inositol:NAD⁺ 2-oxidoreductase
Comments: The enzyme, found in the bacterium *Bacillus subtilis*, has no activity with NADP⁺ [*cf.* EC 1.1.1.371, *scyllo*-inositol 2-dehydrogenase (NADP⁺)]. It is part of a *scyllo*-inositol degradation pathway leading to acetyl-CoA.
References: [2623]

[EC 1.1.1.370 created 2014]

EC 1.1.1.371

- Accepted name:** *scyllo*-inositol 2-dehydrogenase (NADP⁺)
Reaction: *scyllo*-inositol + NADP⁺ = 2,4,6/3,5-pentahydroxycyclohexanone + NADPH + H⁺
Other name(s): *iolW* (gene name)
Systematic name: *scyllo*-inositol:NADP⁺ 2-oxidoreductase
Comments: The enzyme, found in the bacterium *Bacillus subtilis*, has no activity with NAD⁺ [*cf.* EC 1.1.1.370, *scyllo*-inositol 2-dehydrogenase (NAD⁺)].
References: [2623]

[EC 1.1.1.371 created 2014]

EC 1.1.1.372

- Accepted name:** D/L-glyceraldehyde reductase
Reaction: (1) glycerol + NADP⁺ = L-glyceraldehyde + NADPH + H⁺
(2) glycerol + NADP⁺ = D-glyceraldehyde + NADPH + H⁺
Other name(s): *gldI* (gene name); *gaadD* (gene name)
Systematic name: glycerol:NADP⁺ oxidoreductase (D/L-glyceraldehyde-forming)
Comments: The enzyme takes part in a D-galacturonate degradation pathway in the fungi *Aspergillus niger* and *Trichoderma reesei* (*Hypocrea jecorina*). It has equal activity with D- and L-glyceraldehyde, and can also reduce glyoxal and methylglyoxal. The reaction is only observed in the direction of glyceraldehyde reduction.
References: [2249, 2411]

[EC 1.1.1.372 created 2014]

EC 1.1.1.373

- Accepted name:** sulfolactaldehyde 3-reductase
Reaction: 2,3-dihydroxypropane-1-sulfonate + NAD⁺ = 2-hydroxy-3-oxopropane-1-sulfonate + NADH + H⁺
Other name(s): *yihU* (gene name)
Systematic name: 2,3-dihydroxypropane-1-sulfonate:NAD⁺ 3-oxidoreductase
Comments: The enzyme, characterized from the bacterium *Escherichia coli*, is involved in the degradation pathway of sulfoquinovose, the polar headgroup of sulfolipids found in the photosynthetic membranes of all higher plants, mosses, ferns, algae, and most photosynthetic bacteria, as well as the surface layer of some archaea.
References: [795]

[EC 1.1.1.373 created 2014]

EC 1.1.1.374

- Accepted name:** UDP-*N*-acetylglucosamine 3-dehydrogenase
Reaction: UDP-*N*-acetyl- α -D-glucosamine + NAD⁺ = UDP-2-acetamido-3-dehydro-2-deoxy- α -D-glucopyranose + NADH + H⁺

Systematic name: UDP-*N*-acetyl- α -D-glucosamine:NAD⁺ 3-oxidoreductase
Comments: The enzyme from the archaeon *Methanococcus maripaludis* is activated by KCl (200 mM).
References: [2729]

[EC 1.1.1.374 created 2014]

EC 1.1.1.375

Accepted name: L-2-hydroxycarboxylate dehydrogenase [NAD(P)⁺]
Reaction: a (2*S*)-2-hydroxycarboxylate + NAD(P)⁺ = a 2-oxocarboxylate + NAD(P)H + H⁺
Other name(s): MdhII; lactate/malate dehydrogenase
Systematic name: (2*S*)-2-hydroxycarboxylate:NAD(P)⁺ oxidoreductase
Comments: The enzyme from the archaeon *Methanocaldococcus jannaschii* catalyses the reversible oxidation of (2*R*)-3-sulfolactate and (*S*)-malate to 3-sulfonypyruvate and oxaloacetate, respectively (note that (2*R*)-3-sulfolactate has the same stereochemical configuration as (2*S*)-2-hydroxycarboxylates) [1261]. The enzyme can use both NADH and NADPH, although activity is higher with NADPH [1261, 2163, 2353]. The oxidation of (2*R*)-3-sulfolactate was observed only in the presence of NADP⁺ [1261]. The same organism also possesses an NAD⁺-specific enzyme with similar activity, cf. EC 1.1.1.337, L-2-hydroxycarboxylate dehydrogenase (NAD⁺).
References: [1261, 2163, 2353]

[EC 1.1.1.375 created 2014]

EC 1.1.1.376

Accepted name: L-arabinose 1-dehydrogenase [NAD(P)⁺]
Reaction: L-arabinose + NAD(P)⁺ = L-arabinono-1,4-lactone + NAD(P)H + H⁺
Other name(s): L-*arabino*-aldose dehydrogenase
Systematic name: L-arabinose:NAD(P)⁺ 1-oxidoreductase
Comments: The enzymes from the bacterium *Azospirillum brasilense* and the archaeon *Haloferax volcanii* are part of the L-arabinose degradation pathway and prefer NADP⁺ over NAD⁺. *In vitro* the enzyme from *Azospirillum brasilense* shows also high catalytic efficiency with D-galactose.
References: [2822, 4145, 1753]

[EC 1.1.1.376 created 2014]

EC 1.1.1.377

Accepted name: L-rhamnose 1-dehydrogenase (NADP⁺)
Reaction: L-rhamnose + NADP⁺ = L-rhamnono-1,4-lactone + NADPH + H⁺
Systematic name: L-rhamnose:NADP⁺ 1-oxidoreductase
Comments: The enzyme from the archaeon *Thermoplasma acidophilum* is part of the non-phosphorylative degradation pathway for L-rhamnose. The enzyme differs in cofactor specificity from EC 1.1.1.173, L-rhamnose 1-dehydrogenase, which is specific for NAD⁺.
References: [1920]

[EC 1.1.1.377 created 2014]

EC 1.1.1.378

Accepted name: L-rhamnose 1-dehydrogenase [NAD(P)⁺]
Reaction: L-rhamnose + NAD(P)⁺ = L-rhamnono-1,4-lactone + NAD(P)H + H⁺
Systematic name: L-rhamnose:NAD(P)⁺ 1-oxidoreductase
Comments: The enzyme, which occurs in the bacteria *Azotobacter vinelandii* and *Sphingomonas* sp. SKA58, is part of the non-phosphorylative degradation pathway for L-rhamnose. The enzyme differs in cofactor specificity from EC 1.1.1.173, L-rhamnose 1-dehydrogenase, which is specific for NAD⁺ and EC 1.1.1.377, L-rhamnose 1-dehydrogenase (NADP⁺).
References: [4147, 4146]

[EC 1.1.1.378 created 2014]

EC 1.1.1.379

- Accepted name:** (*R*)-mandelate dehydrogenase
Reaction: (*R*)-mandelate + NAD⁺ = phenylglyoxylate + NADH + H⁺
Other name(s): ManDH₂; D-ManDH₂; D-mandelate dehydrogenase (ambiguous)
Systematic name: (*R*)-mandelate:NAD⁺ 2-oxidoreductase
Comments: The enzyme, found in bacteria and fungi, can also accept a number of substituted mandelate derivatives, such as 3-hydroxymandelate, 4-hydroxymandelate, 2-methoxymandelate, 4-hydroxy-3-methoxymandelate and 3-hydroxy-4-methoxymandelate. The enzyme has no activity with (*S*)-mandelate (*cf.* EC 1.1.99.31, (*S*)-mandelate dehydrogenase) [173, 174]. The enzyme transfers the *pro-R*-hydrogen from NADH [174].
References: [173, 174]

[EC 1.1.1.379 created 2014]

EC 1.1.1.380

- Accepted name:** L-gulonate 5-dehydrogenase
Reaction: L-gulonate + NAD⁺ = D-fructuronate + NADH + H⁺
Systematic name: L-gulonate:NAD⁺ 5-oxidoreductase
Comments: The enzyme, characterized from the bacterium *Halomonas elongata*, participates in a pathway for L-gulonate degradation.
References: [656, 4201]

[EC 1.1.1.380 created 2014]

EC 1.1.1.381

- Accepted name:** 3-hydroxy acid dehydrogenase
Reaction: L-*allo*-threonine + NADP⁺ = aminoacetone + CO₂ + NADPH + H⁺ (overall reaction)
(1a) L-*allo*-threonine + NADP⁺ = L-2-amino-3-oxobutanoate + NADPH + H⁺
(1b) L-2-amino-3-oxobutanoate = aminoacetone + CO₂ (spontaneous)
Other name(s): *ydfG* (gene name); YMR226c (gene name)
Systematic name: L-*allo*-threonine:NADP⁺ 3-oxidoreductase
Comments: The enzyme, purified from the bacterium *Escherichia coli* and the yeast *Saccharomyces cerevisiae*, shows activity with a range of 3- and 4-carbon 3-hydroxy acids. The highest activity is seen with L-*allo*-threonine and D-threonine. The enzyme from *Escherichia coli* also shows high activity with L-serine, D-serine, (*S*)-3-hydroxy-2-methylpropanoate and (*R*)-3-hydroxy-2-methylpropanoate. The enzyme has no activity with NAD⁺ or L-threonine (*cf.* EC 1.1.1.103, L-threonine 3-dehydrogenase).
References: [1097]

[EC 1.1.1.381 created 2014, modified 2015]

EC 1.1.1.382

- Accepted name:** ketol-acid reductoisomerase (NAD⁺)
Reaction: (2*R*)-2,3-dihydroxy-3-methylbutanoate + NAD⁺ = (2*S*)-2-hydroxy-2-methyl-3-oxobutanoate + NADH + H⁺
Systematic name: (2*R*)-2,3-dihydroxy-3-methylbutanoate:NAD⁺ oxidoreductase (isomerizing)
Comments: The enzyme, characterized from the bacteria *Thermacetogenium phaeum* and *Desulfococcus oleovorans* and from the archaeon *Archaeoglobus fulgidus*, is specific for NADH [*cf.* EC 1.1.1.86, ketol-acid reductoisomerase (NADP⁺) and EC 1.1.1.383, ketol-acid reductoisomerase [NAD(P)⁺]].
References: [403]

[EC 1.1.1.382 created 2015]

EC 1.1.1.383

- Accepted name:** ketol-acid reductoisomerase [NAD(P)⁺]
Reaction: (2*R*)-2,3-dihydroxy-3-methylbutanoate + NAD(P)⁺ = (2*S*)-2-hydroxy-2-methyl-3-oxobutanoate + NAD(P)H + H⁺
Systematic name: (2*R*)-2,3-dihydroxy-3-methylbutanoate:NAD(P)⁺ oxidoreductase (isomerizing)
Comments: The enzyme, characterized from the bacteria *Hydrogenobaculum* sp. and *Syntrophomonas wolfei* subsp. *wolfei* and from the archaea *Metallosphaera sedula* and *Ignisphaera aggregans*, can use both NADH and NADPH with similar efficiency [*cf.* EC 1.1.1.86, ketol-acid reductoisomerase (NADP⁺) and EC 1.1.1.382, ketol-acid reductoisomerase (NAD⁺)].
References: [403]

[EC 1.1.1.383 created 2015]

EC 1.1.1.384

- Accepted name:** dTDP-3,4-didehydro-2,6-dideoxy- α -D-glucose 3-reductase
Reaction: dTDP-4-dehydro-2,6-dideoxy- α -D-glucose + NADP⁺ = dTDP-3,4-didehydro-2,6-dideoxy- α -D-glucose + NADPH + H⁺
Other name(s): KijD10; dTDP-4-keto-2,6-dideoxy-D-glucose 3-oxidoreductase; dTDP-4-dehydro-2,6-dideoxy- α -D-glucose 3-oxidoreductase
Systematic name: dTDP-4-dehydro-2,6-dideoxy- α -D-glucose:NADP⁺ 3-oxidoreductase
Comments: The enzyme is involved in the biosynthesis of several deoxysugars, including L-digitoxose, L- and D-olivose, L-oliose, D-mycarose and forosamine.
References: [35, 4110, 1553, 2065]

[EC 1.1.1.384 created 2015]

EC 1.1.1.385

- Accepted name:** dihydroantcapsin dehydrogenase
Reaction: L-dihydroantcapsin + NAD⁺ = L-antcapsin + NADH + H⁺
Other name(s): BacC; *ywfD* (gene name)
Systematic name: L-dihydroantcapsin:NAD⁺ oxidoreductase
Comments: The enzyme, characterized from the bacterium *Bacillus subtilis*, is involved in the biosynthesis of the nonribosomally synthesized dipeptide antibiotic bacilysin, composed of L-alanine and L-antcapsin.
References: [2942]

[EC 1.1.1.385 created 2015]

EC 1.1.1.386

- Accepted name:** ipsdienol dehydrogenase
Reaction: (*R*)-ipsdienol + NAD(P)⁺ = ipsdienone + NAD(P)H + H⁺
Other name(s): IDOLDH
Systematic name: (*R*)-ipsdienol:NAD(P)⁺ oxidoreductase
Comments: The enzyme is involved in pheromone production by the pine engraver beetle, *Ips pini*.
References: [1015]

[EC 1.1.1.386 created 2015]

EC 1.1.1.387

- Accepted name:** L-serine 3-dehydrogenase (NAD⁺)
Reaction: L-serine + NAD⁺ = 2-aminoacetaldehyde + CO₂ + NADH + H⁺ (overall reaction)
(1a) L-serine + NAD⁺ = 2-aminomalonate semialdehyde + NADH + H⁺
(1b) 2-aminomalonate semialdehyde = 2-aminoacetaldehyde + CO₂ (spontaneous)
Other name(s): NAD⁺-dependent L-serine dehydrogenase

Systematic name: L-serine:NAD⁺ 3-oxidoreductase
Comments: The enzyme, purified from the bacterium *Pseudomonas aeruginosa*, also shows activity with L-threonine (*cf.* EC 1.1.1.103, L-threonine 3-dehydrogenase). The enzyme has only very low activity with NADP⁺ [*cf.* EC 1.1.1.276, serine 3-dehydrogenase (NADP⁺)].
References: [3837]

[EC 1.1.1.387 created 2015]

EC 1.1.1.388

Accepted name: glucose-6-phosphate dehydrogenase (NAD⁺)
Reaction: D-glucose 6-phosphate + NAD⁺ = 6-phospho-D-glucono-1,5-lactone + NADH + H⁺
Other name(s): Glc6PDH; *azf* (gene name); archaeal zwischenferment
Systematic name: D-glucose-6-phosphate:NAD⁺ 1-oxidoreductase
Comments: The enzyme catalyses a step of the pentose phosphate pathway. The enzyme from the archaeon *Haloferax volcanii* is specific for NAD⁺. *cf.* EC 1.1.1.363, glucose-6-phosphate dehydrogenase [NAD(P)⁺] and EC 1.1.1.49, glucose-6-phosphate dehydrogenase (NADP⁺).
References: [3003]

[EC 1.1.1.388 created 2015]

EC 1.1.1.389

Accepted name: 2-dehydro-3-deoxy-L-galactonate 5-dehydrogenase
Reaction: 2-dehydro-3-deoxy-L-galactonate + NAD⁺ = 3-deoxy-D-*glycero*-2,5-hexodiulosonate + NADH + H⁺
Systematic name: 2-dehydro-3-deoxy-L-galactonate:NAD⁺ 5-oxidoreductase
Comments: The enzyme, characterized from agarose-degrading bacteria, is involved in a degradation pathway for 3,6-anhydro- α -L-galactopyranose, a major component of the polysaccharides of red macroalgae.
References: [2179]

[EC 1.1.1.389 created 2015]

EC 1.1.1.390

Accepted name: sulfoquinovose 1-dehydrogenase
Reaction: sulfoquinovose + NAD⁺ = 6-deoxy-6-sulfo-D-glucono-1,5-lactone + NADH + H⁺
Systematic name: 6-deoxy-6-sulfo-D-glucopyranose:NAD⁺ 1-oxidoreductase
Comments: The enzyme, characterized from the bacterium *Pseudomonas putida* SQ1, participates in a sulfoquinovose degradation pathway. Activity with NADP⁺ is only 4% of that with NAD⁺.
References: [994]

[EC 1.1.1.390 created 2015]

EC 1.1.1.391

Accepted name: 3 β -hydroxycholanate 3-dehydrogenase (NAD⁺)
Reaction: isolithocholate + NAD⁺ = 3-oxo-5 β -cholan-24-oate + NADH + H⁺
Other name(s): 3 β -hydroxysteroid dehydrogenase
Systematic name: isolithocholate:NAD⁺ 3-oxidoreductase
Comments: This bacterial enzyme is involved, along with EC 1.1.1.52, 3 α -hydroxycholanate dehydrogenase (NAD⁺), or EC 1.1.1.392, 3 α -hydroxycholanate dehydrogenase (NADP⁺), in the modification of secondary bile acids to form 3 β -bile acids (also known as iso-bile acids). The enzyme catalyses the reaction in the reduction direction *in vivo*. Also acts on related 3-oxo bile acids. *cf.* EC 1.1.1.393, 3 β -hydroxycholanate 3-dehydrogenase (NADP⁺).
References: [915, 916, 805]

[EC 1.1.1.391 created 2016]

EC 1.1.1.392

- Accepted name:** 3 α -hydroxycholanate dehydrogenase (NADP⁺)
Reaction: lithocholate + NADP⁺ = 3-oxo-5 β -cholan-24-oate + NADPH + H⁺
Other name(s): α -hydroxy-cholanate dehydrogenase (ambiguous)
Systematic name: lithocholate:NADP⁺ 3-oxidoreductase
Comments: This bacterial enzyme is involved in the modification of secondary bile acids to form 3 β -bile acids (also known as iso-bile acids) via a 3-oxo intermediate. The enzyme catalyses a reversible reaction *in vitro*. Also acts on related bile acids. *cf.* EC 1.1.1.52, 3 α -hydroxycholanate dehydrogenase (NAD⁺).
References: [805]

[EC 1.1.1.392 created 2016]

EC 1.1.1.393

- Accepted name:** 3 β -hydroxycholanate 3-dehydrogenase (NADP⁺)
Reaction: isolithocholate + NADP⁺ = 3-oxo-5 β -cholan-24-oate + NADPH + H⁺
Other name(s): 3 β -hydroxysteroid dehydrogenase (ambiguous)
Systematic name: isolithocholate:NADP⁺ 3-oxidoreductase
Comments: This bacterial enzyme is involved, along with EC 1.1.1.52, 3 α -hydroxycholanate dehydrogenase (NAD⁺), or EC 1.1.1.392, 3 α -hydroxycholanate dehydrogenase (NADP⁺), in the modification of secondary bile acids to form 3 β -bile acids (also known as iso-bile acids). The enzyme catalyses the reaction in the reduction direction *in vivo*. Also acts on related 3-oxo bile acids. *cf.* EC 1.1.1.391, 3 β -hydroxycholanate 3-dehydrogenase (NAD⁺).
References: [42, 805]

[EC 1.1.1.393 created 2016]

EC 1.1.1.394

- Accepted name:** aurachin B dehydrogenase
Reaction: aurachin B + NAD⁺ + H₂O = 4-[(2*E*,6*E*)-farnesyl]-4-hydroxy-2-methyl-3-oxo-3,4-dihydroquinoline 1-oxide + NADH + H⁺ (overall reaction)
(1a) 4-[(2*E*,6*E*)-farnesyl]-3,4-dihydroxy-2-methyl-3,4-dihydroquinoline 1-oxide + NAD⁺ = 4-[(2*E*,6*E*)-farnesyl]-4-hydroxy-2-methyl-3-oxo-3,4-dihydroquinoline 1-oxide + NADH + H⁺
(1b) aurachin B + H₂O = 4-[(2*E*,6*E*)-farnesyl]-3,4-dihydroxy-2-methyl-3,4-dihydroquinoline 1-oxide (spontaneous)
Other name(s): AuaH
Systematic name: aurachin B:NAD⁺ 3-oxidoreductase
Comments: The enzyme from the bacterium *Stigmatella aurantiaca* catalyses the final step in the conversion of aurachin C to aurachin B. *In vivo* the enzyme catalyses the reduction of 4-[(2*E*,6*E*)-farnesyl]-4-hydroxy-2-methyl-3-oxo-3,4-dihydroquinoline-1-oxide to form 4-[(2*E*,6*E*)-farnesyl]-2-methyl-1-oxo-3,4-dihydroquinoline-3,4-diol (note that the reactions written above proceed from right to left), which then undergoes a spontaneous dehydration to form aurachin B.
References: [1846]

[EC 1.1.1.394 created 2016]

EC 1.1.1.395

- Accepted name:** 3 α -hydroxy bile acid-CoA-ester 3-dehydrogenase
Reaction: a 3 α -hydroxy bile acid CoA ester + NAD⁺ = a 3-oxo bile acid CoA ester + NADH + H⁺
Other name(s): *baiA1* (gene name); *baiA2* (gene name); *baiA3* (gene name)
Systematic name: 3 α -hydroxy-bile-acid-CoA-ester:NAD⁺ 3-oxidoreductase
Comments: This bacterial enzyme is involved in the 7-dehydroxylation process associated with bile acid degradation. The enzyme has very little activity with unconjugated bile acid substrates. It has similar activity with choloyl-CoA, chenodeoxycholoyl-CoA, deoxycholoyl-CoA, and lithocholoyl-CoA.
References: [2381, 294]

[EC 1.1.1.395 created 2016]

EC 1.1.1.396

- Accepted name:** bacteriochlorophyllide *a* dehydrogenase
Reaction: (1) 3-deacetyl-3-(1-hydroxyethyl)bacteriochlorophyllide *a* + NAD⁺ = bacteriochlorophyllide *a* + NADH + H⁺
(2) 3-devinyl-3-(1-hydroxyethyl)chlorophyllide *a* + NAD⁺ = 3-acetyl-3-devinylchlorophyllide *a* + NADH + H⁺
Other name(s): *bchC* (gene name)
Systematic name: 3-deacetyl-3-(1-hydroxyethyl)bacteriochlorophyllide-*a*:NAD⁺ oxidoreductase (bacteriochlorophyllide *a*-forming)
Comments: The enzyme, together with EC 1.3.7.15, chlorophyllide-*a* reductase, and EC 4.2.1.165, chlorophyllide-*a* 3¹-hydratase, is involved in the conversion of chlorophyllide *a* to bacteriochlorophyllide *a*. The enzymes can act in multiple orders, resulting in the formation of different intermediates, but the final product of the cumulative action of the three enzymes is always bacteriochlorophyllide *a*. The enzyme oxidizes a hydroxyl group on ring A, converting it to an oxo group.
References: [4169, 2485, 2131]

[EC 1.1.1.396 created 2016]

EC 1.1.1.397

- Accepted name:** β-methylindole-3-pyruvate reductase
Reaction: (2*S*,3*R*)-2-hydroxy-3-(indol-3-yl)butanoate + NAD⁺ = (*R*)-3-(indol-3-yl)-2-oxobutanoate + NADH + H⁺
Other name(s): ind2 (gene name)
Systematic name: (2*S*,3*R*)-2-hydroxy-3-(indol-3-yl)butanoate:NAD⁺ oxidoreductase
Comments: The enzyme, characterized from the bacterium *Streptomyces griseus*, participates in the biosynthesis of indolmycin, an antibacterial drug that inhibits the bacterial tryptophan—tRNA ligase (EC 6.1.1.2).
References: [878]

[EC 1.1.1.397 created 2016]

EC 1.1.1.398

- Accepted name:** 2-glutathionyl-2-methylbut-3-en-1-ol dehydrogenase
Reaction: 2-(glutathion-*S*-yl)-2-methylbut-3-en-1-ol + 2 NAD⁺ + H₂O = 2-(glutathion-*S*-yl)-2-methylbut-3-enoate + 2 NADH + 2 H⁺ (overall reaction)
(1a) 2-(glutathion-*S*-yl)-2-methylbut-3-en-1-ol + NAD⁺ = 2-(glutathion-*S*-yl)-2-methylbut-3-enal + NADH + H⁺
(1b) 2-(glutathion-*S*-yl)-2-methylbut-3-enal + NAD⁺ + H₂O = 2-(glutathion-*S*-yl)-2-methylbut-3-enoate + NADH + H⁺
Other name(s): *isoH* (gene name); 4-hydroxy-3-glutathionyl-3-methylbut-1-ene dehydrogenase
Systematic name: 2-(glutathion-*S*-yl)-2-methylbut-3-en-1-ol:NAD⁺ oxidoreductase
Comments: The enzyme, characterized from the bacterium *Rhodococcus* sp. AD45, is involved in isoprene degradation.
References: [4006]

[EC 1.1.1.398 created 2016]

EC 1.1.1.399

- Accepted name:** 2-oxoglutarate reductase
Reaction: (*R*)-2-hydroxyglutarate + NAD⁺ = 2-oxoglutarate + NADH + H⁺
Other name(s): *serA* (gene name)
Systematic name: (*R*)-2-hydroxyglutarate:NAD⁺ 2-oxidoreductase

Comments: The enzyme catalyses a reversible reaction. The enzyme from the bacterium *Peptoniphilus asaccharolyticus* is specific for (*R*)-2-hydroxyglutarate [2202, 1764]. The SerA enzyme from the bacterium *Escherichia coli* can also accept (*S*)-2-hydroxyglutarate with a much higher K_m , and also catalyses the activity of EC 1.1.1.95, phosphoglycerate dehydrogenase [4459].

References: [2202, 1764, 4459]

[EC 1.1.1.399 created 2016]

EC 1.1.1.400

Accepted name: 2-methyl-1,2-propanediol dehydrogenase
Reaction: 2-methylpropane-1,2-diol + NAD⁺ = 2-hydroxy-2-methylpropanal + NADH + H⁺
Other name(s): *mpdB* (gene name)
Systematic name: 2-methylpropane-1,2-diol:NAD⁺ 1-oxidoreductase
Comments: This bacterial enzyme is involved in the degradation pathways of the alkene 2-methylpropene and the fuel additive *tert*-butyl methyl ether (MTBE), a widely occurring groundwater contaminant.
References: [1004, 2044]

[EC 1.1.1.400 created 2016]

EC 1.1.1.401

Accepted name: 2-dehydro-3-deoxy-L-rhamnonate dehydrogenase (NAD⁺)
Reaction: 2-dehydro-3-deoxy-L-rhamnonate + NAD⁺ = 2,4-didehydro-3-deoxy-L-rhamnonate + NADH + H⁺
Other name(s): 2-keto-3-deoxy-L-rhamnonate dehydrogenase
Systematic name: 2-dehydro-3-deoxy-L-rhamnonate:NAD⁺ 4-oxidoreductase
Comments: The enzyme, characterized from the bacteria *Sphingomonas* sp. SKA58 and *Sulfobacillus thermosulfidooxidans*, is involved in the non-phosphorylative degradation pathway for L-rhamnose. It does not show any detectable activity with NADP⁺ or with other aldoses.
References: [4146, 158]

[EC 1.1.1.401 created 2016]

EC 1.1.1.402

Accepted name: D-erythritol 1-phosphate dehydrogenase
Reaction: D-erythritol 1-phosphate + NADP⁺ = D-erythrulose 1-phosphate + NADPH + H⁺
Other name(s): *eryB* (gene name)
Systematic name: D-erythritol-1-phosphate 2-oxidoreductase
Comments: The enzyme, characterized from the pathogenic bacterium *Brucella abortus*, which causes brucellosis in livestock, participates in erythritol catabolism.
References: [3602, 3308, 198]

[EC 1.1.1.402 created 2016]

EC 1.1.1.403

Accepted name: D-threitol dehydrogenase (NAD⁺)
Reaction: D-threitol + NAD⁺ = D-erythrulose + NADH + H⁺
Other name(s): *dthD* (gene name)
Systematic name: D-threitol:NAD⁺ oxidoreductase
Comments: The enzyme, characterized from the bacterium *Mycobacterium smegmatis*, participates in the degradation of D-threitol.
References: [1594]

[EC 1.1.1.403 created 2016]

EC 1.1.1.404

- Accepted name:** tetrachlorobenzoquinone reductase
Reaction: 2,3,5,6-tetrachlorohydroquinone + NAD⁺ = 2,3,5,6-tetrachloro-1,4-benzoquinone + NADH + H⁺
Other name(s): *pcpD* (gene name); TCBQ reductase
Systematic name: 2,3,5,6-tetrachlorohydroquinone:NAD⁺ oxidoreductase
Comments: Contains FMN. The enzyme, characterized from the bacterium *Sphingobium chlorophenolicum*, participates in the degradation of pentachlorophenol.
References: [571, 4296]

[EC 1.1.1.404 created 2017]

EC 1.1.1.405

- Accepted name:** ribitol-5-phosphate 2-dehydrogenase (NADP⁺)
Reaction: D-ribitol 5-phosphate + NADP⁺ = D-ribulose 5-phosphate + NADPH + H⁺
Other name(s): *acs1* (gene name); *bcs1* (gene name); *tarJ* (gene name); ribulose-5-phosphate reductase; ribulose-5-*P* reductase; D-ribulose 5-phosphate reductase
Systematic name: D-ribitol-5-phosphate:NADP⁺ 2-oxidoreductase
Comments: Requires Zn²⁺. The enzyme, characterized in bacteria, is specific for NADP. It is part of the synthesis pathway of CDP-ribitol. In *Haemophilus influenzae* it is part of a multifunctional enzyme also catalysing EC 2.7.7.40, D-ribitol-5-phosphate cytidylyltransferase. *cf.* EC 1.1.1.137, ribitol-5-phosphate 2-dehydrogenase.
References: [4491, 2980, 2981, 222]

[EC 1.1.1.405 created 2017]

EC 1.1.1.406

- Accepted name:** galactitol 2-dehydrogenase (L-tagatose-forming)
Reaction: galactitol + NAD⁺ = L-tagatose + NADH + H⁺
Other name(s): GatDH
Systematic name: galactitol:NAD⁺ 2-oxidoreductase (L-tagatose-forming)
Comments: The enzyme, characterized in the bacterium *Rhodobacter sphaeroides*, has a wide substrate specificity. In addition to galactitol, it primarily oxidizes D-threitol and xylitol, and in addition to L-tagatose, it primarily reduces L-erythrulose, D-ribulose and L-glyceraldehyde. It is specific for NAD⁺. The enzyme also shows activity with D-tagatose (*cf.* EC 1.1.1.16, galactitol 2-dehydrogenase).
References: [3383, 504]

[EC 1.1.1.406 created 2017]

EC 1.1.1.407

- Accepted name:** D-altritol 5-dehydrogenase
Reaction: D-altritol + NAD⁺ = D-tagatose + NADH + H⁺
Systematic name: D-altritol:NAD⁺ 5-oxidoreductase
Comments: The enzyme, characterized in *Agrobacterium fabrum* C58, also has low activity with D-mannitol and D-arabinitol. It is part of a D-altritol degradation pathway.
References: [4202]

[EC 1.1.1.407 created 2017]

EC 1.1.1.408

- Accepted name:** 4-phospho-D-threonate 3-dehydrogenase
Reaction: 4-phospho-D-threonate + NAD⁺ = glycerone phosphate + CO₂ + NADH + H⁺ (overall reaction)
(1a) 4-phospho-D-threonate + NAD⁺ = 3-dehydro-4-phospho-D-erythronate + NADH + H⁺
(1b) 3-dehydro-4-phospho-D-erythronate = glycerone phosphate + CO₂ (spontaneous)

Other name(s): *pdxA2* (gene name) (ambiguous)
Systematic name: 4-phospho-D-threonate:NAD⁺ 3-oxidoreductase
Comments: The enzyme, characterized from bacteria, is involved in a pathway for D-threonate catabolism.
References: [4447]

[EC 1.1.1.408 created 2017]

EC 1.1.1.409

Accepted name: 4-phospho-D-erythronate 3-dehydrogenase
Reaction: 4-phospho-D-erythronate + NAD⁺ = glycerone phosphate + CO₂ + NADH + H⁺ (overall reaction)
(1a) 4-phospho-D-erythronate + NAD⁺ = 3-dehydro-4-phospho-L-threonate + NADH + H⁺
(1b) 3-dehydro-4-phospho-L-threonate = glycerone phosphate + CO₂ (spontaneous)
Other name(s): *pdxA2* (gene name) (ambiguous)
Systematic name: 4-phospho-D-erythronate:NAD⁺ 3-oxidoreductase
Comments: The enzyme, characterized from bacteria, is involved in a pathway for D-erythronate catabolism.
References: [4447]

[EC 1.1.1.409 created 2017]

EC 1.1.1.410

Accepted name: D-erythronate 2-dehydrogenase
Reaction: D-erythronate + NAD⁺ = 2-dehydro-D-erythronate + NADH + H⁺
Other name(s): *denD* (gene name)
Systematic name: D-erythronate:NAD⁺ 2-oxidoreductase
Comments: The enzyme, characterized from bacteria, is involved in D-erythronate catabolism.
References: [4447]

[EC 1.1.1.410 created 2017]

EC 1.1.1.411

Accepted name: L-threonate 2-dehydrogenase
Reaction: L-threonate + NAD⁺ = 2-dehydro-L-erythronate + NADH + H⁺
Other name(s): *ltnD* (gene name)
Systematic name: L-threonate:NAD⁺ 2-oxidoreductase
Comments: The enzyme, characterized from bacteria, is involved in L-threonate catabolism.
References: [4447]

[EC 1.1.1.411 created 2017]

EC 1.1.1.412

Accepted name: 2-alkyl-3-oxoalkanoate reductase
Reaction: a (2*R*,3*S*)-2-alkyl-3-hydroxyalkanoate + NADP⁺ = an (*R*)-2-alkyl-3-oxoalkanoate + NADPH + H⁺
Other name(s): *oleD* (gene name)
Systematic name: (2*R*,3*S*)-2-alkyl-3-hydroxyalkanoate:NADP⁺ oxidoreductase
Comments: The enzyme, found in certain bacterial species, is part of a pathway for the production of olefins.
References: [347]

[EC 1.1.1.412 created 2017]

EC 1.1.1.413

Accepted name: A-factor type γ -butyrolactone 1'-reductase (1*S*-forming)
Reaction: a (3*R*,4*R*)-3-[(1*S*)-1-hydroxyalkyl]-4-(hydroxymethyl)oxolan-2-one + NADP⁺ = a (3*R*,4*R*)-3-alkanoyl-4-(hydroxymethyl)oxolan-2-one + NADPH + H⁺

Other name(s): *barS1* (gene name)
Systematic name: (3*R*,4*R*)-3-[(1*S*)-1-hydroxyalkyl]-4-(hydroxymethyl)oxolan-2-one:NADP⁺ 1'-oxidoreductase
Comments: The enzyme, which is found in bacteria that produce virginiae-butanolide (VB) type γ -butyrolactone autoregulators, reduces its substrate stereospecifically, forming a hydroxyl group in the (S) configuration.
References: [3492]

[EC 1.1.1.413 created 2017]

EC 1.1.1.414

Accepted name: L-galactonate 5-dehydrogenase
Reaction: L-galactonate + NAD⁺ = D-tagaturonate + NADH + H⁺
Other name(s): *lgoD* (gene name); *lgaC* (gene name)
Systematic name: L-galactonate:NAD⁺ 5-oxidoreductase
Comments: The enzyme, reported from the human gut bacteria *Escherichia coli* and *Bacteroides vulgatus*, participates in an L-galactonate degradation pathway.
References: [655, 2073, 1524]

[EC 1.1.1.414 created 2018]

EC 1.1.1.415

Accepted name: noscapine synthase
Reaction: narcotine hemiacetal + NAD⁺ = noscapine + NADH + H⁺
Other name(s): NOS (gene name)
Systematic name: narcotine hemiacetal:NAD⁺ 1-oxidoreductase
Comments: The enzyme, characterized from the plant *Papaver somniferum* (opium poppy), catalyses the last step in the biosynthesis of the isoquinoline alkaloid noscapine.
References: [576, 2237]

[EC 1.1.1.415 created 2018]

EC 1.1.1.416

Accepted name: isopyridoxal dehydrogenase (5-pyridoxolactone-forming)
Reaction: isopyridoxal + NAD⁺ = 5-pyridoxolactone + NADH + H⁺
Systematic name: isopyridoxal:NAD⁺ oxidoreductase (5-pyridoxolactone-forming)
Comments: The enzyme, characterized from the bacterium *Arthrobacter* sp. Cr-7, participates in the degradation of pyridoxine. The enzyme also catalyses the activity of EC 1.2.1.102, isopyridoxal dehydrogenase (5-pyridoxate-forming).
References: [2183]

[EC 1.1.1.416 created 2018]

EC 1.1.2 With a cytochrome as acceptor

[1.1.2.1 Transferred entry. glycerolphosphate dehydrogenase. As the acceptor is now known, the enzyme has been transferred to EC 1.1.5.3, glycerol-3-phosphate dehydrogenase.]

[EC 1.1.2.1 created 1961, deleted 1965]

EC 1.1.2.2

Accepted name: mannitol dehydrogenase (cytochrome)
Reaction: D-mannitol + a ferricytochrome *c* = D-fructose + a ferrocyclochrome *c* + 2 H⁺
Other name(s): polyol dehydrogenase

Systematic name: D-mannitol:cytochrome-*c* 2-oxidoreductase
Comments: The enzyme from the bacterium *Gluconobacter oxydans* acts on polyols with a D-lyxo configuration, such as D-mannitol and D-sorbitol, with preference towards the former.
References: [117, 604]

[EC 1.1.2.2 created 1961]

EC 1.1.2.3

Accepted name: L-lactate dehydrogenase (cytochrome)
Reaction: (*S*)-lactate + 2 ferricytochrome *c* = pyruvate + 2 ferrocyclochrome *c* + 2 H⁺
Other name(s): lactic acid dehydrogenase; cytochrome *b*₂ (flavin-free derivative of flavocytochrome *b*₂); flavocytochrome *b*₂; L-lactate cytochrome *c* reductase; L(+)-lactate:cytochrome *c* oxidoreductase; dehydrogenase, lactate (cytochrome); L-lactate cytochrome *c* oxidoreductase; lactate dehydrogenase (cytochrome); lactic cytochrome *c* reductase
Systematic name: (*S*)-lactate:ferricytochrome-*c* 2-oxidoreductase
Comments: Identical with cytochrome *b*₂; a flavohemoprotein (FMN).
References: [108, 107, 154, 2831]

[EC 1.1.2.3 created 1961]

EC 1.1.2.4

Accepted name: D-lactate dehydrogenase (cytochrome)
Reaction: (*R*)-lactate + 2 ferricytochrome *c* = pyruvate + 2 ferrocyclochrome *c* + 2 H⁺
Other name(s): lactic acid dehydrogenase; D-lactate (cytochrome) dehydrogenase; cytochrome-*dependent* D-(-)-lactate dehydrogenase; D-lactate-cytochrome *c* reductase; D-(-)-lactic cytochrome *c* reductase
Systematic name: (*R*)-lactate:cytochrome-*c* 2-oxidoreductase
Comments: A flavoprotein (FAD).
References: [1277, 1278, 2830, 2831]

[EC 1.1.2.4 created 1961]

EC 1.1.2.5

Accepted name: D-lactate dehydrogenase (cytochrome *c*-553)
Reaction: (*R*)-lactate + 2 ferricytochrome *c*-553 = pyruvate + 2 ferrocyclochrome *c*-553 + 2 H⁺
Systematic name: (*R*)-lactate:cytochrome-*c*-553 2-oxidoreductase
Comments: The enzyme from the sulfate-reducing bacterium *Desulfovibrio vulgaris* can also act on (*R*)-2-hydroxybutanoate.
References: [2842]

[EC 1.1.2.5 created 1989]

EC 1.1.2.6

Accepted name: polyvinyl alcohol dehydrogenase (cytochrome)
Reaction: polyvinyl alcohol + ferricytochrome *c* = oxidized polyvinyl alcohol + ferrocyclochrome *c* + H⁺
Other name(s): PVA dehydrogenase; PVADH
Systematic name: polyvinyl alcohol:ferricytochrome-*c* oxidoreductase
Comments: A quinoprotein. The enzyme is involved in bacterial polyvinyl alcohol degradation. Some Gram-negative bacteria degrade polyvinyl alcohol by importing it into the periplasmic space, where it is oxidized by polyvinyl alcohol dehydrogenase, an enzyme that is coupled to the respiratory chain via cytochrome *c*. The enzyme contains a pyrroloquinoline quinone cofactor.
References: [3497, 3499, 2383, 1520, 1589, 1858]

[EC 1.1.2.6 created 1989 as EC 1.1.99.23, transferred 2010 to EC 1.1.2.6]

EC 1.1.2.7

- Accepted name:** methanol dehydrogenase (cytochrome *c*)
Reaction: a primary alcohol + 2 ferricytochrome *c*_l = an aldehyde + 2 ferrocycytochrome *c*_l + 2 H⁺
Other name(s): methanol dehydrogenase; MDH
Systematic name: methanol:cytochrome *c* oxidoreductase
Comments: A periplasmic quinoprotein alcohol dehydrogenase that only occurs in methylotrophic bacteria. It uses the novel specific cytochrome *c*_l as acceptor. Acts on a wide range of primary alcohols, including ethanol, duodecanol, chloroethanol, cinnamyl alcohol, and also formaldehyde. Activity is stimulated by ammonia or methylamine. It is usually assayed with phenazine methosulfate. Like all other quinoprotein alcohol dehydrogenases it has an 8-bladed 'propeller' structure, a calcium ion bound to the PQQ in the active site and an unusual disulfide ring structure in close proximity to the PQQ. It differs from EC 1.1.2.8, alcohol dehydrogenase (cytochrome *c*), in having a high affinity for methanol and in having a second essential small subunit (no known function).
References: [96, 97, 885, 3298, 680, 311, 4276, 27, 95, 4220]

[EC 1.1.2.7 created 1972 as EC 1.1.99.8, modified 1982, part transferred 2010 to EC 1.1.2.7]

EC 1.1.2.8

- Accepted name:** alcohol dehydrogenase (cytochrome *c*)
Reaction: a primary alcohol + 2 ferricytochrome *c* = an aldehyde + 2 ferrocycytochrome *c* + 2 H⁺
Other name(s): type I quinoprotein alcohol dehydrogenase; quinoprotein ethanol dehydrogenase
Systematic name: alcohol:cytochrome *c* oxidoreductase
Comments: A periplasmic PQQ-containing quinoprotein. Occurs in *Pseudomonas* and *Rhodopseudomonas*. The enzyme from *Pseudomonas aeruginosa* uses a specific inducible cytochrome *c*₅₅₀ as electron acceptor. Acts on a wide range of primary and secondary alcohols, but not methanol. It has a homodimeric structure [contrasting with the heterotetrameric structure of EC 1.1.2.7, methanol dehydrogenase (cytochrome *c*)]. It is routinely assayed with phenazine methosulfate as electron acceptor. Activity is stimulated by ammonia or amines. Like all other quinoprotein alcohol dehydrogenases it has an 8-bladed 'propeller' structure, a calcium ion bound to the PQQ in the active site and an unusual disulfide ring structure in close proximity to the PQQ.
References: [3261, 3920, 3386, 1875, 1864, 2504]

[EC 1.1.2.8 created 1972 as EC 1.1.99.8, modified 1982, part transferred 2010 to EC 1.1.2.8]

EC 1.1.2.9

- Accepted name:** 1-butanol dehydrogenase (cytochrome *c*)
Reaction: butan-1-ol + 2 ferricytochrome *c* = butanal + 2 ferrocycytochrome *c* + 2 H⁺
Other name(s): BDH
Systematic name: butan-1-ol:ferricytochrome *c* oxidoreductase
Comments: This periplasmic quinoprotein alcohol dehydrogenase, characterized from the bacterium *Thauera butanivorans*, is involved in butane degradation. It contains both pyrroloquinoline quinone (PQQ) and heme *c* prosthetic groups. *cf.* EC 1.1.5.11, 1-butanol dehydrogenase (quinone).
References: [4018, 4019, 4020]

[EC 1.1.2.9 created 2016]

EC 1.1.3 With oxygen as acceptor

[1.1.3.1 Deleted entry. glycolate oxidase. Now included with EC 1.1.3.15 (S)-2-hydroxy-acid oxidase]

[EC 1.1.3.1 created 1961, deleted 1984]

EC 1.1.3.2

- Accepted name:** L-lactate oxidase

Reaction: (S)-lactate + O₂ = pyruvate + H₂O₂
Other name(s): *lctO* (gene name); LOX
Systematic name: (S)-lactate:oxygen 2-oxidoreductase
Comments: Contains flavin mononucleotide (FMN). The best characterized enzyme is that from the bacterium *Aerococcus viridans*. The enzyme is widely used in biosensors to measure the lactate concentration in blood and other tissues.
References: [887, 2356, 1198, 3972, 1124, 3659]

[EC 1.1.3.2 created 1961, transferred 1972 to EC 1.13.12.4, reinstated 2018]

[1.1.3.3 Deleted entry. malate oxidase. Now classified as EC 1.1.5.4, malate dehydrogenase (quinone).]

[EC 1.1.3.3 created 1961, deleted 2014]

EC 1.1.3.4

Accepted name: glucose oxidase
Reaction: β-D-glucose + O₂ = D-glucono-1,5-lactone + H₂O₂
Other name(s): glucose oxyhydrase; corylophyline; penatin; glucose aerodehydrogenase; microcid; β-D-glucose oxidase; D-glucose oxidase; D-glucose-1-oxidase; β-D-glucose:quinone oxidoreductase; glucose oxyhydrase; deoxin-1; GOD
Systematic name: β-D-glucose:oxygen 1-oxidoreductase
Comments: A flavoprotein (FAD).
References: [260, 675, 1872, 1873]

[EC 1.1.3.4 created 1961]

EC 1.1.3.5

Accepted name: hexose oxidase
Reaction: D-glucose + O₂ = D-glucono-1,5-lactone + H₂O₂
Systematic name: D-hexose:oxygen 1-oxidoreductase
Comments: A copper glycoprotein. Also oxidizes D-galactose, D-mannose, maltose, lactose and cellobiose.
References: [228, 229, 3724]

[EC 1.1.3.5 created 1961, modified 1976]

EC 1.1.3.6

Accepted name: cholesterol oxidase
Reaction: cholesterol + O₂ = cholest-5-en-3-one + H₂O₂
Other name(s): cholesterol- O₂ oxidoreductase; 3β-hydroxy steroid oxidoreductase; 3β-hydroxysteroid:oxygen oxidoreductase
Systematic name: cholesterol:oxygen oxidoreductase
Comments: Contains FAD. Cholesterol oxidases are secreted bacterial bifunctional enzymes that catalyse the first two steps in the degradation of cholesterol. The enzyme catalyses the oxidation of the 3β-hydroxyl group to a keto group, and the isomerization of the double bond in the oxidized steroid ring system from the Δ⁵ position to Δ⁶ position (*cf.* EC 5.3.3.1, steroid Δ-isomerase).
References: [3181, 3615, 2348, 4069]

[EC 1.1.3.6 created 1961, modified 1982, modified 2012]

EC 1.1.3.7

Accepted name: aryl-alcohol oxidase
Reaction: an aromatic primary alcohol + O₂ = an aromatic aldehyde + H₂O₂
Other name(s): aryl alcohol oxidase; veratryl alcohol oxidase; arom. alcohol oxidase
Systematic name: aryl-alcohol:oxygen oxidoreductase

Comments: Oxidizes many primary alcohols containing an aromatic ring; best substrates are (2-naphthyl)methanol and 3-methoxybenzyl alcohol.

References: [989]

[EC 1.1.3.7 created 1965]

EC 1.1.3.8

Accepted name: L-gulonolactone oxidase

Reaction: L-gulono-1,4-lactone + O₂ = L-ascorbate + H₂O₂ (overall reaction)

(1a) L-gulono-1,4-lactone + O₂ = L-xylo-hex-2-ulono-1,4-lactone + H₂O₂

(1b) L-xylo-hex-2-ulono-1,4-lactone = L-ascorbate (spontaneous)

Other name(s): L-gulono-γ-lactone: O₂ oxidoreductase; L-gulono-γ-lactone oxidase; L-gulono-γ-lactone:oxidoreductase; GLO

Systematic name: L-gulono-1,4-lactone:oxygen 3-oxidoreductase

Comments: A microsomal flavoprotein (FAD). The product spontaneously isomerizes to L-ascorbate. While most higher animals can synthesize ascorbic acid, primates and guinea pigs cannot [2794].

References: [1664, 1951, 2794, 554]

[EC 1.1.3.8 created 1965, modified 2001, modified 2006]

EC 1.1.3.9

Accepted name: galactose oxidase

Reaction: D-galactose + O₂ = D-galacto-hexodialdose + H₂O₂

Other name(s): D-galactose oxidase; β-galactose oxidase

Systematic name: D-galactose:oxygen 6-oxidoreductase

Comments: A copper protein.

References: [144]

[EC 1.1.3.9 created 1965]

EC 1.1.3.10

Accepted name: pyranose oxidase

Reaction: D-glucose + O₂ = 2-dehydro-D-glucose + H₂O₂

Other name(s): glucose 2-oxidase; pyranose-2-oxidase

Systematic name: pyranose:oxygen 2-oxidoreductase

Comments: A flavoprotein (FAD). Also oxidizes D-xylose, L-sorbose and D-glucono-1,5-lactone, which have the same ring conformation and configuration at C-2, C-3 and C-4.

References: [1722, 2346, 2760, 3256]

[EC 1.1.3.10 created 1972]

EC 1.1.3.11

Accepted name: L-sorbose oxidase

Reaction: L-sorbose + O₂ = 5-dehydro-D-fructose + H₂O₂

Systematic name: L-sorbose:oxygen 5-oxidoreductase

Comments: Also acts on D-glucose, D-galactose and D-xylose, but not on D-fructose. 2,6-Dichloroindophenol can act as acceptor.

References: [4304]

[EC 1.1.3.11 created 1972]

EC 1.1.3.12

Accepted name: pyridoxine 4-oxidase
Reaction: pyridoxine + O₂ = pyridoxal + H₂O₂
Other name(s): pyridoxin 4-oxidase; pyridoxol 4-oxidase
Systematic name: pyridoxine:oxygen 4-oxidoreductase
Comments: A flavoprotein. Can also use 2,6-dichloroindophenol as an acceptor.
References: [3736]

[EC 1.1.3.12 created 1972, modified 1976]

EC 1.1.3.13

Accepted name: alcohol oxidase
Reaction: a primary alcohol + O₂ = an aldehyde + H₂O₂
Other name(s): ethanol oxidase; alcohol:oxygen oxidoreductase
Systematic name: alcohol:oxygen oxidoreductase (H₂O₂-forming)
Comments: The enzymes from the fungi *Candida methanosorbosa* and several *Basidiomycetes* species contain an FAD cofactor [1721, 3746]. The enzyme from the phytopathogenic fungi *Colletotrichum graminicola* and *Colletotrichum gloeosporioides* utilize a mononuclear copper-radical mechanism [4361]. The enzyme acts on primary alcohols and unsaturated alcohols, and has much lower activity with branched-chain and secondary alcohols.
References: [1721, 2791, 3746, 4361]

[EC 1.1.3.13 created 1972]

EC 1.1.3.14

Accepted name: catechol oxidase (dimerizing)
Reaction: 4 catechol + 3 O₂ = 2 dibenzo[1,4]dioxin-2,3-dione + 6 H₂O
Systematic name: catechol:oxygen oxidoreductase (dimerizing)
References: [2696]

[EC 1.1.3.14 created 1972]

EC 1.1.3.15

Accepted name: (*S*)-2-hydroxy-acid oxidase
Reaction: an (*S*)-2-hydroxy carboxylate + O₂ = a 2-oxo carboxylate + H₂O₂
Other name(s): hydroxy-acid oxidase A; hydroxy-acid oxidase B; glycolate oxidase; L-2-hydroxy acid oxidase; hydroxyacid oxidase A; L- α -hydroxy acid oxidase
Systematic name: (*S*)-2-hydroxy carboxylate:oxygen 2-oxidoreductase
Comments: A flavoprotein (FMN). Exists as two major isoenzymes; the A form preferentially oxidizes short-chain aliphatic hydroxy acids, and was previously listed as EC 1.1.3.1, glycolate oxidase; the B form preferentially oxidizes long-chain and aromatic hydroxy acids. The rat isoenzyme B also acts as EC 1.4.3.2, L-amino-acid oxidase.
References: [316, 1077, 2076, 2713, 2715, 3002, 3405, 1770]

[EC 1.1.3.15 created 1972 (EC 1.1.3.1 created 1961, incorporated 1984)]

EC 1.1.3.16

Accepted name: ecdysone oxidase
Reaction: ecdysone + O₂ = 3-dehydroecdysone + H₂O₂
Other name(s): β -ecdysone oxidase
Systematic name: ecdysone:oxygen 3-oxidoreductase
Comments: 2,6-Dichloroindophenol can act as an acceptor.
References: [2029]

[EC 1.1.3.16 created 1976]

EC 1.1.3.17

- Accepted name:** choline oxidase
Reaction: $\text{choline} + 2 \text{O}_2 + \text{H}_2\text{O} = \text{betaine} + 2 \text{H}_2\text{O}_2$ (overall reaction)
(1a) $\text{choline} + \text{O}_2 = \text{betaine aldehyde} + \text{H}_2\text{O}_2$
(1b) $\text{betaine aldehyde} + \text{O}_2 + \text{H}_2\text{O} = \text{betaine} + \text{H}_2\text{O}_2$
Systematic name: choline:oxygen 1-oxidoreductase
Comments: A flavoprotein (FAD). In many bacteria, plants and animals, the osmoprotectant betaine is synthesized using different enzymes to catalyse the conversion of (1) choline into betaine aldehyde and (2) betaine aldehyde into betaine. In plants, the first reaction is catalysed by EC 1.14.15.7, choline monooxygenase, whereas in animals and many bacteria, it is catalysed by either membrane-bound choline dehydrogenase (EC 1.1.99.1) or soluble choline oxidase (EC 1.1.3.17) [4077]. The enzyme involved in the second step, EC 1.2.1.8, betaine-aldehyde dehydrogenase, appears to be the same in those plants, animals and bacteria that use two separate enzymes.
References: [1640, 3246, 3122, 1137, 983, 4077, 984, 1134]

[EC 1.1.3.17 created 1978, modified 2005, modified 2007]

EC 1.1.3.18

- Accepted name:** secondary-alcohol oxidase
Reaction: $\text{a secondary alcohol} + \text{O}_2 = \text{a ketone} + \text{H}_2\text{O}_2$
Other name(s): polyvinyl alcohol oxidase; secondary alcohol oxidase
Systematic name: secondary-alcohol:oxygen oxidoreductase
Comments: Acts on secondary alcohols with five or more carbons, and polyvinyl alcohols with molecular mass over 300 Da. The *Pseudomonas* enzyme contains one atom of non-heme iron per molecule.
References: [2625, 3289, 3755, 3756]

[EC 1.1.3.18 created 1981]

EC 1.1.3.19

- Accepted name:** 4-hydroxymandelate oxidase (decarboxylating)
Reaction: $(S)\text{-4-hydroxymandelate} + \text{O}_2 = 4\text{-hydroxybenzaldehyde} + \text{CO}_2 + \text{H}_2\text{O}_2$
Other name(s): L-4-hydroxymandelate oxidase (decarboxylating); (S)-2-hydroxy-2-(4-hydroxyphenyl)acetate:oxygen 1-oxidoreductase; (S)-4-hydroxymandelate:oxygen 1-oxidoreductase; 4-hydroxymandelate oxidase
Systematic name: (S)-4-hydroxymandelate:oxygen 1-oxidoreductase (decarboxylating)
Comments: A flavoprotein (FAD), requires Mn^{2+} . The enzyme from the bacterium *Pseudomonas putida* is involved in the degradation of mandelate.
References: [290]

[EC 1.1.3.19 created 1984, modified 2014]

EC 1.1.3.20

- Accepted name:** long-chain-alcohol oxidase
Reaction: $\text{a long-chain alcohol} + \text{O}_2 = \text{a long-chain aldehyde} + \text{H}_2\text{O}_2$
Other name(s): long-chain fatty alcohol oxidase; fatty alcohol oxidase; fatty alcohol:oxygen oxidoreductase; long-chain fatty acid oxidase
Systematic name: long-chain-alcohol:oxygen oxidoreductase
Comments: Oxidizes long-chain fatty alcohols; best substrate is dodecyl alcohol.
References: [2612, 2613, 583, 4462, 584]

[EC 1.1.3.20 created 1984, modified 2010]

EC 1.1.3.21

Accepted name: glycerol-3-phosphate oxidase
Reaction: *sn*-glycerol 3-phosphate + O₂ = glycerone phosphate + H₂O₂
Other name(s): glycerol phosphate oxidase; glycerol-1-phosphate oxidase; glycerol phosphate oxidase; L- α -glycerophosphate oxidase; α -glycerophosphate oxidase; L- α -glycerol-3-phosphate oxidase
Systematic name: *sn*-glycerol-3-phosphate:oxygen 2-oxidoreductase
Comments: A flavoprotein (FAD).
References: [1150, 1989]

[EC 1.1.3.21 created 1984]

[1.1.3.22 *Transferred entry. xanthine oxidase. Now EC 1.17.3.2, xanthine oxidase. The enzyme was incorrectly classified as acting on a CH-OH group*]

[EC 1.1.3.22 created 1961 as EC 1.2.3.2, transferred 1984 to EC 1.1.3.22, modified 1989, deleted 2004]

EC 1.1.3.23

Accepted name: thiamine oxidase
Reaction: thiamine + 2 O₂ + H₂O = thiamine acetic acid + 2 H₂O₂
Other name(s): thiamin dehydrogenase; thiamine dehydrogenase; thiamin:oxygen 5-oxidoreductase
Systematic name: thiamine:oxygen 5-oxidoreductase
Comments: A flavoprotein (FAD). The product differs from thiamine in replacement of -CH₂.CH₂.OH by -CH₂.COOH; the two-step oxidation proceeds without the release of the intermediate aldehyde from the enzyme.
References: [920, 1234, 2751]

[EC 1.1.3.23 created 1984]

[1.1.3.24 *Transferred entry. L-galactonolactone oxidase. Now EC 1.3.3.12, L-galactonolactone oxidase. The enzyme had been incorrectly classified as acting upon a CH-OH donor rather than a CH-CH donor*]

[EC 1.1.3.24 created 1984, deleted 2006]

[1.1.3.25 *Transferred entry. cellobiose oxidase. Now included with EC 1.1.99.18, cellobiose dehydrogenase (acceptor)*]

[EC 1.1.3.25 created 1986, deleted 2005]

[1.1.3.26 *Transferred entry. columbamine oxidase. Now EC 1.21.3.2, columbamine oxidase*]

[EC 1.1.3.26 created 1989, deleted 2002]

EC 1.1.3.27

Accepted name: hydroxyphytanate oxidase
Reaction: L-2-hydroxyphytanate + O₂ = 2-oxophytanate + H₂O₂
Other name(s): L-2-hydroxyphytanate:oxygen 2-oxidoreductase
Systematic name: L-2-hydroxyphytanate:oxygen 2-oxidoreductase
References: [3991]

[EC 1.1.3.27 created 1990]

EC 1.1.3.28

Accepted name: nucleoside oxidase
Reaction: inosine + O₂ = 9-riburonosylhypoxanthine + H₂O
(1a) 2 inosine + O₂ = 2 5'-dehydroinosine + 2 H₂O
(1b) 2 5'-dehydroinosine + O₂ = 2 9-riburonosylhypoxanthine
Systematic name: nucleoside:oxygen 5'-oxidoreductase

Comments: Other purine and pyrimidine nucleosides (as well as 2'-deoxyribonucleosides) are substrates, but ribose and nucleotides are not substrates. The overall reaction takes place in two separate steps, with the 5'-dehydro nucleoside being released from the enzyme to serve as substrate for the second reaction. This enzyme differs from EC 1.1.3.39, nucleoside oxidase (H₂O₂-forming), as it produces water rather than hydrogen peroxide.

References: [1676, 1675]

[EC 1.1.3.28 created 1992, modified 2001]

EC 1.1.3.29

Accepted name: *N*-acylhexosamine oxidase

Reaction: *N*-acetyl-D-glucosamine + O₂ = *N*-acetyl-D-glucosaminic acid + H₂O₂

Other name(s): *N*-acyl-D-hexosamine oxidase; *N*-acyl-β-D-hexosamine: oxygen 1-oxidoreductase

Systematic name: *N*-acyl-D-hexosamine: oxygen 1-oxidoreductase

Comments: Also acts on *N*-glycolylglucosamine, *N*-acetylgalactosamine and, more slowly, on *N*-acetylmannosamine.

References: [1569]

[EC 1.1.3.29 created 1992]

EC 1.1.3.30

Accepted name: polyvinyl-alcohol oxidase

Reaction: polyvinyl alcohol + O₂ = oxidized polyvinyl alcohol + H₂O₂

Other name(s): dehydrogenase, polyvinyl alcohol; PVA oxidase

Systematic name: polyvinyl-alcohol: oxygen oxidoreductase

References: [3498, 3499]

[EC 1.1.3.30 created 1992]

[1.1.3.31 Deleted entry. methanol oxidase. Cannot be distinguished from EC 1.1.3.13, alcohol oxidase]

[EC 1.1.3.31 created 1992, deleted 2003]

[1.1.3.32 Transferred entry. (*S*)-stylopine synthase. Now EC 1.14.21.1, (*S*)-stylopine synthase]

[EC 1.1.3.32 created 1999, deleted 2002]

[1.1.3.33 Transferred entry. *S*-cheilanthifoline synthase. Now EC 1.14.21.2, (*S*)-cheilanthifoline synthase]

[EC 1.1.3.33 created 1999, deleted 2002]

[1.1.3.34 Transferred entry. berbaminine synthase. Now EC 1.14.21.3, berbaminine synthase]

[EC 1.1.3.34 created 1999, deleted 2002]

[1.1.3.35 Transferred entry. salutaridine synthase. Now EC 1.14.21.4, salutaridine synthase]

[EC 1.1.3.35 created 1999, deleted 2002]

[1.1.3.36 Transferred entry. (*S*)-canadine synthase. Now EC 1.14.21.5, (*S*)-canadine synthase]

[EC 1.1.3.36 created 1999, deleted 2002]

EC 1.1.3.37

Accepted name: D-arabinono-1,4-lactone oxidase

Reaction: D-arabinono-1,4-lactone + O₂ = dehydro-D-arabinono-1,4-lactone + H₂O₂

Other name(s): D-arabinono-γ-lactone oxidase; ALO

Systematic name: D-arabinono-1,4-lactone: oxygen oxidoreductase

Comments: A flavoprotein (FAD). L-Galactono-1,4-lactone, L-gulono-1,4-lactone and L-xylono-1,4-lactone can also act as substrates but D-glucono-1,5-lactone, L-arabinono-1,4-lactone, D-galactono-1,4-lactone and D-gulono-1,4-lactone cannot [1605]. With L-galactono-1,4-lactone as substrate, the product is L-ascorbate [2162]. The product dehydro-D-arabinono-1,4-lactone had previously been referred to erroneously as D-erythroascorbate (CAS no.: 5776-48-7; formula: C₆H₈O₆), although it was referred to as a five-carbon compound [1605].

References: [1605, 1606, 2162]

[EC 1.1.3.37 created 1999]

EC 1.1.3.38

Accepted name: vanillyl-alcohol oxidase

Reaction: vanillyl alcohol + O₂ = vanillin + H₂O₂

Other name(s): 4-hydroxy-2-methoxybenzyl alcohol oxidase

Systematic name: vanillyl alcohol:oxygen oxidoreductase

Comments: Vanillyl-alcohol oxidase from *Penicillium simplicissimum* contains covalently bound FAD. It converts a wide range of 4-hydroxybenzyl alcohols and 4-hydroxybenzylamines into the corresponding aldehydes. The allyl group of 4-allylphenols is also converted into the -CH=CH-CH₂OH group.

References: [761, 1047]

[EC 1.1.3.38 created 1999]

EC 1.1.3.39

Accepted name: nucleoside oxidase (H₂O₂-forming)

Reaction: adenosine + 2 O₂ + H₂O = 9-riburonosyladenine + 2 H₂O₂ (overall reaction)

(1a) adenosine + O₂ = 5'-dehydroadenosine + H₂O₂

(1b) 5'-dehydroadenosine + O₂ + H₂O = 9-riburonosyladenine + H₂O₂

Systematic name: nucleoside:oxygen 5'-oxidoreductase (H₂O₂-forming)

Comments: A heme-containing flavoprotein (FAD). Other purine and pyrimidine nucleosides (as well as 2'-deoxyribonucleosides and arabinosides) are substrates, but ribose and nucleotides are not substrates. The overall reaction takes place in two separate steps, with the 5'-dehydro nucleoside being released from the enzyme to serve as substrate for the second reaction. This enzyme differs from EC 1.1.3.28, nucleoside oxidase, as it produces hydrogen peroxide rather than water.

References: [1999]

[EC 1.1.3.39 created 2001]

EC 1.1.3.40

Accepted name: D-mannitol oxidase

Reaction: mannitol + O₂ = mannose + H₂O₂

Other name(s): mannitol oxidase; D-arabitol oxidase

Systematic name: mannitol:oxygen oxidoreductase (cyclizing)

Comments: Also catalyses the oxidation of D-arabinitol and, to a lesser extent, D-glucitol (sorbitol), whereas L-arabinitol is not a good substrate. The enzyme from the snails *Helix aspersa* and *Arion ater* is found in a specialised tubular organelle that has been termed the mannosome.

References: [4065, 2138]

[EC 1.1.3.40 created 2001]

EC 1.1.3.41

Accepted name: alditol oxidase

Reaction: an alditol + O₂ = an aldose + H₂O₂

Other name(s): xylitol oxidase; xylitol:oxygen oxidoreductase; AldO

Systematic name: alditol:oxygen oxidoreductase
Comments: The enzyme from *Streptomyces* sp. IKD472 and from *Streptomyces coelicolor* is a monomeric oxidase containing one molecule of FAD per molecule of protein [4326, 1484]. While xylitol (five carbons) and sorbitol (6 carbons) are the preferred substrates, other alditols, including L-threitol (four carbons), D-arabinitol (five carbons), D-galactitol (six carbons) and D-mannitol (six carbons) can also act as substrates, but more slowly [4326, 1484]. Belongs in the vanillyl-alcohol-oxidase family of enzymes [1484].
References: [4326, 1484, 1036]

[EC 1.1.3.41 created 2002, modified 2008]

EC 1.1.3.42

Accepted name: prosolanapyrone-II oxidase
Reaction: prosolanapyrone II + O₂ = prosolanapyrone III + H₂O₂
Other name(s): Sol5 (ambiguous); SPS (ambiguous); solanapyrone synthase (bifunctional enzyme: prosolanapyrone II oxidase/prosolanapyrone III cycloisomerase); prosolanapyrone II oxidase
Systematic name: prosolanapyrone-II:oxygen 3'-oxidoreductase
Comments: The enzyme is involved in the biosynthesis of the phytotoxin solanapyrone by some fungi. The bifunctional enzyme catalyses the oxidation of prosolanapyrone II and the subsequent Diels Alder cycloisomerization of the product prosolanapyrone III to (-)-solanapyrone A (cf. EC 5.5.1.20, prosolanapyrone III cycloisomerase).
References: [1822, 1832, 1831]

[EC 1.1.3.42 created 2011]

EC 1.1.3.43

Accepted name: paromamine 6'-oxidase
Reaction: paromamine + O₂ = 6'-dehydroparomamine + H₂O₂
Other name(s): *btrQ* (gene name); *neoG* (gene name); *kanI* (gene name); *tacB* (gene name); *neoQ* (obsolete gene name)
Systematic name: paromamine:oxygen 6'-oxidoreductase
Comments: Contains FAD. Involved in the biosynthetic pathways of several clinically important aminocyclitol antibiotics, including kanamycin, butirosin, neomycin and ribostamycin. Works in combination with EC 2.6.1.93, neamine transaminase, to replace the 6'-hydroxy group of paromamine with an amino group. The enzyme from the bacterium *Streptomyces fradiae* also catalyses EC 1.1.3.44, 6'''-hydroxyneomycin C oxidase.
References: [1592, 4406, 631]

[EC 1.1.3.43 created 2012]

EC 1.1.3.44

Accepted name: 6'''-hydroxyneomycin C oxidase
Reaction: 6'''-deamino-6'''-hydroxyneomycin C + O₂ = 6'''-deamino-6'''-oxoneomycin C + H₂O₂
Other name(s): *neoG* (gene name); *neoQ* (obsolete gene name)
Systematic name: 6'''-deamino-6'''-hydroxyneomycin C:oxygen 6'''-oxidoreductase
Comments: Contains FAD. Involved in the biosynthetic pathway of aminoglycoside antibiotics of the neomycin family. Works in combination with EC 2.6.1.95, neomycin C transaminase, to replace the 6'''-hydroxy group of 6'''-hydroxyneomycin C with an amino group. Also catalyses EC 1.1.3.43, paromamine 6'-oxidase.
References: [1592, 631]

[EC 1.1.3.44 created 2012]

EC 1.1.3.45

- Accepted name:** aclacinomycin-N oxidase
Reaction: aclacinomycin N + O₂ = aclacinomycin A + H₂O₂
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: [60, 3725]

[EC 1.1.3.45 created 2013]

EC 1.1.3.46

- Accepted name:** 4-hydroxymandelate oxidase
Reaction: (S)-4-hydroxymandelate + O₂ = 2-(4-hydroxyphenyl)-2-oxoacetate + H₂O₂
Other name(s): 4HmO; HmO
Systematic name: (S)-4-hydroxymandelate:oxygen 1-oxidoreductase
Comments: A flavoprotein (FMN). The enzyme from the bacterium *Amycolatopsis orientalis* is involved in the biosynthesis of L-(4-hydroxyphenyl)glycine and L-(3,5-dihydroxyphenyl)glycine, two non-proteinogenic amino acids occurring in the vancomycin group of antibiotics.
References: [1599, 2234]

[EC 1.1.3.46 created 2014]

EC 1.1.3.47

- Accepted name:** 5-(hydroxymethyl)furfural oxidase
Reaction: 5-(hydroxymethyl)furfural + 3 O₂ + 2 H₂O = furan-2,5-dicarboxylate + 3 H₂O₂ (overall reaction)
(1a) 5-(hydroxymethyl)furfural + O₂ = furan-2,5-dicarbalddehyde + H₂O₂
(1b) furan-2,5-dicarbalddehyde + H₂O = 5-(dihydroxymethyl)furan-2-carbalddehyde (spontaneous)
(1c) 5-(dihydroxymethyl)furan-2-carbalddehyde + O₂ = 5-formylfuran-2-carboxylate + H₂O₂
(1d) 5-formylfuran-2-carboxylate + H₂O = 5-(dihydroxymethyl)furan-2-carboxylate (spontaneous)
(1e) 5-(dihydroxymethyl)furan-2-carboxylate + O₂ = furan-2,5-dicarboxylate + H₂O₂
Systematic name: 5-(hydroxymethyl)furfural:oxygen oxidoreductase
Comments: The enzyme, characterized from the bacterium *Methylovorus* sp. strain MP688, is involved in the degradation and detoxification of 5-(hydroxymethyl)furfural. The enzyme acts only on alcohol groups and requires the spontaneous hydration of aldehyde groups for their oxidation [826]. The enzyme has a broad substrate range that overlaps with EC 1.1.3.7, aryl-alcohol oxidase.
References: [2030, 825, 826]

[EC 1.1.3.47 created 2014]

EC 1.1.3.48

- Accepted name:** 3-deoxy- α -D-manno-octulosonate 8-oxidase
Reaction: 3-deoxy- α -D-manno-octulopyranosonate + O₂ = 3,8-dideoxy-8-oxo- α -D-manno-octulosonate + H₂O₂
Other name(s): *kdnB* (gene name)
Systematic name: 3-deoxy- α -D-manno-octulopyranosonate:oxygen 8-oxidoreductase
Comments: The enzyme, characterized from the bacterium *Shewanella oneidensis*, is involved in the formation of 8-amino-3,8-dideoxy- α -D-manno-octulosonate, an aminated form of Kdo found in lipopolysaccharides of members of the *Shewanella* genus. *cf.* EC 2.6.1.109, 8-amino-3,8-dideoxy- α -D-manno-octulosonate transaminase.
References: [1162]

[EC 1.1.3.48 created 2015]

EC 1.1.3.49

Accepted name: (*R*)-mandelonitrile oxidase
Reaction: (*R*)-mandelonitrile + O₂ = benzoyl cyanide + H₂O₂
Other name(s): ChuaMOX (gene name)
Systematic name: (*R*)-mandelonitrile:oxygen oxidoreductase
Comments: Contains FAD. The enzyme, characterized from the millipede *Chamberlinius huaiienensis*, is segregated from its substrate, which is contained in special sacs. The sacs are ruptured during defensive behavior, allowing the enzyme and substrate to mix in special reaction chambers leading to production of the defensive chemical benzoyl cyanide.
References: [1667]

[EC 1.1.3.49 created 2016]

EC 1.1.4 With a disulfide as acceptor

[1.1.4.1 *Transferred entry. vitamin-K-epoxide reductase (warfarin-sensitive). Now EC 1.17.4.4, vitamin-K-epoxide reductase (warfarin-sensitive)*]

[EC 1.1.4.1 created 1989, deleted 2014]

[1.1.4.2 *Transferred entry. vitamin-K-epoxide reductase (warfarin-insensitive). Now EC 1.17.4.5, vitamin-K-epoxide reductase (warfarin-insensitive)*]

[EC 1.1.4.2 created 1989, deleted 2014]

EC 1.1.5 With a quinone or similar compound as acceptor

[1.1.5.1 *Deleted entry. cellobiose dehydrogenase (quinone). Now known to be proteolytic product of EC 1.1.99.18, cellobiose dehydrogenase (acceptor)*]

[EC 1.1.5.1 created 1983, deleted 2002]

EC 1.1.5.2

Accepted name: glucose 1-dehydrogenase (PQQ, quinone)
Reaction: D-glucose + ubiquinone = D-glucono-1,5-lactone + ubiquinol
Other name(s): quinoprotein glucose dehydrogenase; membrane-bound glucose dehydrogenase; mGDH; glucose dehydrogenase (PQQ-dependent); glucose dehydrogenase (pyrroloquinoline-quinone); quinoprotein D-glucose dehydrogenase
Systematic name: D-glucose:ubiquinone oxidoreductase
Comments: Integral membrane protein containing PQQ as prosthetic group. It also contains bound ubiquinone and Mg²⁺ or Ca²⁺. Electron acceptor is membrane ubiquinone but usually assayed with phenazine methosulfate. Like in all other quinoprotein alcohol dehydrogenases the catalytic domain has an 8-bladed propeller structure. It occurs in a wide range of bacteria. Catalyses a direct oxidation of the pyranose form of D-glucose to the lactone and thence to D-gluconate in the periplasm. Oxidizes other monosaccharides including the pyranose forms of pentoses.
References: [4302, 806, 886, 72, 683, 685, 938, 1717, 937, 2676]

[EC 1.1.5.2 created 1982 as EC 1.1.99.17, transferred 2003 to EC 1.1.5.2, modified 2010]

EC 1.1.5.3

Accepted name: glycerol-3-phosphate dehydrogenase
Reaction: *sn*-glycerol 3-phosphate + a quinone = glycerone phosphate + a quinol

Other name(s): α -glycerophosphate dehydrogenase; α -glycerophosphate dehydrogenase (acceptor); anaerobic glycerol-3-phosphate dehydrogenase; DL-glycerol 3-phosphate oxidase (misleading); FAD-dependent glycerol-3-phosphate dehydrogenase; FAD-dependent *sn*-glycerol-3-phosphate dehydrogenase; FAD-GPDH; FAD-linked glycerol 3-phosphate dehydrogenase; FAD-linked L-glycerol-3-phosphate dehydrogenase; flavin-linked glycerol-3-phosphate dehydrogenase; flavoprotein-linked L-glycerol 3-phosphate dehydrogenase; glycerol 3-phosphate cytochrome *c* reductase (misleading); glycerol phosphate dehydrogenase; glycerol phosphate dehydrogenase (acceptor); glycerol phosphate dehydrogenase (FAD); glycerol-3-phosphate CoQ reductase; glycerol-3-phosphate dehydrogenase (flavin-linked); glycerol-3-phosphate:CoQ reductase; glycerophosphate dehydrogenase; L-3-glycerophosphate-ubiquinone oxidoreductase; L-glycerol-3-phosphate dehydrogenase (ambiguous); L-glycerophosphate dehydrogenase; mGPD; mitochondrial glycerol phosphate dehydrogenase; NAD⁺-independent glycerol phosphate dehydrogenase; pyridine nucleotide-independent L-glycerol 3-phosphate dehydrogenase; *sn*-glycerol 3-phosphate oxidase (misleading); *sn*-glycerol-3-phosphate dehydrogenase; *sn*-glycerol-3-phosphate:(acceptor) 2-oxidoreductase; *sn*-glycerol-3-phosphate:acceptor 2-oxidoreductase

Systematic name: *sn*-glycerol 3-phosphate:quinone oxidoreductase

Comments: This flavin-dependent dehydrogenase is an essential membrane enzyme, functioning at the central junction of glycolysis, respiration and phospholipid biosynthesis. In bacteria, the enzyme is localized to the cytoplasmic membrane [4100], while in eukaryotes it is tightly bound to the outer surface of the inner mitochondrial membrane [3394]. In eukaryotes, this enzyme, together with the cytosolic enzyme EC 1.1.1.8, glycerol-3-phosphate dehydrogenase (NAD⁺), forms the glycerol-3-phosphate shuttle by which NADH produced in the cytosol, primarily from glycolysis, can be reoxidized to NAD⁺ by the mitochondrial electron-transport chain [2343]. This shuttle plays a critical role in transferring reducing equivalents from cytosolic NADH into the mitochondrial matrix [94, 2145]. Insect flight muscle uses only CoQ₁₀ as the physiological quinone whereas hamster and rat mitochondria use mainly CoQ₉ [3132]. The enzyme is activated by calcium [2343].

References: [3192, 3394, 2343, 3132, 3476, 4100, 94, 2145]

[EC 1.1.5.3 created 1961 as EC 1.1.2.1, transferred 1965 to EC 1.1.99.5, transferred 2009 to EC 1.1.5.3]

EC 1.1.5.4

Accepted name: malate dehydrogenase (quinone)

Reaction: (*S*)-malate + a quinone = oxaloacetate + reduced quinone

Other name(s): FAD-dependent malate-vitamin K reductase; malate-vitamin K reductase; (*S*)-malate:(acceptor) oxidoreductase; L-malate-quinone oxidoreductase; malate:quinone oxidoreductase; malate quinone oxidoreductase; MQO; malate:quinone reductase; malate dehydrogenase (acceptor); FAD-dependent malate dehydrogenase

Systematic name: (*S*)-malate:quinone oxidoreductase

Comments: A flavoprotein (FAD). Vitamin K and several other quinones can act as acceptors. Different from EC 1.1.1.37 (malate dehydrogenase (NAD⁺)), EC 1.1.1.82 (malate dehydrogenase (NADP⁺)) and EC 1.1.1.299 (malate dehydrogenase [NAD(P)⁺]).

References: [1641, 1642, 3149, 2594, 1833]

[EC 1.1.5.4 created 1978 as EC 1.1.99.16, transferred 2009 to EC 1.1.5.4]

EC 1.1.5.5

Accepted name: alcohol dehydrogenase (quinone)

Reaction: ethanol + ubiquinone = acetaldehyde + ubiquinol

Other name(s): type III ADH; membrane associated quinohaemoprotein alcohol dehydrogenase

Systematic name: alcohol:quinone oxidoreductase

Comments: Only described in acetic acid bacteria where it is involved in acetic acid production. Associated with membrane. Electron acceptor is membrane ubiquinone. A model structure suggests that, like all other quinoprotein alcohol dehydrogenases, the catalytic subunit has an 8-bladed propeller structure, a calcium ion bound to the PQQ in the active site and an unusual disulfide ring structure in close proximity to the PQQ; the catalytic subunit also has a heme *c* in the C-terminal domain. The enzyme has two additional subunits, one of which contains three molecules of heme *c*. It does not require amines for activation. It has a restricted substrate specificity, oxidizing a few primary alcohols (C₂ to C₆), but not methanol, secondary alcohols and some aldehydes. It is assayed with phenazine methosulfate or with ferricyanide.

References: [1233, 3512, 593, 1061, 2457, 2463, 2460, 2461, 684]

[EC 1.1.5.5 created 2009, modified 2010]

[1.1.5.6 *Transferred entry. formate dehydrogenase-N. Now EC 1.17.5.3, formate dehydrogenase-N*]

[EC 1.1.5.6 created 2010, deleted 2017]

EC 1.1.5.7

Accepted name: cyclic alcohol dehydrogenase (quinone)
Reaction: a cyclic alcohol + a quinone = a cyclic ketone + a quinol
Other name(s): cyclic alcohol dehydrogenase; MCAD
Systematic name: cyclic alcohol:quinone oxidoreductase
Comments: This enzyme oxidizes a wide variety of cyclic alcohols. Some minor enzyme activity is found with aliphatic secondary alcohols and sugar alcohols, but not primary alcohols. The enzyme is unable to catalyse the reverse reaction of cyclic ketones or aldehydes to cyclic alcohols. This enzyme differs from EC 1.1.5.5, alcohol dehydrogenase (quinone), which shows activity with ethanol [2604].
References: [2604]

[EC 1.1.5.7 created 2010]

EC 1.1.5.8

Accepted name: quinate dehydrogenase (quinone)
Reaction: quinate + quinone = 3-dehydroquinate + quinol
Other name(s): NAD(P)⁺-independent quinate dehydrogenase; quinate:pyrroloquinoline-quinone 5-oxidoreductase
Systematic name: quinate:quinol 3-oxidoreductase
Comments: The enzyme is membrane-bound. Does not use NAD(P)⁺ as acceptor. Contains pyrroloquinoline-quinone.
References: [4008, 16, 4021]

[EC 1.1.5.8 created 1992 as EC 1.1.99.25, modified 2004, transferred 2010 to EC 1.1.5.8]

EC 1.1.5.9

Accepted name: glucose 1-dehydrogenase (FAD, quinone)
Reaction: D-glucose + a quinone = D-glucono-1,5-lactone + a quinol
Other name(s): glucose dehydrogenase (*Aspergillus*); FAD-dependent glucose dehydrogenase; D-glucose:(acceptor) 1-oxidoreductase; glucose dehydrogenase (acceptor); *gdh* (gene name)
Systematic name: D-glucose:quinone 1-oxidoreductase
Comments: A glycoprotein containing one mole of FAD per mole of enzyme. 2,6-Dichloroindophenol can act as acceptor. *cf.* EC 1.1.5.2, glucose 1-dehydrogenase (PQQ, quinone).
References: [171, 526, 2303, 1650, 3764, 3765]

[EC 1.1.5.9 created 1972 as EC 1.1.99.10, modified 1976, transferred 2013 to EC 1.1.5.9]

EC 1.1.5.10

Accepted name: D-2-hydroxyacid dehydrogenase (quinone)
Reaction: (R)-2-hydroxyacid + a quinone = 2-oxoacid + a quinol
Other name(s): (R)-2-hydroxy acid dehydrogenase; (R)-2-hydroxy-acid:(acceptor) 2-oxidoreductase; D-lactate dehydrogenase (ambiguous)
Systematic name: (R)-2-hydroxyacid:quinone oxidoreductase
Comments: The enzyme from mammalian kidney contains one mole of FAD per mole of enzyme.(R)-lactate, (R)-malate and *meso*-tartrate are good substrates. Ubiquinone-1 and the dye 2,6-dichloroindophenol can act as acceptors; NAD⁺ and NADP⁺ are not acceptors.
References: [3944, 3945, 485, 486]

[EC 1.1.5.10 created 2014]

EC 1.1.5.11

Accepted name: 1-butanol dehydrogenase (quinone)
Reaction: butan-1-ol + a quinone = butanal + a quinol
Other name(s): BOH
Systematic name: butan-1-ol:quinone oxidoreductase
Comments: This periplasmic quinoprotein alcohol dehydrogenase, characterized from the bacterium *Thauera butanivorans*, is involved in butane degradation. It contains a pyrroloquinoline quinone (PQQ) prosthetic group. *cf.* EC 1.1.2.9, 1-butanol dehydrogenase (cytochrome *c*).
References: [4019, 4020]

[EC 1.1.5.11 created 2016]

EC 1.1.5.12

Accepted name: D-lactate dehydrogenase (quinone)
Reaction: (R)-lactate + a quinone = pyruvate + a quinol
Other name(s): *dld* (gene name)
Systematic name: (R)-lactate:quinone 2-oxidoreductase
Comments: The enzyme is an FAD-dependent peripheral membrane dehydrogenase that participates in respiration. Electrons derived from D-lactate oxidation are transferred to the membrane soluble quinone pool.
References: [2007, 1126, 2456, 2974, 899]

[EC 1.1.5.12 created 2017]

EC 1.1.9 With a copper protein as acceptor

EC 1.1.9.1

Accepted name: alcohol dehydrogenase (azurin)
Reaction: a primary alcohol + azurin = an aldehyde + reduced azurin
Other name(s): type II quinoprotein alcohol dehydrogenase; quinohaemoprotein ethanol dehydrogenase; QHEDH; ADHIIB
Systematic name: alcohol:azurin oxidoreductase
Comments: A soluble, periplasmic PQQ-containing quinohemoprotein. Also contains a single heme *c*. Occurs in *Comamonas* and *Pseudomonas*. Does not require an amine activator. Oxidizes a wide range of primary and secondary alcohols, and also aldehydes and large substrates such as sterols; methanol is not a substrate. Usually assayed with phenazine methosulfate or ferricyanide. Like all other quinoprotein alcohol dehydrogenases it has an 8-bladed propeller structure, a calcium ion bound to the PQQ in the active site and an unusual disulfide ring structure in close proximity to the PQQ.
References: [1291, 762, 3920, 2464, 580, 2915]

[EC 1.1.9.1 created 2010 as EC 1.1.98.1; transferred 2011 to EC 1.1.9.1]

EC 1.1.98 With other, known, physiological acceptors

[1.1.98.1 Transferred entry. Now EC 1.1.9.1, alcohol dehydrogenase (azurin)]

[EC 1.1.98.1 created 2010, deleted 2011]

EC 1.1.98.2

Accepted name: glucose-6-phosphate dehydrogenase (coenzyme-F₄₂₀)
Reaction: D-glucose 6-phosphate + oxidized coenzyme F₄₂₀ = 6-phospho-D-glucono-1,5-lactone + reduced coenzyme F₄₂₀
Other name(s): coenzyme F₄₂₀-dependent glucose-6-phosphate dehydrogenase; F₄₂₀-dependent glucose-6-phosphate dehydrogenase; FGD1; Rv0407; F₄₂₀-dependent glucose-6-phosphate dehydrogenase 1
Systematic name: D-glucose-6-phosphate:F₄₂₀ 1-oxidoreductase
Comments: The enzyme is very specific for D-glucose 6-phosphate. No activity with NAD⁺, NADP⁺, FAD and FMN [3076].
References: [3076, 209, 3077]

[EC 1.1.98.2 created 2010 as EC 1.1.99.34, transferred 2011 to EC 1.1.98.2]

EC 1.1.98.3

Accepted name: decaprenylphospho-β-D-ribofuranose 2-dehydrogenase
Reaction: *trans*,*octacis*-decaprenylphospho-β-D-ribofuranose + FAD = *trans*,*octacis*-decaprenylphospho-β-D-erythro-pentofuranosid-2-ulose + FADH₂
Other name(s): decaprenylphosphoryl-β-D-ribofuranose 2'-epimerase; Rv3790; DprE1; decaprenylphospho-β-D-ribofuranose 2-oxidase
Systematic name: *trans*,*octacis*-decaprenylphospho-β-D-ribofuranose:FAD 2-oxidoreductase
Comments: The enzyme, isolated from the bacterium *Mycobacterium smegmatis*, is involved, along with EC 1.1.1.333, decaprenylphospho-D-erythro-pentofuranosid-2-ulose 2-reductase, in the epimerization of *trans*,*octacis*-decaprenylphospho-β-D-ribofuranose to *trans*,*octacis*-decaprenylphospho-β-D-arabinofuranose, the arabinosyl donor for the biosynthesis of mycobacterial cell wall arabinan polymers.
References: [3179, 3925]

[EC 1.1.98.3 created 2012, modified 2014]

EC 1.1.98.4

Accepted name: F₄₂₀H₂:quinone oxidoreductase
Reaction: a quinol + oxidized coenzyme F₄₂₀ = a quinone + reduced coenzyme F₄₂₀
Other name(s): FqoF protein
Systematic name: quinol:coenzyme-F₄₂₀ oxidoreductase
Comments: An enzyme complex that contains FAD and iron-sulfur clusters. The enzyme has been described in the archaea *Methanosarcina mazei* and *Archaeoglobus fulgidus*.
References: [422, 2082, 3]

[EC 1.1.98.4 created 2013]

EC 1.1.98.5

Accepted name: secondary-alcohol dehydrogenase (coenzyme-F₄₂₀)
Reaction: R-CHOH-R' + oxidized coenzyme F₄₂₀ = R-CO-R' + reduced coenzyme F₄₂₀
Other name(s): F₄₂₀-dependent alcohol dehydrogenase; secondary alcohol:F₄₂₀ oxidoreductase; F₄₂₀-dependent secondary alcohol dehydrogenase
Systematic name: secondary-alcohol:coenzyme F₄₂₀ oxidoreductase
Comments: The enzyme isolated from the methanogenic archaea *Methanogenium liminatans* catalyses the reversible oxidation of various secondary and cyclic alcohols to the corresponding ketones.

References: [322, 139]

[EC 1.1.98.5 created 2013]

EC 1.1.98.6

Accepted name: ribonucleoside-triphosphate reductase (formate)
Reaction: ribonucleoside 5'-triphosphate + formate = 2'-deoxyribonucleoside 5'-triphosphate + CO₂ + H₂O
Other name(s): *nrdD* (gene name); class III ribonucleoside-triphosphate reductase; anaerobic ribonucleotide reductase; anaerobic ribonucleoside-triphosphate reductase
Systematic name: ribonucleoside-5'-triphosphate:formate 2'-oxidoreductase
Comments: The enzyme, which is expressed in the bacterium *Escherichia coli* during anaerobic growth, contains an iron sulfur center. The active form of the enzyme contains an oxygen-sensitive glycylyl (1-amino-2-oxoethan-1-yl) radical that is generated by the activating enzyme NrdG via chemistry involving *S*-adenosylmethionine (SAM) and a [4Fe-4S] cluster. The glycylyl radical is involved in generation of a transient thiyl (sulfanyl) radical on a cysteine residue, which attacks the substrate, forming a ribonucleotide 3'-radical, followed by water loss to form a ketyl (α -oxoalkyl) radical. The ketyl radical gains an electron from a cysteine residue and a proton from formic acid, forming 3'-keto-deoxyribonucleotide and generating a thiosulfuranyl (1 λ^4 -disulfan-1-yl) radical bridge between methionine and cysteine residues. Oxidation of formate by the thiosulfuranyl radical results in the release of CO₂ and regeneration of the thiyl radical. *cf.* EC 1.17.4.1, ribonucleoside-diphosphate reductase and EC 1.17.4.2, ribonucleoside-triphosphate reductase (thioredoxin).
References: [939, 2658, 2659, 2876, 4162]

[EC 1.1.98.6 created 2017]

EC 1.1.99 With unknown physiological acceptors

EC 1.1.99.1

Accepted name: choline dehydrogenase
Reaction: choline + acceptor = betaine aldehyde + reduced acceptor
Other name(s): choline oxidase; choline-cytochrome *c* reductase; choline:(acceptor) oxidoreductase; choline:(acceptor) 1-oxidoreductase
Systematic name: choline:acceptor 1-oxidoreductase
Comments: A quinoprotein. In many bacteria, plants and animals, the osmoprotectant betaine is synthesized using different enzymes to catalyse the conversion of (1) choline into betaine aldehyde and (2) betaine aldehyde into betaine. In plants, the first reaction is catalysed by EC 1.14.15.7, choline monooxygenase, whereas in animals and many bacteria, it is catalysed by either membrane-bound choline dehydrogenase (EC 1.1.99.1) or soluble choline oxidase (EC 1.1.3.17) [4077]. The enzyme involved in the second step, EC 1.2.1.8, betaine-aldehyde dehydrogenase, appears to be the same in plants, animals and bacteria.
References: [75, 912, 1136, 4077]

[EC 1.1.99.1 created 1961, modified 1989, modified 2005]

EC 1.1.99.2

Accepted name: L-2-hydroxyglutarate dehydrogenase
Reaction: (*S*)-2-hydroxyglutarate + acceptor = 2-oxoglutarate + reduced acceptor
Other name(s): α -ketoglutarate reductase; α -hydroxyglutarate dehydrogenase; L- α -hydroxyglutarate dehydrogenase; hydroxyglutaric dehydrogenase; α -hydroxyglutarate oxidoreductase; L- α -hydroxyglutarate:NAD⁺ 2-oxidoreductase; α -hydroxyglutarate dehydrogenase (NAD⁺ specific); (*S*)-2-hydroxyglutarate:(acceptor) 2-oxidoreductase
Systematic name: (*S*)-2-hydroxyglutarate:acceptor 2-oxidoreductase
References: [4163]

[EC 1.1.99.2 created 1961, modified 2013]

EC 1.1.99.3

Accepted name: gluconate 2-dehydrogenase (acceptor)
Reaction: D-gluconate + acceptor = 2-dehydro-D-gluconate + reduced acceptor
Other name(s): gluconate oxidase; gluconate dehydrogenase; gluconic dehydrogenase; D-gluconate dehydrogenase; gluconic acid dehydrogenase; 2-ketogluconate reductase; D-gluconate dehydrogenase, 2-keto-D-gluconate-yielding; D-gluconate:(acceptor) 2-oxidoreductase
Systematic name: D-gluconate:acceptor 2-oxidoreductase
Comments: A flavoprotein (FAD).
References: [2459, 3117]

[EC 1.1.99.3 created 1961, modified 1976, modified 1989]

EC 1.1.99.4

Accepted name: dehydrogluconate dehydrogenase
Reaction: 2-dehydro-D-gluconate + acceptor = 2,5-didehydro-D-gluconate + reduced acceptor
Other name(s): ketogluconate dehydrogenase; α -ketogluconate dehydrogenase; 2-keto-D-gluconate dehydrogenase; 2-oxogluconate dehydrogenase
Systematic name: 2-dehydro-D-gluconate:acceptor 2-oxidoreductase
Comments: A flavoprotein.
References: [747, 3510]

[EC 1.1.99.4 created 1961, modified 1989]

[1.1.99.5 *Transferred entry. glycerol-3-phosphate dehydrogenase. As the acceptor is now known, the enzyme has been transferred to EC 1.1.5.3, glycerol-3-phosphate dehydrogenase.*]

[EC 1.1.99.5 created 1961 as EC 1.1.2.1, transferred 1965 to EC 1.1.99.5, deleted 2009]

EC 1.1.99.6

Accepted name: D-lactate dehydrogenase (acceptor)
Reaction: (R)-lactate + acceptor = pyruvate + reduced acceptor
Other name(s): D-2-hydroxy acid dehydrogenase; D-2-hydroxy-acid dehydrogenase; (R)-2-hydroxy-acid:acceptor 2-oxidoreductase
Systematic name: (R)-lactate:acceptor 2-oxidoreductase
Comments: The zinc flavoprotein (FAD) from the archaeon *Archaeoglobus fulgidus* cannot utilize NAD⁺, cytochrome *c*, methylene blue or dimethylnaphthoquinone as acceptors. *In vitro* it is active with artificial electron acceptors such as 2,6-dichlorophenolindophenol, but the physiological acceptor is not yet known.
References: [3151]

[EC 1.1.99.6 created 1965, modified 2013]

EC 1.1.99.7

Accepted name: lactate—malate transhydrogenase
Reaction: (S)-lactate + oxaloacetate = pyruvate + malate
Other name(s): malate-lactate transhydrogenase
Systematic name: (S)-lactate:oxaloacetate oxidoreductase
Comments: Catalyses hydrogen transfer from C₃ or C₄ (S)-2-hydroxy acids to 2-oxo acids. It contains tightly bound nicotinamide nucleotide in its active centre. This prosthetic group cannot be removed without denaturation of the protein.
References: [63, 64]

[EC 1.1.99.7 created 1972]

[1.1.99.8 *Transferred entry. alcohol dehydrogenase (acceptor). Now EC 1.1.2.7, methanol dehydrogenase (cytochrome c) and EC 1.1.2.8, alcohol dehydrogenase (cytochrome c).*]

[EC 1.1.99.8 created 1972, modified 1982, deleted 2010]

EC 1.1.99.9

Accepted name: pyridoxine 5-dehydrogenase
Reaction: pyridoxine + acceptor = isopyridoxal + reduced acceptor
Other name(s): pyridoxal-5-dehydrogenase; pyridoxol 5-dehydrogenase; pyridoxin 5-dehydrogenase; pyridoxine dehydrogenase; pyridoxine 5'-dehydrogenase; pyridoxine:(acceptor) 5-oxidoreductase
Systematic name: pyridoxine:acceptor 5-oxidoreductase
Comments: A flavoprotein (FAD).
References: [3736]

[EC 1.1.99.9 created 1972, modified 1976]

[1.1.99.10 *Transferred entry. glucose dehydrogenase (acceptor). Now EC 1.1.5.9, glucose 1-dehydrogenase (FAD, quinone)*]

[EC 1.1.99.10 created 1972, modified 1976, deleted 2013]

EC 1.1.99.11

Accepted name: fructose 5-dehydrogenase
Reaction: D-fructose + acceptor = 5-dehydro-D-fructose + reduced acceptor
Other name(s): fructose 5-dehydrogenase (acceptor); D-fructose dehydrogenase; D-fructose:(acceptor) 5-oxidoreductase
Systematic name: D-fructose:acceptor 5-oxidoreductase
Comments: 2,6-Dichloroindophenol can act as acceptor.
References: [71, 4303]

[EC 1.1.99.11 created 1972]

EC 1.1.99.12

Accepted name: sorbose dehydrogenase
Reaction: L-sorbose + acceptor = 5-dehydro-D-fructose + reduced acceptor
Other name(s): L-sorbose:(acceptor) 5-oxidoreductase
Systematic name: L-sorbose:acceptor 5-oxidoreductase
Comments: 2,6-Dichloroindophenol can act as acceptor.
References: [3317]

[EC 1.1.99.12 created 1972]

EC 1.1.99.13

Accepted name: glucoside 3-dehydrogenase
Reaction: sucrose + acceptor = 3-dehydro- α -D-glucosyl- β -D-fructofuranoside + reduced acceptor
Other name(s): D-glucoside 3-dehydrogenase; D-aldohepyranoside dehydrogenase; D-aldohexoside:cytochrome *c* oxidoreductase; D-glucoside 3-dehydrogenase; hexopyranoside-cytochrome *c* oxidoreductase; D-aldohexoside:(acceptor) 3-oxidoreductase
Systematic name: D-aldohexoside:acceptor 3-oxidoreductase
Comments: A flavoprotein (FAD). The enzyme acts on D-glucose, D-galactose, D-glucosides and D-galactosides, but D-glucosides react more rapidly than D-galactosides.
References: [1436]

[EC 1.1.99.13 created 1972]

EC 1.1.99.14

Accepted name: glycolate dehydrogenase
Reaction: glycolate + acceptor = glyoxylate + reduced acceptor
Other name(s): glycolate oxidoreductase; glycolic acid dehydrogenase; glycolate:(acceptor) 2-oxidoreductase
Systematic name: glycolate:acceptor 2-oxidoreductase
Comments: Also acts on (*R*)-lactate. 2,6-Dichloroindophenol and phenazine methosulfate can act as acceptors.
References: [2297]

[EC 1.1.99.14 created 1978]

[1.1.99.15 *Transferred entry. 5,10-methylenetetrahydrofolate reductase (FADH₂). Now EC 1.5.1.20, methylenetetrahydrofolate reductase [NAD(P)H]*]

[EC 1.1.99.15 created 1978, deleted 1980]

[1.1.99.16 *Transferred entry. malate dehydrogenase (acceptor). As the acceptor is now known, the enzyme has been transferred to EC 1.1.5.4, malate dehydrogenase (quinone).*]

[EC 1.1.99.16 created 1978, deleted 2009]

[1.1.99.17 *Transferred entry. glucose dehydrogenase (pyrroloquinoline-quinone). Now EC 1.1.5.2, quinoprotein glucose dehydrogenase*]

[EC 1.1.99.17 created 1982, deleted 2003]

EC 1.1.99.18

Accepted name: cellobiose dehydrogenase (acceptor)
Reaction: cellobiose + acceptor = cellobiono-1,5-lactone + reduced acceptor
Other name(s): cellobiose dehydrogenase; cellobiose oxidoreductase; *Phanerochaete chrysosporium* cellobiose oxidoreductase; CBOR; cellobiose oxidase; cellobiose:oxygen 1-oxidoreductase; CDH; cellobiose:(acceptor) 1-oxidoreductase
Systematic name: cellobiose:acceptor 1-oxidoreductase
Comments: Also acts, more slowly, on cello-oligosaccharides, lactose and D-glucosyl-1,4-β-D-mannose. The enzyme from the white rot fungus *Phanerochaete chrysosporium* is unusual in having two redoxin domains, one containing a flavin and the other a protoheme group. It transfers reducing equivalents from cellobiose to two types of redox acceptor: two-electron oxidants, including redox dyes, benzoquinones, and molecular oxygen, and one-electron oxidants, including semiquinone species, iron(II) complexes, and the model acceptor cytochrome *c* [2430]. 2,6-Dichloroindophenol can act as acceptor *in vitro*.
References: [673, 782, 783, 1331, 186, 1348, 151, 152, 2430]

[EC 1.1.99.18 created 1983, modified 2002 (EC 1.1.5.1 created 1983, incorporated 2002, EC 1.1.3.25 created 1986, incorporated 2005)]

[1.1.99.19 *Transferred entry. uracil dehydrogenase. Now EC 1.17.99.4, uracil/thymine dehydrogenase*]

[EC 1.1.99.19 created 1961 as EC 1.2.99.1, transferred 1984 to EC 1.1.99.19, deleted 2006]

EC 1.1.99.20

Accepted name: alkan-1-ol dehydrogenase (acceptor)
Reaction: primary alcohol + acceptor = aldehyde + reduced acceptor
Other name(s): polyethylene glycol dehydrogenase; alkan-1-ol:(acceptor) oxidoreductase
Systematic name: alkan-1-ol:acceptor oxidoreductase
Comments: A quinoprotein. Acts on C₃-C₁₆ linear-chain saturated primary alcohols, C₄-C₇ aldehydes and on non-ionic surfactants containing polyethylene glycol residues, such as Tween 40 and 60, but not on methanol and only very slowly on ethanol. 2,6-Dichloroindophenol can act as acceptor. *cf.* EC 1.1.99.8 alcohol dehydrogenase (acceptor).

References: [1859, 1860]

[EC 1.1.99.20 created 1989]

EC 1.1.99.21

Accepted name: D-sorbitol dehydrogenase (acceptor)
Reaction: D-sorbitol + acceptor = L-sorbose + reduced acceptor
Other name(s): D-sorbitol:(acceptor) 1-oxidoreductase
Systematic name: D-sorbitol:acceptor 1-oxidoreductase
Comments: A flavoprotein (FAD).
References: [3511]

[EC 1.1.99.21 created 1989]

EC 1.1.99.22

Accepted name: glycerol dehydrogenase (acceptor)
Reaction: glycerol + acceptor = glycerone + reduced acceptor
Other name(s): glycerol:(acceptor) 1-oxidoreductase
Systematic name: glycerol:acceptor 1-oxidoreductase
Comments: A quinoprotein. Also acts, more slowly, on a number of other polyols including D-sorbitol, D-arabinitol, *meso*-erythritol, ribitol and propane-1,2-diol.
References: [76]

[EC 1.1.99.22 created 1989]

[1.1.99.23 *Transferred entry. polyvinyl-alcohol dehydrogenase (acceptor). Now EC 1.1.2.6, polyvinyl alcohol dehydrogenase (cytochrome)*]

[EC 1.1.99.23 created 1989, deleted 2010]

EC 1.1.99.24

Accepted name: hydroxyacid-oxoacid transhydrogenase
Reaction: (*S*)-3-hydroxybutanoate + 2-oxoglutarate = acetoacetate + (*R*)-2-hydroxyglutarate
Other name(s): transhydrogenase, hydroxy acid-oxo acid
Systematic name: (*S*)-3-hydroxybutanoate:2-oxoglutarate oxidoreductase
Comments: 4-Hydroxybutanoate and (*R*)-2-hydroxyglutarate can also act as donors; 4-oxobutanoate can also act as acceptor.
References: [1850]

[EC 1.1.99.24 created 1992]

[1.1.99.25 *Transferred entry. quinate dehydrogenase (pyrroloquinoline-quinone). Now EC 1.1.5.8, quinate dehydrogenase (quinone)*]

[EC 1.1.99.25 created 1992, modified 2004, deleted 2010]

EC 1.1.99.26

Accepted name: 3-hydroxycyclohexanone dehydrogenase
Reaction: 3-hydroxycyclohexanone + acceptor = cyclohexane-1,3-dione + reduced acceptor
Systematic name: 3-hydroxycyclohexanone:acceptor 1-oxidoreductase
Comments: 2,6-Dichloroindophenol and methylene blue can act as acceptors.
References: [741]

[EC 1.1.99.26 created 1992]

EC 1.1.99.27

- Accepted name:** (*R*)-pantolactone dehydrogenase (flavin)
Reaction: (*R*)-pantolactone + acceptor = 2-dehydropantolactone + reduced acceptor
Other name(s): 2-dehydropantolactone reductase (flavin); 2-dehydropantoyl-lactone reductase (flavin); (*R*)-pantoyllactone dehydrogenase (flavin)
Systematic name: (*R*)-pantolactone:acceptor oxidoreductase (flavin-containing)
Comments: High specificity for (*R*)-pantolactone. Phenazine methosulfate (PMS) can act as acceptor. The enzyme has been studied in the bacterium *Nocardia asteroides* and shown to be membrane-bound and induced by 1,2-propanediol. The FMN cofactor is non-covalently bound.
References: [1830]

[EC 1.1.99.27 created 1999]

EC 1.1.99.28

- Accepted name:** glucose-fructose oxidoreductase
Reaction: D-glucose + D-fructose = D-gluconolactone + D-glucitol
Systematic name: D-glucose:D-fructose oxidoreductase
Comments: D-mannose, D-xylose, D-galactose, 2-deoxy-D-glucose and L-arabinose will function as aldose substrates, but with low affinities. The ketose substrate must be in the open-chain form. The apparent affinity for fructose is low, because little of the fructose substrate is in the open-chain form. Xylulose and glycerone (dihydroxyacetone) will replace fructose, but they are poor substrates. The enzyme from *Zymomonas mobilis* contains tightly bound NADP⁺.
References: [4419, 1394, 1808]

[EC 1.1.99.28 created 1999]

EC 1.1.99.29

- Accepted name:** pyranose dehydrogenase (acceptor)
Reaction: (1) a pyranose + acceptor = a pyranos-2-ulose (or a pyranos-3-ulose or a pyranos-2,3-diulose) + reduced acceptor
(2) a pyranoside + acceptor = a pyranosid-3-ulose (or a pyranosid-3,4-diulose) + reduced acceptor
Other name(s): pyranose dehydrogenase; pyranose-quinone oxidoreductase; quinone-dependent pyranose dehydrogenase; PDH
Systematic name: pyranose:acceptor oxidoreductase
Comments: Requires FAD. A number of aldoses and ketoses in pyranose form, as well as glycosides, gluco-oligosaccharides, sucrose and lactose can act as a donor. 1,4-Benzoquinone or ferricenium ion (ferrocene oxidized by removal of one electron) can serve as acceptor. Unlike EC 1.1.3.10, pyranose oxidase, this fungal enzyme does not interact with O₂ and exhibits extremely broad substrate tolerance with variable regioselectivity (C-3, C-2 or C-3 + C-2 or C-3 + C-4) for (di)oxidation of different sugars. D-Glucose is exclusively or preferentially oxidized at C-3 (depending on the enzyme source), but can also be oxidized at C-2 + C-3. The enzyme also acts on 1→4- α - and 1→4- β -gluco-oligosaccharides, non-reducing gluco-oligosaccharides and L-arabinose, which are not substrates of EC 1.1.3.10. Sugars are oxidized in their pyranose but not in their furanose form.
References: [4055, 4057, 4058, 4054, 4056]

[EC 1.1.99.29 created 2004]

EC 1.1.99.30

- Accepted name:** 2-oxo-acid reductase
Reaction: a (2*R*)-hydroxy-carboxylate + acceptor = a 2-oxo-carboxylate + reduced acceptor
Other name(s): (2*R*)-hydroxycarboxylate-viologen-oxidoreductase; HVOR; 2-oxoacid reductase
Systematic name: (2*R*)-hydroxy-carboxylate:acceptor oxidoreductase

Comments: Contains [4Fe-4S] and a mononucleotide molybdenum (pyranopterin) cofactor. Has broad substrate specificity, with 2-oxo-monocarboxylates and 2-oxo-dicarboxylates acting as substrates. Branching in a substrate at the C-3 position results in loss of activity. The enzyme from *Proteus* sp. is inactivated by oxygen.

References: [3923, 2771]

[EC 1.1.99.30 created 2004]

EC 1.1.99.31

Accepted name: (*S*)-mandelate dehydrogenase

Reaction: (*S*)-mandelate + acceptor = phenylglyoxylate + reduced acceptor

Other name(s): MDH

Systematic name: (*S*)-mandelate:acceptor 2-oxidoreductase

Comments: This enzyme is a member of the FMN-dependent α -hydroxy-acid oxidase/dehydrogenase family [2190]. While all enzymes of this family oxidize the (*S*)-enantiomer of an α -hydroxy acid to an α -oxo acid, the ultimate oxidant (oxygen, intramolecular heme or some other acceptor) depends on the particular enzyme. This enzyme transfers the electron pair from FMNH₂ to a component of the electron transport chain, most probably ubiquinone [2190, 808]. It is part of a metabolic pathway in Pseudomonads that allows these organisms to utilize mandelic acid, derivatized from the common soil metabolite amygdalin, as the sole source of carbon and energy [808]. The enzyme has a large active-site pocket and preferentially binds substrates with longer sidechains, e.g. 2-hydroxyoctanoate rather than 2-hydroxybutyrate [2190]. It also prefers substrates that, like (*S*)-mandelate, have β unsaturation, e.g. (indol-3-yl)glycolate compared with (indol-3-yl)lactate [2190]. Esters of mandelate, such as methyl (*S*)-mandelate, are also substrates [807].

References: [2190, 808, 807]

[EC 1.1.99.31 created 2006]

EC 1.1.99.32

Accepted name: L-sorbose 1-dehydrogenase

Reaction: L-sorbose + acceptor = 1-dehydro-L-sorbose + reduced acceptor

Other name(s): SDH

Systematic name: L-sorbose:acceptor 1-oxidoreductase

Comments: The product, L-sorbose, is an intermediate in bacterial 2-keto-L-gulonic-acid formation. The activity of this membrane-bound enzyme is stimulated by Fe(III) or Co²⁺ but is inhibited by Cu²⁺. The enzyme is highly specific for L-sorbose as other sugars, such as glucose, mannitol and sorbitol, are not substrates. Phenazine methosulfate and DCIP can act as artificial acceptors.

References: [3714]

[EC 1.1.99.32 created 2008]

[1.1.99.33] *Transferred entry. formate dehydrogenase (acceptor). Now EC 1.17.99.7, formate dehydrogenase (acceptor)]*

[EC 1.1.99.33 created 2010, deleted 2017]

[1.1.99.34] *Transferred entry. glucose-6-phosphate dehydrogenase (coenzyme-F₄₂₀). As the acceptor is now known, the enzyme has been transferred to EC 1.1.98.2, glucose-6-phosphate dehydrogenase (coenzyme-F₄₂₀)]*

[EC 1.1.99.34 created 2010, deleted 2011]

EC 1.1.99.35

Accepted name: soluble quinoprotein glucose dehydrogenase

Reaction: D-glucose + acceptor = D-glucono-1,5-lactone + reduced acceptor

Other name(s): soluble glucose dehydrogenase; sGDH; glucose dehydrogenase (PQQ-dependent)

Systematic name: D-glucose:acceptor oxidoreductase

Comments: Soluble periplasmic enzyme containing PQQ as prosthetic group, bound to a calcium ion. Electron acceptor is not known. It is assayed with Wurster's Blue or phenazine methosulfate. It has negligible sequence or structure similarity to other quinoproteins. It catalyses an exceptionally high rate of oxidation of a wide range of aldose sugars, including D-glucose, galactose, arabinose and xylose, and also the disaccharides lactose, cellobiose and maltose. It has been described only in *Acinetobacter calcoaceticus*.

References: [1178, 848, 632, 2458, 2914, 2462]

[EC 1.1.99.35 created 2010]

EC 1.1.99.36

Accepted name: alcohol dehydrogenase (nicotinoprotein)

Reaction: ethanol + acceptor = acetaldehyde + reduced acceptor

Other name(s): NDMA-dependent alcohol dehydrogenase; nicotinoprotein alcohol dehydrogenase; np-ADH; ethanol:*N,N*-dimethyl-4-nitrosoaniline oxidoreductase

Systematic name: ethanol:acceptor oxidoreductase

Comments: Contains Zn²⁺. Nicotinoprotein alcohol dehydrogenases are unique medium-chain dehydrogenases/reductases (MDR) alcohol dehydrogenases that have a tightly bound NAD⁺/NADH cofactor that does not dissociate during the catalytic process. Instead, the cofactor is regenerated by a second substrate or electron carrier. While the *in vivo* electron acceptor is not known, *N,N*-dimethyl-4-nitrosoaniline (NDMA), which is reduced to 4-(hydroxylamino)-*N,N*-dimethylaniline, can serve this function *in vitro*. The enzyme from the Gram-positive bacterium *Amycolatopsis methanolica* can accept many primary alcohols as substrates, including benzylalcohol [2892].

References: [2892, 3008, 3358, 3007, 2820]

[EC 1.1.99.36 created 2010]

EC 1.1.99.37

Accepted name: methanol dehydrogenase (nicotinoprotein)

Reaction: methanol + acceptor = formaldehyde + reduced acceptor

Other name(s): NDMA-dependent methanol dehydrogenase; nicotinoprotein methanol dehydrogenase; methanol:*N,N*-dimethyl-4-nitrosoaniline oxidoreductase

Systematic name: methanol:acceptor oxidoreductase

Comments: Contains Zn²⁺ and Mg²⁺. Nicotinoprotein methanol dehydrogenases have a tightly bound NADP⁺/NADPH cofactor that does not dissociate during the catalytic process. Instead, the cofactor is regenerated by a second substrate or electron carrier. While the *in vivo* electron acceptor is not known, *N,N*-dimethyl-4-nitrosoaniline (NDMA), which is reduced to 4-(hydroxylamino)-*N,N*-dimethylaniline, can serve this function *in vitro*. The enzyme has been detected in several Gram-positive methylotrophic bacteria, including *Amycolatopsis methanolica*, *Rhodococcus rhodochrous* and *Rhodococcus erythropolis* [4064, 2892, 464]. These enzymes are decameric, and possess a 5-fold symmetry [1467]. Some of the enzymes can also dismutate formaldehyde to methanol and formate [2940].

References: [4064, 2892, 464, 1467, 2940]

[EC 1.1.99.37 created 2010]

EC 1.1.99.38

Accepted name: 2-deoxy-*scyllo*-inosamine dehydrogenase (AdoMet-dependent)

Reaction: 2-deoxy-*scyllo*-inosamine + *S*-adenosyl-L-methionine = 3-amino-2,3-dideoxy-*scyllo*-inosose + 5'-deoxyadenosine + L-methionine

Other name(s): *btrN* (gene name); 2-deoxy-*scyllo*-inosamine dehydrogenase (SAM-dependent)

Systematic name: 2-deoxy-*scyllo*-inosamine:*S*-adenosyl-L-methionine 1-oxidoreductase

Comments: Involved in the biosynthetic pathway of the aminoglycoside antibiotics of the butirosin family. The enzyme from *Bacillus circulans* was shown to be a radical *S*-adenosyl-L-methionine (SAM) enzyme. *cf.* EC 1.1.1.329, 2-deoxy-*scyllo*-inosamine dehydrogenase.

References: [4364, 4365]

[EC 1.1.99.38 created 2012, modified 2013]

EC 1.1.99.39

Accepted name: D-2-hydroxyglutarate dehydrogenase
Reaction: (R)-2-hydroxyglutarate + acceptor = 2-oxoglutarate + reduced acceptor
Other name(s): D2HGDH (gene name)
Systematic name: (R)-2-hydroxyglutarate:acceptor 2-oxidoreductase
Comments: Contains FAD. The enzyme has no activity with NAD⁺ or NADP⁺, and was assayed *in vitro* using artificial electron acceptors. It has lower activity with (R)-lactate, (R)-2-hydroxybutyrate and *meso*-tartrate, and no activity with the (S) isomers. The mammalian enzyme is stimulated by Zn²⁺, Co²⁺ and Mn²⁺.
References: [952, 7]

[EC 1.1.99.39 created 2013]

EC 1.1.99.40

Accepted name: (R)-2-hydroxyglutarate—pyruvate transhydrogenase
Reaction: (R)-2-hydroxyglutarate + pyruvate = 2-oxoglutarate + (R)-lactate
Other name(s): DLD3 (gene name)
Systematic name: (R)-2-hydroxyglutarate:pyruvate oxidoreductase [(R)-lactate-forming]
Comments: The enzyme, characterized in the yeast *Saccharomyces cerevisiae*, also functions as EC 1.1.2.4, D-lactate dehydrogenase (cytochrome), and is active with oxaloacetate as electron acceptor forming (R)-malate.
References: [237]

[EC 1.1.99.40 created 2017]

EC 1.1.99.41

Accepted name: 3-hydroxy-1,2-didehydro-2,3-dihydrotabersonine reductase
Reaction: (1) (3R)-3-hydroxy-16-methoxy-2,3-dihydrotabersonine + acceptor = (3R)-3-hydroxy-16-methoxy-1,2-didehydro-2,3-dihydrotabersonine + reduced acceptor
(2) (3R)-3-hydroxy-2,3-dihydrotabersonine + acceptor = (3R)-3-hydroxy-1,2-didehydro-2,3-dihydrotabersonine + reduced acceptor
Other name(s): T3R; tabersonine 3-reductase
Systematic name: (3R)-3-hydroxy-16-methoxy-2,3-dihydrotabersonine:acceptor oxidoreductase
Comments: This enzyme is involved in the biosynthesis of vindoline and vindorosine in the plant *Catharanthus roseus* (Madagascar periwinkle). *In vivo*, it functions in the direction of reduction. It has no activity with 3-epoxylated compounds, which can form spontaneously from its unstable substrates.
References: [3085]

[EC 1.1.99.41 created 2017]

EC 1.1.99.42

Accepted name: 4-pyridoxic acid dehydrogenase
Reaction: 4-pyridoxate + acceptor = 5-formyl-3-hydroxy-2-methylpyridine-4-carboxylate + reduced acceptor
Other name(s): mlr6792 (locus name)
Systematic name: 4-pyridoxate:acceptor 5-oxidoreductase
Comments: The enzyme, characterized from the bacteria *Pseudomonas* sp. MA-1 and *Mesorhizobium loti*, participates in the degradation of pyridoxine (vitamin B₆). It is membrane bound and contains FAD. The enzyme has been assayed *in vitro* in the presence of the artificial electron acceptor dichloroindophenol (DCPIP).
References: [4299, 1173]

[EC 1.1.99.42 created 2018]

EC 1.2 Acting on the aldehyde or oxo group of donors

This subclass contains enzymes that oxidize aldehydes to the corresponding acids; when this acid is concomitantly phosphorylated or acetylates CoA, this is indicated in parentheses. Oxo groups may be oxidized either with addition of water and cleavage of a carbon-carbon bond or, in the case of ring compounds, by addition of the elements of water and dehydrogenation. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.2.1), a cytochrome (EC 1.2.2), oxygen (EC 1.2.3), a disulfide (EC 1.2.4), an iron-sulfur protein (EC 1.2.7), or some other acceptor (EC 1.2.99).

EC 1.2.1 With NAD⁺ or NADP⁺ as acceptor

[1.2.1.1 Deleted entry. *glutathione-dependent formaldehyde dehydrogenase*. This enzyme was classified on the basis of an incorrect reaction. It has been replaced by two enzymes, EC 1.1.1.284, *S*-(hydroxymethyl)glutathione dehydrogenase and EC 4.4.1.22, *S*-(hydroxymethyl)glutathione synthase]

[EC 1.2.1.1 created 1961, modified 1982, modified 2002, deleted 2005]

[1.2.1.2 Transferred entry. *formate dehydrogenase*. Now EC 1.17.1.9, *formate dehydrogenase*]

[EC 1.2.1.2 created 1961, deleted 2017]

EC 1.2.1.3

Accepted name: aldehyde dehydrogenase (NAD⁺)
Reaction: an aldehyde + NAD⁺ + H₂O = a carboxylate + NADH + H⁺
Other name(s): CoA-independent aldehyde dehydrogenase; *m*-methylbenzaldehyde dehydrogenase; NAD-aldehyde dehydrogenase; NAD-dependent 4-hydroxynonanal dehydrogenase; NAD-dependent aldehyde dehydrogenase; NAD-linked aldehyde dehydrogenase; propionaldehyde dehydrogenase; aldehyde dehydrogenase (NAD)
Systematic name: aldehyde:NAD⁺ oxidoreductase
Comments: Wide specificity, including oxidation of D-glucuronolactone to D-glucarate.
References: [1712, 3096]

[EC 1.2.1.3 created 1961 (EC 1.1.1.70 created 1965, incorporated 1978)]

EC 1.2.1.4

Accepted name: aldehyde dehydrogenase (NADP⁺)
Reaction: an aldehyde + NADP⁺ + H₂O = a carboxylate + NADPH + H⁺
Other name(s): NADP-acetaldehyde dehydrogenase; NADP-dependent aldehyde dehydrogenase; aldehyde dehydrogenase (NADP)
Systematic name: aldehyde:NADP⁺ oxidoreductase
References: [15, 1712, 2721, 3425]

[EC 1.2.1.4 created 1961]

EC 1.2.1.5

Accepted name: aldehyde dehydrogenase [NAD(P)⁺]
Reaction: an aldehyde + NAD(P)⁺ + H₂O = a carboxylate + NAD(P)H + H⁺
Other name(s): ALDH
Systematic name: aldehyde:NAD(P)⁺ oxidoreductase
References: [307, 1712, 1933, 3637, 3806]

[EC 1.2.1.5 created 1961]

[1.2.1.6 Deleted entry. benzaldehyde dehydrogenase]

[EC 1.2.1.6 created 1961, deleted 1965]

EC 1.2.1.7

Accepted name: benzaldehyde dehydrogenase (NADP⁺)
Reaction: benzaldehyde + NADP⁺ + H₂O = benzoate + NADPH + 2 H⁺
Other name(s): NADP-linked benzaldehyde dehydrogenase; benzaldehyde dehydrogenase (NADP)
Systematic name: benzaldehyde:NADP⁺ oxidoreductase
References: [1312, 3612]

[EC 1.2.1.7 created 1961]

EC 1.2.1.8

Accepted name: betaine-aldehyde dehydrogenase
Reaction: betaine aldehyde + NAD⁺ + H₂O = betaine + NADH + 2 H⁺
Other name(s): betaine aldehyde oxidase; BADH; betaine aldehyde dehydrogenase; BetB
Systematic name: betaine-aldehyde:NAD⁺ oxidoreductase
Comments: In many bacteria, plants and animals, the osmoprotectant betaine is synthesized in two steps: (1) choline to betaine aldehyde and (2) betaine aldehyde to betaine. This enzyme is involved in the second step and appears to be the same in plants, animals and bacteria. In contrast, different enzymes are involved in the first reaction. In plants, this reaction is catalysed by EC 1.14.15.7 (choline monooxygenase), whereas in animals and many bacteria it is catalysed by either membrane-bound EC 1.1.99.1 (choline dehydrogenase) or soluble EC 1.1.3.17 (choline oxidase) [4077]. In some bacteria, betaine is synthesized from glycine through the actions of EC 2.1.1.156 (glycine/sarcosine *N*-methyltransferase) and EC 2.1.1.157 (sarcosine/dimethylglycine *N*-methyltransferase).
References: [3240, 2287, 2824, 1751, 4077]

[EC 1.2.1.8 created 1961, modified 2005, modified 2011]

EC 1.2.1.9

Accepted name: glyceraldehyde-3-phosphate dehydrogenase (NADP⁺)
Reaction: D-glyceraldehyde 3-phosphate + NADP⁺ + H₂O = 3-phospho-D-glycerate + NADPH + 2 H⁺
Other name(s): triosephosphate dehydrogenase; dehydrogenase, glyceraldehyde phosphate (nicotinamide adenine dinucleotide phosphate); glyceraldehyde phosphate dehydrogenase (NADP); glyceraldehyde 3-phosphate dehydrogenase (NADP); NADP-glyceraldehyde phosphate dehydrogenase; NADP-glyceraldehyde-3-phosphate dehydrogenase; glyceraldehyde-3-phosphate:NADP reductase; nonphosphorylating glyceraldehyde-3-phosphate dehydrogenase; glyceraldehyde-3-phosphate dehydrogenase (NADP)
Systematic name: D-glyceraldehyde-3-phosphate:NADP⁺ oxidoreductase
References: [3235]

[EC 1.2.1.9 created 1961]

EC 1.2.1.10

Accepted name: acetaldehyde dehydrogenase (acetylating)
Reaction: acetaldehyde + CoA + NAD⁺ = acetyl-CoA + NADH + H⁺
Other name(s): aldehyde dehydrogenase (acylating); ADA; acylating acetaldehyde dehydrogenase; DmpF; BphJ
Systematic name: acetaldehyde:NAD⁺ oxidoreductase (CoA-acetylating)

Comments: Also acts, more slowly, on glycolaldehyde, propanal and butanal. In several bacterial species this enzyme forms a bifunctional complex with EC 4.1.3.39, 4-hydroxy-2-oxovalerate aldolase. The enzymes from the bacteria *Burkholderia xenovorans* and *Thermus thermophilus* also perform the reaction of EC 1.2.1.87, propanal dehydrogenase (propanoylating). Involved in the *meta*-cleavage pathway for the degradation of phenols, methylphenols and catechols. NADP⁺ can replace NAD⁺ but the rate of reaction is much slower [3049].

References: [457, 3558, 3049, 178, 177]

[EC 1.2.1.10 created 1961, modified 2006, modified 2011]

EC 1.2.1.11

Accepted name: aspartate-semialdehyde dehydrogenase

Reaction: L-aspartate 4-semialdehyde + phosphate + NADP⁺ = L-4-aspartyl phosphate + NADPH + H⁺

Other name(s): aspartate semialdehyde dehydrogenase; aspartic semialdehyde dehydrogenase; L-aspartate-β-semialdehyde:NADP⁺ oxidoreductase (phosphorylating); aspartic β-semialdehyde dehydrogenase; ASA dehydrogenase

Systematic name: L-aspartate-4-semialdehyde:NADP⁺ oxidoreductase (phosphorylating)

References: [309, 1712]

[EC 1.2.1.11 created 1961]

EC 1.2.1.12

Accepted name: glyceraldehyde-3-phosphate dehydrogenase (phosphorylating)

Reaction: D-glyceraldehyde 3-phosphate + phosphate + NAD⁺ = 3-phospho-D-glyceroyl phosphate + NADH + H⁺

Other name(s): triosephosphate dehydrogenase; dehydrogenase, glyceraldehyde phosphate; phosphoglyceraldehyde dehydrogenase; 3-phosphoglyceraldehyde dehydrogenase; NAD⁺-dependent glyceraldehyde phosphate dehydrogenase; glyceraldehyde phosphate dehydrogenase (NAD⁺); glyceraldehyde-3-phosphate dehydrogenase (NAD⁺); NADH-glyceraldehyde phosphate dehydrogenase; glyceraldehyde-3-*P*-dehydrogenase

Systematic name: D-glyceraldehyde-3-phosphate:NAD⁺ oxidoreductase (phosphorylating)

Comments: Also acts very slowly on D-glyceraldehyde and some other aldehydes; thiols can replace phosphate.

References: [496, 662, 1338, 4026, 4129]

[EC 1.2.1.12 created 1961]

EC 1.2.1.13

Accepted name: glyceraldehyde-3-phosphate dehydrogenase (NADP⁺) (phosphorylating)

Reaction: D-glyceraldehyde 3-phosphate + phosphate + NADP⁺ = 3-phospho-D-glyceroyl phosphate + NADPH + H⁺

Other name(s): triosephosphate dehydrogenase (NADP⁺); dehydrogenase, glyceraldehyde phosphate (nicotinamide adenine dinucleotide phosphate) (phosphorylating); glyceraldehyde phosphate dehydrogenase (nicotinamide adenine dinucleotide phosphate) (phosphorylating); NADP⁺-glyceraldehyde-3-phosphate dehydrogenase; NADP⁺-glyceraldehyde phosphate dehydrogenase; NADP⁺-dependent glyceraldehyde phosphate dehydrogenase; NADP⁺-triose phosphate dehydrogenase; glyceraldehyde-3-phosphate dehydrogenase (NADP⁺) (phosphorylating); GAPDH

Systematic name: D-glyceraldehyde-3-phosphate:NADP⁺ oxidoreductase (phosphorylating)

References: [398, 1197, 3235]

[EC 1.2.1.13 created 1961]

[1.2.1.14 Transferred entry. IMP dehydrogenase. Now EC 1.1.1.205, IMP dehydrogenase]

[EC 1.2.1.14 created 1961, deleted 1984]

EC 1.2.1.15

Accepted name: malonate-semialdehyde dehydrogenase
Reaction: 3-oxopropanoate + NAD(P)⁺ + H₂O = malonate + NAD(P)H + 2 H⁺
Systematic name: 3-oxopropanoate:NAD(P)⁺ oxidoreductase
References: [2702]

[EC 1.2.1.15 created 1965]

EC 1.2.1.16

Accepted name: succinate-semialdehyde dehydrogenase [NAD(P)⁺]
Reaction: succinate semialdehyde + NAD(P)⁺ + H₂O = succinate + NAD(P)H + 2 H⁺
Other name(s): succinate semialdehyde dehydrogenase (nicotinamide adenine dinucleotide (phosphate)); succinate-semialdehyde dehydrogenase [NAD(P)]
Systematic name: succinate-semialdehyde:NAD(P)⁺ oxidoreductase
References: [1712, 1715, 2790]

[EC 1.2.1.16 created 1965]

EC 1.2.1.17

Accepted name: glyoxylate dehydrogenase (acylating)
Reaction: glyoxylate + CoA + NADP⁺ = oxalyl-CoA + NADPH + H⁺
Systematic name: glyoxylate:NADP⁺ oxidoreductase (CoA-oxalylating)
References: [3091]

[EC 1.2.1.17 created 1965]

EC 1.2.1.18

Accepted name: malonate-semialdehyde dehydrogenase (acetylating)
Reaction: 3-oxopropanoate + CoA + NAD(P)⁺ = acetyl-CoA + CO₂ + NAD(P)H
Other name(s): malonic semialdehyde oxidative decarboxylase
Systematic name: 3-oxopropanoate:NAD(P)⁺ oxidoreductase (decarboxylating, CoA-acetylating)
References: [1433, 1712, 4300]

[EC 1.2.1.18 created 1965]

EC 1.2.1.19

Accepted name: aminobutyraldehyde dehydrogenase
Reaction: 4-aminobutanal + NAD⁺ + H₂O = 4-aminobutanoate + NADH + 2 H⁺
Other name(s): γ-guanidinobutyraldehyde dehydrogenase (ambiguous); ABAL dehydrogenase; 4-aminobutyraldehyde dehydrogenase; 4-aminobutanal dehydrogenase; γ-aminobutyraldehyde dehydrogenase; 1-pyrroline dehydrogenase; ABALDH; YdcW
Systematic name: 4-aminobutanal:NAD⁺ 1-oxidoreductase
Comments: The enzyme from some species exhibits broad substrate specificity and has a marked preference for straight-chain aldehydes (up to 7 carbon atoms) as substrates [1305]. The plant enzyme also acts on 4-guanidinobutanal (*cf.* EC 1.2.1.54 γ-guanidinobutyraldehyde dehydrogenase). As 1-pyrroline and 4-aminobutanal are in equilibrium and can be interconverted spontaneously, 1-pyrroline may act as the starting substrate. The enzyme forms part of the arginine-catabolism pathway [3301] and belongs in the aldehyde dehydrogenase superfamily [1305].
References: [478, 1712, 1713, 2443, 4372, 3066, 3065, 3301, 1305]

[EC 1.2.1.19 created 1965, modified 1989 (EC 1.5.1.35 created 2006, incorporated 2007)]

EC 1.2.1.20

Accepted name: glutarate-semialdehyde dehydrogenase
Reaction: 5-oxopentanoate + NAD⁺ + H₂O = glutarate + NADH + 2 H⁺
Other name(s): glutarate semialdehyde dehydrogenase
Systematic name: glutarate-semialdehyde:NAD⁺ oxidoreductase
References: [1626]

[EC 1.2.1.20 created 1965]

EC 1.2.1.21

Accepted name: glycolaldehyde dehydrogenase
Reaction: glycolaldehyde + NAD⁺ + H₂O = glycolate + NADH + 2 H⁺
Other name(s): glycol aldehyde dehydrogenase
Systematic name: glycolaldehyde:NAD⁺ oxidoreductase
References: [755]

[EC 1.2.1.21 created 1972]

EC 1.2.1.22

Accepted name: lactaldehyde dehydrogenase
Reaction: (S)-lactaldehyde + NAD⁺ + H₂O = (S)-lactate + NADH + 2 H⁺
Other name(s): L-lactaldehyde:NAD oxidoreductase; nicotinamide adenine dinucleotide (NAD)-linked dehydrogenase
Systematic name: (S)-lactaldehyde:NAD⁺ oxidoreductase
References: [3165, 3610]

[EC 1.2.1.22 created 1972]

EC 1.2.1.23

Accepted name: 2-oxoaldehyde dehydrogenase (NAD⁺)
Reaction: a 2-oxoaldehyde + NAD⁺ + H₂O = a 2-oxo carboxylate + NADH + H⁺
Other name(s): α-ketoaldehyde dehydrogenase; methylglyoxal dehydrogenase; NAD⁺-linked α-ketoaldehyde dehydrogenase; 2-ketoaldehyde dehydrogenase; NAD⁺-dependent α-ketoaldehyde dehydrogenase
Systematic name: 2-oxoaldehyde:NAD⁺ 2-oxidoreductase
Comments: Not identical with EC 1.2.1.49 2-oxoaldehyde dehydrogenase (NADP⁺).
References: [2598, 3139, 3141]

[EC 1.2.1.23 created 1972, modified 1986]

EC 1.2.1.24

Accepted name: succinate-semialdehyde dehydrogenase (NAD⁺)
Reaction: succinate semialdehyde + NAD⁺ + H₂O = succinate + NADH + 2 H⁺
Other name(s): succinate semialdehyde dehydrogenase (NAD⁺); succinic semialdehyde dehydrogenase (NAD⁺); succinyl semialdehyde dehydrogenase (NAD⁺); succinate semialdehyde:NAD⁺ oxidoreductase
Systematic name: succinate-semialdehyde:NAD⁺ oxidoreductase
Comments: This enzyme participates in the degradation of glutamate and 4-aminobutyrate. It is similar to EC 1.2.1.79 [succinate-semialdehyde dehydrogenase (NADP⁺)], and EC 1.2.1.16 [succinate-semialdehyde dehydrogenase (NAD(P)⁺)], but is specific for NAD⁺.
References: [52, 3269, 458]

[EC 1.2.1.24 created 1972, modified 2010]

EC 1.2.1.25

Accepted name: 2-oxoisovalerate dehydrogenase (acylating)
Reaction: 3-methyl-2-oxobutanoate + CoA + NAD⁺ = 2-methylpropanoyl-CoA + CO₂ + NADH
Other name(s): 2-oxoisovalerate dehydrogenase; α-ketoisovalerate dehydrogenase
Systematic name: 3-methyl-2-oxobutanoate:NAD⁺ 2-oxidoreductase (CoA-methyl-propanoylating)
Comments: Also acts on (*S*)-3-methyl-2-oxopentanoate and 4-methyl-2-oxopentanoate.
References: [2727]

[EC 1.2.1.25 created 1972]

EC 1.2.1.26

Accepted name: 2,5-dioxovalerate dehydrogenase
Reaction: 2,5-dioxopentanoate + NADP⁺ + H₂O = 2-oxoglutarate + NADPH + 2 H⁺
Other name(s): 2-oxoglutarate semialdehyde dehydrogenase; α-ketoglutaric semialdehyde dehydrogenase
Systematic name: 2,5-dioxopentanoate:NADP⁺ 5-oxidoreductase
References: [22]

[EC 1.2.1.26 created 1972]

EC 1.2.1.27

Accepted name: methylmalonate-semialdehyde dehydrogenase (CoA-acylating)
Reaction: 2-methyl-3-oxopropanoate + CoA + H₂O + NAD⁺ = propanoyl-CoA + HCO₃⁻ + NADH
Other name(s): MSDH; MMSA dehydrogenase; *iolA* (gene name); methylmalonate-semialdehyde dehydrogenase (acylating)
Systematic name: 2-methyl-3-oxopropanoate:NAD⁺ 3-oxidoreductase (CoA-propanoylating)
Comments: Also converts 3-oxopropanoate into acetyl-CoA [3651]. The reaction occurs in two steps with the decarboxylation process preceding CoA-binding [3651]. Bicarbonate rather than CO₂ is released as a final product [3651].
References: [3573, 882, 3651]

[EC 1.2.1.27 created 1972, modified 2014]

EC 1.2.1.28

Accepted name: benzaldehyde dehydrogenase (NAD⁺)
Reaction: benzaldehyde + NAD⁺ + H₂O = benzoate + NADH + 2 H⁺
Other name(s): benzaldehyde (NAD) dehydrogenase; benzaldehyde dehydrogenase (NAD)
Systematic name: benzaldehyde:NAD⁺ oxidoreductase
References: [1312]

[EC 1.2.1.28 created 1972]

EC 1.2.1.29

Accepted name: aryl-aldehyde dehydrogenase
Reaction: an aromatic aldehyde + NAD⁺ + H₂O = an aromatic acid + NADH + H⁺
Systematic name: aryl-aldehyde:NAD⁺ oxidoreductase
Comments: Oxidizes a number of aromatic aldehydes, but not aliphatic aldehydes.
References: [3109]

[EC 1.2.1.29 created 1972]

EC 1.2.1.30

Accepted name: aryl-aldehyde dehydrogenase (NADP⁺)

Reaction: an aromatic aldehyde + NADP⁺ + AMP + diphosphate + H₂O = an aromatic acid + NADPH + H⁺ + ATP
Other name(s): aromatic acid reductase; aryl-aldehyde dehydrogenase (NADP)
Systematic name: aryl-aldehyde:NADP⁺ oxidoreductase (ATP-forming)
References: [1297, 1299]

[EC 1.2.1.30 created 1972]

EC 1.2.1.31

Accepted name: L-aminoadipate-semialdehyde dehydrogenase
Reaction: (S)-2-amino-6-oxohexanoate + NAD(P)⁺ + H₂O = L-2-aminoadipate + NAD(P)H + H⁺ (overall reaction)
(1a) (S)-2-amino-6-oxohexanoate = (S)-2,3,4,5-tetrahydropyridine-2-carboxylate + H₂O (spontaneous)
(1b) (S)-2,3,4,5-tetrahydropyridine-2-carboxylate + NAD(P)⁺ + 2 H₂O = L-2-aminoadipate + NAD(P)H + H⁺
Other name(s): aminoadipate semialdehyde dehydrogenase; 2-aminoadipate semialdehyde dehydrogenase; α-aminoadipate-semialdehyde dehydrogenase; α-aminoadipate reductase; 2-aminoadipic semialdehyde dehydrogenase; L-α-aminoadipate δ-semialdehyde oxidoreductase; L-α-aminoadipate δ-semialdehyde:NAD⁺ oxidoreductase; L-α-aminoadipate δ-semialdehyde:nicotinamide adenine dinucleotide oxidoreductase; L-2-aminoadipate 6-semialdehyde:NAD(P)⁺ 6-oxidoreductase
Systematic name: (S)-2-amino-6-oxohexanoate:NAD(P)⁺ 6-oxidoreductase
Comments: (S)-2-amino-6-oxohexanoate undergoes a spontaneous dehydration forming the cyclic (S)-2,3,4,5-tetrahydropyridine-2-carboxylate, which serves as a substrate for the hydrogenation reaction.
References: [479, 3214, 764, 1091]

[EC 1.2.1.31 created 1972, modified 2011]

EC 1.2.1.32

Accepted name: aminomuconate-semialdehyde dehydrogenase
Reaction: 2-aminomuconate 6-semialdehyde + NAD⁺ + H₂O = 2-aminomuconate + NADH + 2 H⁺
Other name(s): 2-aminomuconate semialdehyde dehydrogenase; 2-hydroxymuconic acid semialdehyde dehydrogenase; 2-hydroxymuconate semialdehyde dehydrogenase; α-aminomuconic ε-semialdehyde dehydrogenase; α-hydroxymuconic ε-semialdehyde dehydrogenase; 2-hydroxymuconic semialdehyde dehydrogenase
Systematic name: 2-aminomuconate-6-semialdehyde:NAD⁺ 6-oxidoreductase
Comments: Also acts on 2-hydroxymuconate semialdehyde.
References: [1627]

[EC 1.2.1.32 created 1972]

EC 1.2.1.33

Accepted name: (R)-dehydropantoate dehydrogenase
Reaction: (R)-4-dehydropantoate + NAD⁺ + H₂O = (R)-3,3-dimethylmalate + NADH + 2 H⁺
Other name(s): D-aldopantoate dehydrogenase; D-2-hydroxy-3,3-dimethyl-3-formylpropionate:diphosphopyridine nucleotide (DPN⁺) oxidoreductase
Systematic name: (R)-4-dehydropantoate:NAD⁺ 4-oxidoreductase
References: [2360]

[EC 1.2.1.33 created 1972]

[1.2.1.34 Transferred entry. D-mannonate dehydrogenase (NAD(P)⁺). Now EC 1.1.1.131, mannuronate reductase]

[EC 1.2.1.34 created 1972, deleted 1983 [transferred to EC 1.1.1.180, deleted 1984]]

[1.2.1.35 Transferred entry. uronate dehydrogenase. Now EC 1.1.1.203, uronate dehydrogenase]

[EC 1.2.1.35 created 1972, deleted 1984]

EC 1.2.1.36

Accepted name: retinal dehydrogenase
Reaction: retinal + NAD⁺ + H₂O = retinoate + NADH + 2 H⁺
Other name(s): cytosolic retinal dehydrogenase
Systematic name: retinal:NAD⁺ oxidoreductase
Comments: A metalloflavoprotein (FAD). Acts on both the 11-*trans*- and 13-*cis*-forms of retinal.
References: [2587]

[EC 1.2.1.36 created 1972]

[1.2.1.37 Transferred entry. xanthine dehydrogenase. Now EC 1.17.1.4, xanthine dehydrogenase]

[EC 1.2.1.37 created 1972, deleted 1984]

EC 1.2.1.38

Accepted name: *N*-acetyl- γ -glutamyl-phosphate reductase
Reaction: *N*-acetyl-L-glutamate 5-semialdehyde + NADP⁺ + phosphate = *N*-acetyl-L-glutamyl 5-phosphate + NADPH + H⁺
Other name(s): reductase, acetyl- γ -glutamyl phosphate; *N*-acetylglutamate 5-semialdehyde dehydrogenase; *N*-acetylglutamic γ -semialdehyde dehydrogenase; *N*-acetyl-L-glutamate γ -semialdehyde:NADP⁺ oxidoreductase (phosphorylating)
Systematic name: *N*-acetyl-L-glutamate-5-semialdehyde:NADP⁺ 5-oxidoreductase (phosphorylating)
References: [163, 1217]

[EC 1.2.1.38 created 1972]

EC 1.2.1.39

Accepted name: phenylacetaldehyde dehydrogenase
Reaction: phenylacetaldehyde + NAD⁺ + H₂O = phenylacetate + NADH + 2 H⁺
Systematic name: phenylacetaldehyde:NAD⁺ oxidoreductase
References: [1092]

[EC 1.2.1.39 created 1976]

[1.2.1.40 Deleted entry. 3 α ,7 α ,12 α -trihydroxycholestan-26-al 26-oxidoreductase. The activity is part of EC 1.14.13.15, cholestanetriol 26-monoxygenase]

[EC 1.2.1.40 created 1976, deleted 2012]

EC 1.2.1.41

Accepted name: glutamate-5-semialdehyde dehydrogenase
Reaction: L-glutamate 5-semialdehyde + phosphate + NADP⁺ = L-glutamyl 5-phosphate + NADPH + H⁺
Other name(s): β -glutamylphosphate reductase; γ -glutamyl phosphate reductase; β -glutamylphosphate reductase; glutamate semialdehyde dehydrogenase; glutamate- γ -semialdehyde dehydrogenase
Systematic name: L-glutamate-5-semialdehyde:NADP⁺ 5-oxidoreductase (phosphorylating)
References: [162]

[EC 1.2.1.41 created 1976]

EC 1.2.1.42

Accepted name: hexadecanal dehydrogenase (acylating)
Reaction: hexadecanal + CoA + NAD⁺ = hexadecanoyl-CoA + NADH + H⁺

Other name(s): fatty acyl-CoA reductase
Systematic name: hexadecanal:NAD⁺ oxidoreductase (CoA-acylating)
Comments: Also acts, more slowly, on octadecanoyl-CoA.
References: [1763]

[EC 1.2.1.42 created 1978]

[1.2.1.43 *Transferred entry. formate dehydrogenase (NADP⁺). Now EC 1.17.1.10, formate dehydrogenase (NADP⁺)*]

[EC 1.2.1.43 created 1978, deleted 2017]

EC 1.2.1.44

Accepted name: cinnamoyl-CoA reductase
Reaction: cinnamaldehyde + CoA + NADP⁺ = cinnamoyl-CoA + NADPH + H⁺
Other name(s): feruloyl-CoA reductase; cinnamoyl-coenzyme A reductase; feruloyl-CoA reductase; feruloyl coenzyme A reductase; *p*-hydroxycinnamoyl coenzyme A reductase; cinnamoyl-CoA:NADPH reductase
Systematic name: cinnamaldehyde:NADP⁺ oxidoreductase (CoA-cinnamoylating)
Comments: Acts also on a number of substituted cinnamoyl esters of coenzyme A.
References: [1298, 3314, 4175]

[EC 1.2.1.44 created 1978]

[1.2.1.45 *Transferred entry. 4-carboxy-2-hydroxy-6-semialdehyde dehydrogenase. Now EC 1.1.1.312, 2-hydroxy-4-carboxymuconate semialdehyde hemiacetal dehydrogenase.*]

[EC 1.2.1.45 created 1978, deleted 2011]

EC 1.2.1.46

Accepted name: formaldehyde dehydrogenase
Reaction: formaldehyde + NAD⁺ + H₂O = formate + NADH + 2 H⁺
Other name(s): NAD-linked formaldehyde dehydrogenase; NAD-dependent formaldehyde dehydrogenase
Systematic name: formaldehyde:NAD⁺ oxidoreductase
References: [1535]

[EC 1.2.1.46 created 1982]

EC 1.2.1.47

Accepted name: 4-trimethylammoniobutyraldehyde dehydrogenase
Reaction: 4-trimethylammoniobutanal + NAD⁺ + H₂O = 4-trimethylammoniobutanoate + NADH + 2 H⁺
Other name(s): 4-trimethylaminobutyraldehyde dehydrogenase; 4-*N*-trimethylaminobutyraldehyde dehydrogenase
Systematic name: 4-trimethylammoniobutanal:NAD⁺ 1-oxidoreductase
References: [3143]

[EC 1.2.1.47 created 1983]

EC 1.2.1.48

Accepted name: long-chain-aldehyde dehydrogenase
Reaction: a long-chain aldehyde + NAD⁺ + H₂O = a long-chain carboxylate + NADH + 2 H⁺
Other name(s): long-chain aliphatic aldehyde dehydrogenase; long-chain fatty aldehyde dehydrogenase; fatty aldehyde:NAD⁺ oxidoreductase
Systematic name: long-chain-aldehyde:NAD⁺ oxidoreductase
Comments: The best substrate is dodecylaldehyde.
References: [234, 2612, 2613]

[EC 1.2.1.48 created 1984]

EC 1.2.1.49

Accepted name: 2-oxoaldehyde dehydrogenase (NADP⁺)
Reaction: a 2-oxoaldehyde + NADP⁺ + H₂O = a 2-oxo carboxylate + NADPH + H⁺
Other name(s): α-ketoaldehyde dehydrogenase; methylglyoxal dehydrogenase; NADP⁺-linked α-ketoaldehyde dehydrogenase; 2-ketoaldehyde dehydrogenase; NADP⁺-dependent α-ketoaldehyde dehydrogenase
Systematic name: 2-oxoaldehyde:NADP⁺ 2-oxidoreductase
Comments: Not identical with EC 1.2.1.23 2-oxoaldehyde dehydrogenase (NAD⁺).
References: [3139, 3141]

[EC 1.2.1.49 created 1986]

EC 1.2.1.50

Accepted name: long-chain acyl-protein thioester reductase
Reaction: a long-chain aldehyde + [protein]-L-cysteine + NADP⁺ = a [protein]-S-(long-chain fatty acyl)-L-cysteine + NADPH + H⁺
Other name(s): *luxC* (gene name); acyl-CoA reductase; acyl coenzyme A reductase; long-chain-aldehyde:NADP⁺ oxidoreductase (acyl-CoA-forming); long-chain-fatty-acyl-CoA reductase
Systematic name: long-chain-aldehyde:NADP⁺ oxidoreductase (protein thioester-forming)
Comments: Together with a hydrolase component (EC 3.1.2.2 and EC 3.1.2.14) and a synthetase component (EC 6.2.1.19), this enzyme forms a multienzyme fatty acid reductase complex that produces the long-chain aldehyde substrate of the bacterial luciferase enzyme (EC 1.14.14.3). The enzyme is acylated by receiving an acyl group from EC 6.2.1.19, and catalyses the reduction of the acyl group, releasing the aldehyde product. The enzyme is also able to accept the acyl group from a long-chain acyl-CoA.
References: [3187, 4091, 2255]

[EC 1.2.1.50 created 1986, modified 2016]

EC 1.2.1.51

Accepted name: pyruvate dehydrogenase (NADP⁺)
Reaction: pyruvate + CoA + NADP⁺ = acetyl-CoA + CO₂ + NADPH
Systematic name: pyruvate:NADP⁺ 2-oxidoreductase (CoA-acetylating)
Comments: The *Euglena* enzyme can also use FAD or methylviologen as acceptor, more slowly. The enzyme is inhibited by oxygen.
References: [1658, 1659]

[EC 1.2.1.51 created 1989]

EC 1.2.1.52

Accepted name: oxoglutarate dehydrogenase (NADP⁺)
Reaction: 2-oxoglutarate + CoA + NADP⁺ = succinyl-CoA + CO₂ + NADPH
Other name(s): oxoglutarate dehydrogenase (NADP)
Systematic name: 2-oxoglutarate:NADP⁺ 2-oxidoreductase (CoA-succinylating)
Comments: The *Euglena* enzyme can also use NAD⁺ as acceptor, but more slowly.
References: [1658]

[EC 1.2.1.52 created 1989]

EC 1.2.1.53

Accepted name: 4-hydroxyphenylacetaldehyde dehydrogenase

Reaction: 4-hydroxyphenylacetaldehyde + NAD⁺ + H₂O = 4-hydroxyphenylacetate + NADH + 2 H⁺
Other name(s): 4-HPAL dehydrogenase
Systematic name: 4-hydroxyphenylacetaldehyde:NAD⁺ oxidoreductase
Comments: With EC 4.2.1.87 octopamine dehydratase, brings about the metabolism of octopamine in *Pseudomonas*.
References: [712]

[EC 1.2.1.53 created 1989]

EC 1.2.1.54

Accepted name: γ-guanidinobutyraldehyde dehydrogenase
Reaction: 4-guanidinobutanal + NAD⁺ + H₂O = 4-guanidinobutanoate + NADH + 2 H⁺
Other name(s): α-guanidinobutyraldehyde dehydrogenase; 4-guanidinobutyraldehyde dehydrogenase; GBAL dehydrogenase
Systematic name: 4-guanidinobutanal:NAD⁺ 1-oxidoreductase
Comments: Involved in the degradation of arginine in *Pseudomonas putida* (cf. EC 1.2.1.19 aminobutyraldehyde dehydrogenase).
References: [4372]

[EC 1.2.1.54 created 1989]

[1.2.1.55 Transferred entry. (R)-3-hydroxyacid ester dehydrogenase. Now EC 1.1.1.279, (R)-3-hydroxyacid-ester dehydrogenase]

[EC 1.2.1.55 created 1990, deleted 2003]

[1.2.1.56 Transferred entry. (S)-3-hydroxyacid ester dehydrogenase. Now EC 1.1.1.280, (S)-3-hydroxyacid-ester dehydrogenase]

[EC 1.2.1.56 created 1990, deleted 2003]

EC 1.2.1.57

Accepted name: butanal dehydrogenase
Reaction: butanal + CoA + NAD(P)⁺ = butanoyl-CoA + NAD(P)H + H⁺
Systematic name: butanal:NAD(P)⁺ oxidoreductase (CoA-acylating)
Comments: Also acts on acetaldehyde, but more slowly.
References: [2927]

[EC 1.2.1.57 created 1992]

EC 1.2.1.58

Accepted name: phenylglyoxylate dehydrogenase (acylating)
Reaction: phenylglyoxylate + NAD⁺ + CoA = benzoyl-S-CoA + CO₂ + NADH
Systematic name: phenylglyoxylate:NAD⁺ oxidoreductase
Comments: Requires thiamine diphosphate as cofactor. The enzyme from the denitrifying bacterium *Azoarcus evansii* is specific for phenylglyoxylate. 2-Oxoisovalerate is oxidized at 15% of the rate for phenylglyoxylate. Also reduces viologen dyes. Contains iron-sulfur centres and FAD.
References: [1521]

[EC 1.2.1.58 created 1999]

EC 1.2.1.59

Accepted name: glyceraldehyde-3-phosphate dehydrogenase (NAD(P)⁺) (phosphorylating)
Reaction: D-glyceraldehyde 3-phosphate + phosphate + NAD(P)⁺ = 3-phospho-D-glyceroyl phosphate + NAD(P)H + H⁺

Other name(s): triosephosphate dehydrogenase (NAD(P)); glyceraldehyde-3-phosphate dehydrogenase (NAD(P)) (phosphorylating)
Systematic name: D-glyceraldehyde 3-phosphate:NAD(P)⁺ oxidoreductase (phosphorylating)
Comments: NAD⁺ and NADP⁺ can be used as cofactors with similar efficiency, unlike EC 1.2.1.12 glyceraldehyde-3-phosphate dehydrogenase (phosphorylating) and EC 1.2.1.13 glyceraldehyde-3-phosphate dehydrogenase (NADP⁺) (phosphorylating), which are NAD⁺- and NADP⁺-dependent, respectively.
References: [3989, 3990]

[EC 1.2.1.59 created 1999]

EC 1.2.1.60

Accepted name: 5-carboxymethyl-2-hydroxyumuconic-semialdehyde dehydrogenase
Reaction: 5-carboxymethyl-2-hydroxyumuconate semialdehyde + H₂O + NAD⁺ = 5-carboxymethyl-2-hydroxyumuconate + NADH + 2 H⁺
Other name(s): carboxymethylhydroxyumuconic semialdehyde dehydrogenase
Systematic name: 5-carboxymethyl-2-hydroxyumuconic-semialdehyde:NAD⁺ oxidoreductase
Comments: Involved in the tyrosine degradation pathway in *Arthrobacter* sp.
References: [313, 66, 657, 1159]

[EC 1.2.1.60 created 2000]

EC 1.2.1.61

Accepted name: 4-hydroxyumuconic-semialdehyde dehydrogenase
Reaction: 4-hydroxyumuconic semialdehyde + NAD⁺ + H₂O = maleylacetate + NADH + 2 H⁺
Systematic name: 4-hydroxyumuconic-semialdehyde:NAD⁺ oxidoreductase
Comments: Involved in the 4-nitrophenol degradation pathway.
References: [3589]

[EC 1.2.1.61 created 2000]

EC 1.2.1.62

Accepted name: 4-formylbenzenesulfonate dehydrogenase
Reaction: 4-formylbenzenesulfonate + NAD⁺ + H₂O = 4-sulfobenzoate + NADH + 2 H⁺
Systematic name: 4-formylbenzenesulfonate:NAD⁺ oxidoreductase
Comments: Involved in the toluene-4-sulfonate degradation pathway.
References: [1789, 1787]

[EC 1.2.1.62 created 2000]

EC 1.2.1.63

Accepted name: 6-oxohexanoate dehydrogenase
Reaction: 6-oxohexanoate + NADP⁺ + H₂O = adipate + NADPH + 2 H⁺
Systematic name: 6-oxohexanoate:NADP⁺ oxidoreductase
Comments: Last step in the cyclohexanol degradation pathway in *Acinetobacter* sp.
References: [752, 857]

[EC 1.2.1.63 created 2000]

EC 1.2.1.64

Accepted name: 4-hydroxybenzaldehyde dehydrogenase (NAD⁺)
Reaction: 4-hydroxybenzaldehyde + NAD⁺ + H₂O = 4-hydroxybenzoate + NADH + 2 H⁺

Other name(s): *p*-hydroxybenzaldehyde dehydrogenase (ambiguous); 4-hydroxybenzaldehyde dehydrogenase (ambiguous)
Systematic name: 4-hydroxybenzaldehyde:NAD⁺ oxidoreductase
Comments: The bacterial enzyme (characterized from an unidentified denitrifying bacterium) is involved in an anaerobic toluene degradation pathway. The plant enzyme is involved in formation of 4-hydroxybenzoate, a cell wall-bound phenolic acid that plays a major role in plant defense against pathogens. *cf.* EC 1.2.1.96, 4-hydroxybenzaldehyde dehydrogenase (NADP⁺).
References: [362, 3541]

[EC 1.2.1.64 created 2000, modified 2015]

EC 1.2.1.65

Accepted name: salicylaldehyde dehydrogenase
Reaction: salicylaldehyde + NAD⁺ + H₂O = salicylate + NADH + 2 H⁺
Systematic name: salicylaldehyde:NAD⁺ oxidoreductase
Comments: Involved in the naphthalene degradation pathway in some bacteria.
References: [908]

[EC 1.2.1.65 created 2000, modified 2011]

[1.2.1.66 *Transferred entry. mycothiol-dependent formaldehyde dehydrogenase. Now EC 1.1.1.306, S-(hydroxymethyl)mycothiol dehydrogenase*]

[EC 1.2.1.66 created 2000, deleted 2010]

EC 1.2.1.67

Accepted name: vanillin dehydrogenase
Reaction: vanillin + NAD⁺ + H₂O = vanillate + NADH + 2 H⁺
Systematic name: vanillin:NAD⁺ oxidoreductase
References: [3036]

[EC 1.2.1.67 created 2000]

EC 1.2.1.68

Accepted name: coniferyl-aldehyde dehydrogenase
Reaction: coniferyl aldehyde + H₂O + NAD(P)⁺ = ferulate + NAD(P)H + 2 H⁺
Systematic name: coniferyl aldehyde:NAD(P)⁺ oxidoreductase
Comments: Also oxidizes other aromatic aldehydes, but not aliphatic aldehydes.
References: [9]

[EC 1.2.1.68 created 2000]

EC 1.2.1.69

Accepted name: fluoroacetaldehyde dehydrogenase
Reaction: fluoroacetaldehyde + NAD⁺ + H₂O = fluoroacetate + NADH + 2 H⁺
Systematic name: fluoroacetaldehyde:NAD⁺ oxidoreductase
Comments: The enzyme from *Streptomyces cattleya* has a high affinity for fluoroacetate and glycolaldehyde but not for acetaldehyde.
References: [2670, 2671]

[EC 1.2.1.69 created 2003]

EC 1.2.1.70

Accepted name: glutamyl-tRNA reductase
Reaction: L-glutamate 1-semialdehyde + NADP⁺ + tRNA^{Glu} = L-glutamyl-tRNA^{Glu} + NADPH + H⁺
Systematic name: L-glutamate-semialdehyde:NADP⁺ oxidoreductase (L-glutamyl-tRNA^{Glu}-forming)
Comments: This enzyme forms part of the pathway for the biosynthesis of 5-aminolevulinic acid from glutamate, known as the C5 pathway. The route shown in the diagram is used in most eubacteria, and in all archaeobacteria, algae and plants. However, in the α -proteobacteria, EC 2.3.1.37, 5-aminolevulinic acid synthase, is used in an alternative route to produce the product 5-aminolevulinic acid from succinyl-CoA and glycine. This route is found in the mitochondria of fungi and animals, organelles that are considered to be derived from an endosymbiotic α -proteobacterium. Although higher plants do not possess EC 2.3.1.37, the protistan *Euglena gracilis* possesses both the C5 pathway and EC 2.3.1.37.
References: [4063, 3037, 3353]

[EC 1.2.1.70 created 2004]

EC 1.2.1.71

Accepted name: succinylglutamate-semialdehyde dehydrogenase
Reaction: *N*-succinyl-L-glutamate 5-semialdehyde + NAD⁺ + H₂O = *N*-succinyl-L-glutamate + NADH + 2 H⁺
Other name(s): succinylglutamic semialdehyde dehydrogenase; *N*-succinylglutamate 5-semialdehyde dehydrogenase; SGS; AruD; AstD
Systematic name: *N*-succinyl-L-glutamate 5-semialdehyde:NAD⁺ oxidoreductase
Comments: This is the fourth enzyme in the arginine succinyltransferase (AST) pathway for the catabolism of arginine [4151]. This pathway converts the carbon skeleton of arginine into glutamate, with the concomitant production of ammonia and conversion of succinyl-CoA into succinate and CoA. The five enzymes involved in this pathway are EC 2.3.1.109 (arginine *N*-succinyltransferase), EC 3.5.3.23 (*N*-succinylarginine dihydrolase), EC 2.6.1.11 (acetylornithine transaminase), EC 1.2.1.71 (succinylglutamate-semialdehyde dehydrogenase) and EC 3.5.1.96 (succinylglutamate desuccinylase) [3927, 704].
References: [4151, 4152, 3927, 1685, 3379, 704, 705]

[EC 1.2.1.71 created 2006]

EC 1.2.1.72

Accepted name: erythrose-4-phosphate dehydrogenase
Reaction: D-erythrose 4-phosphate + NAD⁺ + H₂O = 4-phosphoerythronate + NADH + 2 H⁺
Other name(s): erythrose 4-phosphate dehydrogenase; E4PDH; GapB; Epd dehydrogenase; E4P dehydrogenase
Systematic name: D-erythrose 4-phosphate:NAD⁺ oxidoreductase
Comments: This enzyme was originally thought to be a glyceraldehyde-3-phosphate dehydrogenase (EC 1.2.1.12), but this has since been disproved, as glyceraldehyde 3-phosphate is not a substrate [4458, 359]. Forms part of the pyridoxal-5'-phosphate coenzyme biosynthesis pathway in *Escherichia coli*, along with EC 1.1.1.290 (4-phosphoerythronate dehydrogenase), EC 2.6.1.52 (phosphoserine transaminase), EC 1.1.1.262 (4-hydroxythreonine-4-phosphate dehydrogenase), EC 2.6.99.2 (pyridoxine 5'-phosphate synthase) and EC 1.4.3.5 (pyridoxamine-phosphate oxidase).
References: [4458, 359, 4342]

[EC 1.2.1.72 created 2006]

EC 1.2.1.73

Accepted name: sulfoacetaldehyde dehydrogenase
Reaction: 2-sulfoacetaldehyde + H₂O + NAD⁺ = sulfoacetate + NADH + 2 H⁺
Other name(s): SafD
Systematic name: 2-sulfoacetaldehyde:NAD⁺ oxidoreductase

Comments: This reaction is part of a bacterial pathway that can utilize the amino group of taurine as a sole source of nitrogen for growth. At physiological concentrations, NAD⁺ cannot be replaced by NADP⁺. The enzyme is specific for sulfoacetaldehyde, as formaldehyde, acetaldehyde, betaine aldehyde, propanal, glyceraldehyde, phosphonoacetaldehyde, glyoxylate, glycolaldehyde and 2-oxobutyrate are not substrates.

References: [2056]

[EC 1.2.1.73 created 2008]

EC 1.2.1.74

Accepted name: abieta-7,13-dien-18-al dehydrogenase

Reaction: abieta-7,13-dien-18-al + H₂O + NAD⁺ = abieta-7,13-dien-18-oate + NADH + H⁺

Other name(s): abietadienal dehydrogenase (ambiguous)

Systematic name: abieta-7,13-dien-18-al:NAD⁺ oxidoreductase

Comments: Abietic acid is the principle component of conifer resin. This enzyme catalyses the last step of the pathway of abietic acid biosynthesis in *Abies grandis* (grand fir). The activity has been demonstrated in cell-free stem extracts of *A. grandis*, was present in the cytoplasm, and required NAD⁺ as cofactor [1115]. The enzyme is expressed constitutively at a high level, and is not inducible by wounding of the plant tissue [1117].

References: [1115, 1117]

[EC 1.2.1.74 created 2009, modified 2012]

EC 1.2.1.75

Accepted name: malonyl-CoA reductase (malonate semialdehyde-forming)

Reaction: malonate semialdehyde + CoA + NADP⁺ = malonyl-CoA + NADPH + H⁺

Other name(s): NADP-dependent malonyl CoA reductase; malonyl CoA reductase (NADP); malonyl CoA reductase (malonate semialdehyde-forming)

Systematic name: malonate semialdehyde:NADP⁺ oxidoreductase (malonate semialdehyde-forming)

Comments: Requires Mg²⁺. Catalyses the reduction of malonyl-CoA to malonate semialdehyde, a key step in the 3-hydroxypropanoate and the 3-hydroxypropanoate/4-hydroxybutanoate cycles, autotrophic CO₂ fixation pathways found in some green non-sulfur phototrophic bacteria and some thermoacidophilic archaea, respectively [3671, 265]. The enzyme from *Sulfolobus tokodaii* has been purified, and found to contain one RNA molecule per two subunits [51]. The enzyme from *Chloroflexus aurantiacus* is bifunctional, and also catalyses the next reaction in the pathway, EC 1.1.1.298 [3-hydroxypropionate dehydrogenase (NADP⁺)] [1604].

References: [3671, 265, 51, 1604]

[EC 1.2.1.75 created 2009]

EC 1.2.1.76

Accepted name: succinate-semialdehyde dehydrogenase (acylating)

Reaction: succinate semialdehyde + CoA + NADP⁺ = succinyl-CoA + NADPH + H⁺

Other name(s): succinyl-coA reductase; coenzyme-A-dependent succinate-semialdehyde dehydrogenase

Systematic name: succinate semialdehyde:NADP⁺ oxidoreductase (CoA-acylating)

Comments: Catalyses the NADPH-dependent reduction of succinyl-CoA to succinate semialdehyde. The enzyme has been described in *Clostridium kluyveri*, where it participates in succinate fermentation [3571], and in *Metallosphaera sedula*, where it participates in the 3-hydroxypropanoate/4-hydroxybutanoate cycle, an autotrophic CO₂ fixation pathway found in some thermoacidophilic archaea [51, 265].

References: [3571, 51, 265]

[EC 1.2.1.76 created 2009]

EC 1.2.1.77

- Accepted name:** 3,4-dehydroadipyl-CoA semialdehyde dehydrogenase (NADP⁺)
Reaction: 3,4-didehydroadipyl-CoA semialdehyde + NADP⁺ + H₂O = 3,4-didehydroadipyl-CoA + NADPH + H⁺
Other name(s): BoxD; 3,4-dehydroadipyl-CoA semialdehyde dehydrogenase
Systematic name: 3,4-didehydroadipyl-CoA semialdehyde:NADP⁺ oxidoreductase
Comments: This enzyme catalyses a step in the aerobic benzoyl-coenzyme A catabolic pathway in *Azoarcus evansii* and *Burkholderia xenovorans*.
References: [1187, 167]

[EC 1.2.1.77 created 2010]

EC 1.2.1.78

- Accepted name:** 2-formylbenzoate dehydrogenase
Reaction: 2-formylbenzoate + NAD⁺ + H₂O = *o*-phthalic acid + NADH + H⁺
Other name(s): 2-carboxybenzaldehyde dehydrogenase; 2CBAL dehydrogenase; PhdK
Systematic name: 2-formylbenzoate:NAD⁺ oxidoreductase
Comments: The enzyme is involved in phenanthrene degradation.
References: [1692, 1955]

[EC 1.2.1.78 created 2010]

EC 1.2.1.79

- Accepted name:** succinate-semialdehyde dehydrogenase (NADP⁺)
Reaction: succinate semialdehyde + NADP⁺ + H₂O = succinate + NADPH + 2 H⁺
Other name(s): succinic semialdehyde dehydrogenase (NADP⁺); succinyl semialdehyde dehydrogenase (NADP⁺); succinate semialdehyde:NADP⁺ oxidoreductase; NADP-dependent succinate-semialdehyde dehydrogenase; GabD
Systematic name: succinate-semialdehyde:NADP⁺ oxidoreductase
Comments: This enzyme participates in the degradation of glutamate and 4-aminobutyrate. It is similar to EC 1.2.1.24 [succinate-semialdehyde dehydrogenase (NAD⁺)], and EC 1.2.1.16 [succinate-semialdehyde dehydrogenase (NAD(P)⁺)], but is specific for NADP⁺. The enzyme from *Escherichia coli* is 20-fold more active with NADP⁺ than NAD⁺ [1707].
References: [208, 1707]

[EC 1.2.1.79 created 2010]

EC 1.2.1.80

- Accepted name:** long-chain acyl-[acyl-carrier-protein] reductase
Reaction: a long-chain aldehyde + an [acyl-carrier protein] + NAD(P)⁺ = a long-chain acyl-[acyl-carrier protein] + NAD(P)H + H⁺
Other name(s): long-chain acyl-[acp] reductase; fatty acyl-[acyl-carrier-protein] reductase; acyl-[acp] reductase
Systematic name: long-chain-aldehyde:NAD(P)⁺ oxidoreductase (acyl-[acyl-carrier protein]-forming)
Comments: Catalyses the reaction in the opposite direction. This enzyme, purified from the cyanobacterium *Synechococcus elongatus* PCC 7942, catalyses the NAD(P)H-dependent reduction of an activated fatty acid (acyl-[acp]) to the corresponding aldehyde. Together with EC 4.1.99.5, octadecanal decarboxylase, it is involved in alkane biosynthesis. The natural substrates of the enzyme are C₁₆ and C₁₈ activated fatty acids. Requires Mg²⁺.
References: [3365]

[EC 1.2.1.80 created 2011]

EC 1.2.1.81

Accepted name: sulfoacetaldehyde dehydrogenase (acylating)
Reaction: 2-sulfoacetaldehyde + CoA + NADP⁺ = sulfoacetyl-CoA + NADPH + H⁺
Other name(s): SauS
Systematic name: 2-sulfoacetaldehyde:NADP⁺ oxidoreductase (CoA-acylating)
Comments: The enzyme is involved in degradation of sulfoacetate. In this pathway the reaction is catalysed in the reverse direction. The enzyme is specific for sulfoacetaldehyde and NADP⁺.
References: [4165]

[EC 1.2.1.81 created 2011]

EC 1.2.1.82

Accepted name: β-apo-4'-carotenal oxygenase
Reaction: 4'-apo-β,ψ-caroten-4'-al + NAD⁺ + H₂O = neurosporaxanthin + NADH + 2 H⁺
Other name(s): β-apo-4'-carotenal dehydrogenase; YLO-1; *carD* (gene name)
Systematic name: 4'-apo-β,ψ-carotenal:NAD⁺ oxidoreductase
Comments: Neurosporaxanthin is responsible for the orange color of of *Neurospora*.
References: [968, 814]

[EC 1.2.1.82 created 2011]

EC 1.2.1.83

Accepted name: 3-succinoylsemialdehyde-pyridine dehydrogenase
Reaction: 4-oxo-4-(pyridin-3-yl)butanal + NADP⁺ + H₂O = 4-oxo-4-(pyridin-3-yl)butanoate + NADPH + H⁺
Systematic name: 4-oxo-4-(pyridin-3-yl)butanal:NADP⁺ oxidoreductase
Comments: The enzyme has been characterized from the soil bacterium *Pseudomonas* sp. HZN6. It participates in the nicotine degradation pathway.
References: [3080]

[EC 1.2.1.83 created 2012]

EC 1.2.1.84

Accepted name: alcohol-forming fatty acyl-CoA reductase
Reaction: a long-chain acyl-CoA + 2 NADPH + 2 H⁺ = a long-chain alcohol + 2 NADP⁺ + CoA
Other name(s): FAR (gene name); long-chain acyl-CoA:NADPH reductase
Systematic name: NADPH:long-chain acyl-CoA reductase
Comments: The enzyme has been characterized from the plant *Simmondsia chinensis* (jojoba). The alcohol is formed by a four-electron reduction of fatty acyl-CoA. Although the reaction proceeds through an aldehyde intermediate, a free aldehyde is not released. The recombinant enzyme was shown to accept saturated and mono-unsaturated fatty acyl-CoAs of 16 to 22 carbons.
References: [2514]

[EC 1.2.1.84 created 2012]

EC 1.2.1.85

Accepted name: 2-hydroxyomuconate-6-semialdehyde dehydrogenase
Reaction: 2-hydroxyomuconate-6-semialdehyde + NAD⁺ + H₂O = (2Z,4E)-2-hydroxyhexa-2,4-dienedioate + NADH + 2 H⁺
Other name(s): *xyIG* (gene name); *praB* (gene name)
Systematic name: 2-hydroxyomuconate-6-semialdehyde:NAD⁺ oxidoreductase
Comments: This substrate for this enzyme is formed by *meta* ring cleavage of catechol (EC 1.13.11.2, catechol 2,3-dioxygenase), and is an intermediate in the bacterial degradation of several aromatic compounds. Has lower activity with benzaldehyde [1653]. Activity with NAD⁺ is more than 10-fold higher than with NADP⁺ [1824]. *cf.* EC 1.2.1.32, aminomuconate-semialdehyde dehydrogenase.
References: [1653, 2895, 1824]

[EC 1.2.1.85 created 2012]

EC 1.2.1.86

Accepted name: geranial dehydrogenase
Reaction: geranial + H₂O + NAD⁺ = geranate + NADH + H⁺
Other name(s): GaDH; *geoB* (gene name)
Systematic name: geranial:NAD⁺ oxidoreductase
Comments: Does not act on neral.
References: [4242, 2312]

[EC 1.2.1.86 created 2012]

EC 1.2.1.87

Accepted name: propanal dehydrogenase (CoA-propanoylating)
Reaction: propanal + CoA + NAD⁺ = propanoyl-CoA + NADH + H⁺
Other name(s): BphJ
Systematic name: propanal:NAD⁺ oxidoreductase (CoA-propanoylating)
Comments: The enzyme forms a bifunctional complex with EC 4.1.3.43, 4-hydroxy-2-oxohexanoate aldolase, with a tight channel connecting the two subunits [1,2,3]. Also acts, more slowly, on glycolaldehyde and butanal. In *Pseudomonas* species the enzyme forms a bifunctional complex with EC 4.1.3.39, 4-hydroxy-2-oxovalerate aldolase. The enzymes from the bacteria *Burkholderia xenovorans* and *Thermus thermophilus* also perform the reaction of EC 1.2.1.10, acetaldehyde dehydrogenase (acetylating). NADP⁺ can replace NAD⁺ with a much slower rate [177].
References: [178, 503, 177]

[EC 1.2.1.87 created 2013]

EC 1.2.1.88

Accepted name: L-glutamate γ -semialdehyde dehydrogenase
Reaction: L-glutamate 5-semialdehyde + NAD⁺ + H₂O = L-glutamate + NADH + H⁺
Other name(s): 1-pyrroline-5-carboxylate dehydrogenase; Δ^1 -pyrroline-5-carboxylate dehydrogenase; 1-pyrroline dehydrogenase; pyrroline-5-carboxylate dehydrogenase; pyrroline-5-carboxylic acid dehydrogenase; L-pyrroline-5-carboxylate-NAD⁺ oxidoreductase; 1-pyrroline-5-carboxylate:NAD⁺ oxidoreductase; Δ^1 -pyrroline-5-carboxylic acid dehydrogenase
Systematic name: L-glutamate γ -semialdehyde:NAD⁺ oxidoreductase
Comments: This enzyme catalyses the irreversible oxidation of glutamate- γ -semialdehyde to glutamate as part of the proline degradation pathway. (*S*)-1-pyrroline-5-carboxylate, the product of the first enzyme of the pathway (EC 1.5.5.2, proline dehydrogenase) is in spontaneous equilibrium with its tautomer L-glutamate γ -semialdehyde. In many bacterial species, both activities are carried out by a single bifunctional enzyme [1034, 416]. The enzyme can also oxidize other 1-pyrrolines, e.g. 3-hydroxy-1-pyrroline-5-carboxylate is converted into 4-hydroxyglutamate and (*R*)-1-pyrroline-5-carboxylate is converted into D-glutamate. NADP⁺ can also act as acceptor, but with lower activity [1646].
References: [21, 3673, 1034, 416, 1646]

[EC 1.2.1.88 created 1972 as EC 1.5.1.12, modified 2008, transferred 2013 to EC 1.2.1.88]

EC 1.2.1.89

Accepted name: D-glyceraldehyde dehydrogenase (NADP⁺)
Reaction: D-glyceraldehyde + NADP⁺ + H₂O = D-glycerate + NADPH + H⁺
Other name(s): glyceraldehyde dehydrogenase; GADH
Systematic name: D-glyceraldehyde:NADP⁺ oxidoreductase
Comments: The enzyme from the archaea *Thermoplasma acidophilum* and *Picrophilus torridus* is involved in the non-phosphorylative Entner-Doudoroff pathway. *cf.* EC 1.2.99.8, glyceraldehyde dehydrogenase (FAD-containing).

References: [1784, 3158]

[EC 1.2.1.89 created 2014]

EC 1.2.1.90

Accepted name: glyceraldehyde-3-phosphate dehydrogenase [NAD(P)⁺]
Reaction: D-glyceraldehyde 3-phosphate + NAD(P)⁺ + H₂O = 3-phospho-D-glycerate + NAD(P)H + 2 H⁺
Other name(s): non-phosphorylating glyceraldehyde-3-phosphate dehydrogenase; GAPN
Systematic name: D-glyceraldehyde-3-phosphate:NAD(P)⁺ oxidoreductase
Comments: The enzyme is part of the modified Embden-Meyerhof-Parnas pathway of the archaeon *Thermoproteus tenax*. cf. EC 1.2.1.9 [glyceraldehyde-3-phosphate dehydrogenase (NADP⁺)].
References: [430, 431, 3026, 2298]

[EC 1.2.1.90 created 2014]

EC 1.2.1.91

Accepted name: 3-oxo-5,6-dehydrosuberyl-CoA semialdehyde dehydrogenase
Reaction: 3-oxo-5,6-dehydrosuberyl-CoA semialdehyde + NADP⁺ + H₂O = 3-oxo-5,6-dehydrosuberyl-CoA + NADPH + H⁺
Other name(s): *paaZ* (gene name)
Systematic name: 3-oxo-5,6-dehydrosuberyl-CoA semialdehyde:NADP⁺ oxidoreductase
Comments: The enzyme from *Escherichia coli* is a bifunctional fusion protein that also catalyses EC 3.3.2.12, oxepin-CoA hydrolase. Combined the two activities result in a two-step conversion of oxepin-CoA to 3-oxo-5,6-dehydrosuberyl-CoA, part of an aerobic phenylacetate degradation pathway.
References: [1001, 1673, 3853]

[EC 1.2.1.91 created 2011 as EC 1.17.1.7, transferred 2014 to EC 1.2.1.91]

EC 1.2.1.92

Accepted name: 3,6-anhydro- α -L-galactose dehydrogenase
Reaction: 3,6-anhydro- α -L-galactopyranose + NAD(P)⁺ + H₂O = 3,6-anhydro-L-galactonate + NAD(P)H + H⁺
Systematic name: 3,6-anhydro- α -L-galactopyranose:NAD(P)⁺ 1-oxidoreductase
Comments: The enzyme, characterized from the marine bacterium *Vibrio* sp. EJY3, is involved in a degradation pathway for 3,6-anhydro- α -L-galactose, a major component of the polysaccharides produced by red macroalgae, such as agarose and porphyran.
References: [4413]

[EC 1.2.1.92 created 2014]

[1.2.1.93 Transferred entry. formate dehydrogenase (NAD⁺, ferredoxin). Now EC 1.17.1.11, formate dehydrogenase (NAD⁺, ferredoxin)]

[EC 1.2.1.93 created 2015, deleted 2017]

EC 1.2.1.94

Accepted name: farnesal dehydrogenase
Reaction: (2E,6E)-farnesal + NAD⁺ + H₂O = (2E,6E)-farnesoate + NADH + 2 H⁺
Other name(s): AaALDH3
Systematic name: farnesal:NAD⁺ oxidoreductase
Comments: Involved in juvenile hormone production in insects. The enzyme was described from the corpora allata of *Drosophila melanogaster* (fruit fly), *Manduca sexta* (tobacco hornworm) and *Aedes aegypti* (dengue mosquito).
References: [2354, 175, 3197]

[EC 1.2.1.94 created 2015]

EC 1.2.1.95

- Accepted name:** L-2-aminoadipate reductase
Reaction: (S)-2-amino-6-oxohexanoate + NADP⁺ + AMP + diphosphate = L-2-aminoadipate + NADPH + H⁺ + ATP (overall reaction)
(1a) L-2-aminoadipyl-[LYS2 peptidyl-carrier-protein] + AMP + diphosphate = L-2-aminoadipate + holo-[LYS2 peptidyl-carrier-protein] + ATP
(1b) (S)-2-amino-6-oxohexanoate + holo-[LYS2 peptidyl-carrier-protein] + NADP⁺ = L-2-aminoadipyl-[LYS2 peptidyl-carrier-protein] + NADPH + H⁺
Other name(s): LYS2; α-aminoadipate reductase
Systematic name: (S)-2-amino-6-oxohexanoate:NADP⁺ oxidoreductase (ATP-forming)
Comments: This enzyme, characterized from the yeast *Saccharomyces cerevisiae*, catalyses the reduction of L-2-aminoadipate to (S)-2-amino-6-oxohexanoate during L-lysine biosynthesis. An adenylation domain activates the substrate at the expense of ATP hydrolysis, and forms L-2-aminoadipate adenylate, which is attached to a peptidyl-carrier protein (PCP) domain. Binding of NADPH results in reductive cleavage of the acyl-S-enzyme intermediate, releasing (S)-2-amino-6-oxohexanoate. Different from EC 1.2.1.31, L-aminoadipate-semialdehyde dehydrogenase, which catalyses a similar transformation in the opposite direction without ATP hydrolysis.
References: [927]

[EC 1.2.1.95 created 2015]

EC 1.2.1.96

- Accepted name:** 4-hydroxybenzaldehyde dehydrogenase (NADP⁺)
Reaction: 4-hydroxybenzaldehyde + NADP⁺ + H₂O = 4-hydroxybenzoate + NADPH + 2 H⁺
Other name(s): p-hydroxybenzaldehyde dehydrogenase (ambiguous); *pchA* (gene name)
Systematic name: 4-hydroxybenzaldehyde:NADP⁺ oxidoreductase
Comments: Involved in the aerobic pathway for degradation of toluene, 4-methylphenol, and 2,4-xyleneol by several *Pseudomonas* strains. The enzyme is also active with 4-hydroxy-3-methylbenzaldehyde. *cf.* EC 1.2.1.64, 4-hydroxybenzaldehyde dehydrogenase (NAD⁺).
References: [4192, 578]

[EC 1.2.1.96 created 2015]

EC 1.2.1.97

- Accepted name:** 3-sulfolactaldehyde dehydrogenase
Reaction: (2S)-3-sulfolactaldehyde + NAD(P)⁺ + H₂O = (2S)-3-sulfolactate + NAD(P)H + H⁺
Other name(s): SLA dehydrogenase
Systematic name: (2S)-3-sulfolactaldehyde:NAD(P)⁺ oxidoreductase
Comments: The enzyme, characterized from the bacterium *Pseudomonas putida* SQ1, participates in a sulfoquinovose degradation pathway. Also acts on succinate semialdehyde.
References: [994]

[EC 1.2.1.97 created 2015]

EC 1.2.1.98

- Accepted name:** 2-hydroxy-2-methylpropanal dehydrogenase
Reaction: 2-hydroxy-2-methylpropanal + NAD⁺ + H₂O = 2-hydroxy-2-methylpropanoate + NADH + H⁺
Other name(s): *mpdC* (gene name)
Systematic name: 2-hydroxy-2-methylpropanal:NAD⁺ oxidoreductase
Comments: This bacterial enzyme is involved in the degradation pathways of the alkene 2-methylpropene and the fuel additive *tert*-butyl methyl ether (MTBE), a widely occurring groundwater contaminant.
References: [1004]

[EC 1.2.1.98 created 2016]

EC 1.2.1.99

- Accepted name:** 4-(γ -glutamylamino)butanal dehydrogenase
Reaction: 4-(γ -L-glutamylamino)butanal + NAD(P)⁺ + H₂O = 4-(γ -L-glutamylamino)butanoate + NAD(P)H + H⁺
Other name(s): *puuC* (gene name)
Systematic name: 4-(γ -L-glutamylamino)butanal:NAD(P)⁺ oxidoreductase
Comments: The enzyme, characterized from the bacterium *Escherichia coli*, is involved in a putrescine catabolic pathway. It has a broad substrate range, and can also catalyse the activities of EC 1.2.1.19, aminobutyraldehyde dehydrogenase, and EC 1.2.1.24, succinate-semialdehyde dehydrogenase (NAD⁺).
References: [2090, 1748, 3380]

[EC 1.2.1.99 created 2017]

EC 1.2.1.100

- Accepted name:** 5-formyl-3-hydroxy-2-methylpyridine 4-carboxylic acid 5-dehydrogenase
Reaction: 5-formyl-3-hydroxy-2-methylpyridine-4-carboxylate + NAD⁺ + H₂O = 3-hydroxy-2-methylpyridine-4,5-dicarboxylate + NADH + H⁺
Other name(s): mlr6793 (locus name)
Systematic name: 5-formyl-3-hydroxy-2-methylpyridine-4-carboxylate:NAD⁺ 5-oxidoreductase
Comments: The enzyme, characterized from the bacteria *Pseudomonas* sp. MA-1 and *Mesorhizobium loti*, participates in the degradation of pyridoxine (vitamin B₆).
References: [2183, 4363, 2646]

[EC 1.2.1.100 created 2018]

EC 1.2.1.101

- Accepted name:** L-tyrosine reductase
Reaction: L-tyrosinal + NADP⁺ + AMP + diphosphate = L-tyrosine + NADPH + H⁺ + ATP
Other name(s): *InaA* (gene name); *InbA* (gene name)
Systematic name: (2S)-2-amino-3-(4-hydroxyphenyl)propanal:NADP⁺ oxidoreductase (ATP-forming)
Comments: The enzyme, characterized from the ascomycete fungus *Aspergillus flavus*, is specific for L-tyrosine. It contains three domains - an adenylation domain, a peptidyl-carrier protein (PCP) domain, and a reductase domain, and requires activation by attachment of a phosphopantetheinyl group. The enzyme activates its substrate to an adenylate form, followed by a transfer to the PCP domain. The resulting thioester is subsequently transferred to the reductase domain, where it is reduced to the aldehyde.
References: [1039]

[EC 1.2.1.101 created 2018]

EC 1.2.1.102

- Accepted name:** isopyridoxal dehydrogenase (5-pyridoxate-forming)
Reaction: isopyridoxal + NAD⁺ + H₂O = 5-pyridoxate + NADH + H⁺
Systematic name: isopyridoxal:NAD⁺ oxidoreductase (5-pyridoxate-forming)
Comments: The enzyme, characterized from the bacterium *Arthrobacter* sp. Cr-7, participates in the degradation of pyridoxine. The enzyme also catalyses the activity of EC 1.1.1.416, isopyridoxal dehydrogenase (5-pyridoxolactone-forming).
References: [2183]

[EC 1.2.1.102 created 2018]

EC 1.2.2 With a cytochrome as acceptor

EC 1.2.2.1

Accepted name: formate dehydrogenase (cytochrome)
Reaction: formate + 2 ferricytochrome b_1 = CO₂ + 2 ferrocycytochrome b_1 + 2 H⁺
Other name(s): formate dehydrogenase; formate:cytochrome b_1 oxidoreductase
Systematic name: formate:ferricytochrome- b_1 oxidoreductase
References: [1142]

[EC 1.2.2.1 created 1961]

[1.2.2.2 Deleted entry. pyruvate dehydrogenase (cytochrome). Now covered by EC 1.2.5.1, pyruvate dehydrogenase (quinone)]

[EC 1.2.2.2 created 1961, deleted 2010]

[1.2.2.3 Transferred entry. formate dehydrogenase (cytochrome-c-553). Now EC 1.17.2.3, formate dehydrogenase (cytochrome-c-553)]

[EC 1.2.2.3 created 1981, deleted 2017]

EC 1.2.2.4

Accepted name: carbon-monoxide dehydrogenase (cytochrome b -561)
Reaction: CO + H₂O + 2 ferricytochrome b -561 = CO₂ + 2 H⁺ + 2 ferrocycytochrome b -561
Other name(s): carbon monoxide oxidase; carbon monoxide oxygenase (cytochrome b -561); carbon monoxide:methylene blue oxidoreductase; CO dehydrogenase; carbon-monoxide dehydrogenase
Systematic name: carbon monoxide,water:cytochrome b -561 oxidoreductase
Comments: Contains molybdopterin cytosine dinucleotide, FAD and [2Fe-2S]-clusters. Oxygen, methylene blue and iodinitrotetrazolium chloride can act as nonphysiological electron acceptors.
References: [2518, 1706, 2519, 844, 1384]

[EC 1.2.2.4 created 1999 (EC 1.2.3.10 created 1990, incorporated 2003), modified 2003]

EC 1.2.3 With oxygen as acceptor

EC 1.2.3.1

Accepted name: aldehyde oxidase
Reaction: an aldehyde + H₂O + O₂ = a carboxylate + H₂O₂
Other name(s): quinoline oxidase; retinal oxidase
Systematic name: aldehyde:oxygen oxidoreductase
Comments: Contains molybdenum, [2Fe-2S] centres and FAD. The enzyme from liver exhibits a broad substrate specificity, and is involved in the metabolism of xenobiotics, including the oxidation of N -heterocycles and aldehydes and the reduction of N -oxides, nitrosamines, hydroxamic acids, azo dyes, nitropolycyclic aromatic hydrocarbons, and sulfoxides [2057, 4383]. The enzyme is also responsible for the oxidation of retinal, an activity that was initially attributed to a distinct enzyme (EC 1.2.3.11, retinal oxidase) [3904, 1591].
References: [1245, 1979, 2368, 2057, 3904, 4383, 1591, 3955]

[EC 1.2.3.1 created 1961, modified 2002, modified 2004, modified 2012]

[1.2.3.2 Transferred entry. xanthine oxidase. Now EC 1.17.3.2, xanthine oxidase]

[EC 1.2.3.2 created 1961, deleted 1984]

EC 1.2.3.3

Accepted name: pyruvate oxidase
Reaction: pyruvate + phosphate + O₂ = acetyl phosphate + CO₂ + H₂O₂
Other name(s): pyruvic oxidase; phosphate-dependent pyruvate oxidase
Systematic name: pyruvate:oxygen 2-oxidoreductase (phosphorylating)
Comments: A flavoprotein (FAD) requiring thiamine diphosphate. Two reducing equivalents are transferred from the resonant carbanion/enamine forms of 2-hydroxyethyl-thiamine-diphosphate to the adjacent flavin cofactor, yielding 2-acetyl-thiamine diphosphate (AcThDP) and reduced flavin. FADH₂ is reoxidized by O₂ to yield H₂O₂ and FAD and AcThDP is cleaved phosphorolytically to acetyl phosphate and thiamine diphosphate [3898].
References: [4218, 3898]

[EC 1.2.3.3 created 1961]

EC 1.2.3.4

Accepted name: oxalate oxidase
Reaction: oxalate + O₂ + 2 H⁺ = 2 CO₂ + H₂O₂
Other name(s): aero-oxalo dehydrogenase; oxalic acid oxidase
Systematic name: oxalate:oxygen oxidoreductase
Comments: Contains Mn²⁺ as a cofactor. The enzyme is not a flavoprotein as had been thought [3171].
References: [748, 2043, 3171]

[EC 1.2.3.4 created 1961]

EC 1.2.3.5

Accepted name: glyoxylate oxidase
Reaction: glyoxylate + H₂O + O₂ = oxalate + H₂O₂
Systematic name: glyoxylate:oxygen oxidoreductase
References: [1825]

[EC 1.2.3.5 created 1972]

EC 1.2.3.6

Accepted name: pyruvate oxidase (CoA-acetylating)
Reaction: pyruvate + CoA + O₂ = acetyl-CoA + CO₂ + H₂O₂
Systematic name: pyruvate:oxygen 2-oxidoreductase (CoA-acetylating)
Comments: A flavoprotein (FAD). May be identical with EC 1.2.7.1 pyruvate synthase.
References: [3157, 3793]

[EC 1.2.3.6 created 1976]

EC 1.2.3.7

Accepted name: indole-3-acetaldehyde oxidase
Reaction: (indol-3-yl)acetaldehyde + H₂O + O₂ = (indol-3-yl)acetate + H₂O₂
Other name(s): indoleacetaldehyde oxidase; IAALd oxidase; AO1; indole-3-acetaldehyde:oxygen oxidoreductase
Systematic name: (indol-3-yl)acetaldehyde:oxygen oxidoreductase
Comments: A hemoprotein. This enzyme is an isoform of aldehyde oxidase (EC 1.2.3.1). It has a preference for aldehydes having an indole-ring structure as substrate [3436, 3440]. It may play a role in plant hormone biosynthesis as its activity is higher in the auxin-overproducing mutant, *super-root1*, than in wild-type *Arabidopsis thaliana* [3440]. While (indol-3-yl)acetaldehyde is the preferred substrate, it also oxidizes indole-3-carbaldehyde and acetaldehyde, but more slowly. The enzyme from maize contains FAD, iron and molybdenum [2037].
References: [372, 2573, 3110, 2037, 2036, 3436, 3440]

[EC 1.2.3.7 created 1984, modified 2004, modified 2006]

EC 1.2.3.8

Accepted name: pyridoxal oxidase
Reaction: pyridoxal + H₂O + O₂ = 4-pyridoxate + (?)
Systematic name: pyridoxal:oxygen 4-oxidoreductase
Comments: A molybdenum protein.
References: [1370, 4136]

[EC 1.2.3.8 created 1984]

EC 1.2.3.9

Accepted name: aryl-aldehyde oxidase
Reaction: an aromatic aldehyde + O₂ + H₂O = an aromatic carboxylate + H₂O₂
Systematic name: aryl-aldehyde:oxygen oxidoreductase
Comments: Acts on benzaldehyde, vanillin and a number of other aromatic aldehydes, but not on aliphatic aldehydes or sugars.
References: [692]

[EC 1.2.3.9 created 1986, modified 2002]

[1.2.3.10 Deleted entry. carbon-monoxide oxidase. Activity due to EC 1.2.2.4 carbon-monoxide dehydrogenase (cytochrome b-561)]

[EC 1.2.3.10 created 1990, deleted 2003]

[1.2.3.11 Deleted entry. retinal oxidase. Now included with EC 1.2.3.1, aldehyde oxidase]

[EC 1.2.3.11 created 1990, modified 2002, deleted 2011]

[1.2.3.12 Transferred entry. vanillate demethylase. Now EC 1.14.13.82, vanillate monooxygenase]

[EC 1.2.3.12 created 2000, deleted 2003]

EC 1.2.3.13

Accepted name: 4-hydroxyphenylpyruvate oxidase
Reaction: 2 4-hydroxyphenylpyruvate + O₂ = 2 4-hydroxyphenylacetate + 2 CO₂
Systematic name: 4-hydroxyphenylpyruvate:oxygen oxidoreductase (decarboxylating)
Comments: Involved in tyrosine degradation pathway in *Arthrobacter sp.*
References: [313]

[EC 1.2.3.13 created 2000]

EC 1.2.3.14

Accepted name: abscisic-aldehyde oxidase
Reaction: abscisic aldehyde + H₂O + O₂ = abscisate + H₂O₂
Other name(s): abscisic aldehyde oxidase; AAO3; AOd; AOδ
Systematic name: abscisic-aldehyde:oxygen oxidoreductase
Comments: Acts on both (+)- and (-)-abscisic aldehyde. Involved in the abscisic-acid biosynthesis pathway in plants, along with EC 1.1.1.288, (xanthoxin dehydrogenase), EC 1.13.11.51 (9-*cis*-epoxycarotenoid dioxygenase) and EC 1.14.13.93 [(+)-abscisic acid 8'-hydroxylase]. While abscisic aldehyde is the best substrate, the enzyme also acts with indole-3-aldehyde, 1-naphthaldehyde and benzaldehyde as substrates, but more slowly [3441].
References: [3281, 3442, 3441]

[EC 1.2.3.14 created 2005]

EC 1.2.3.15

- Accepted name:** (methyl)glyoxal oxidase
Reaction: (1) glyoxal + H₂O + O₂ = glyoxylate + H₂O₂
(2) 2-oxopropanal + H₂O + O₂ = pyruvate + H₂O₂
Other name(s): glx1 (gene name); glx2 (gene name)
Systematic name: (methyl)glyoxal:oxygen oxidoreductase
Comments: The enzyme, originally characterized from the white rot fungus *Phanerochaete chrysosporium*, utilizes a free radical-coupled copper complex for catalysis.
References: [1886, 1885, 1888, 4198]

[EC 1.2.3.15 created 2016]

EC 1.2.4 With a disulfide as acceptor

EC 1.2.4.1

- Accepted name:** pyruvate dehydrogenase (acetyl-transferring)
Reaction: pyruvate + [dihydrolipoyllysine-residue acetyltransferase] lipoyllysine = [dihydrolipoyllysine-residue acetyltransferase] S-acetyldihydrolipoyllysine + CO₂
Other name(s): *MtPDC* (mitochondrial pyruvate dehydrogenase complex); pyruvate decarboxylase; pyruvate dehydrogenase; pyruvate dehydrogenase (lipoamide); pyruvate dehydrogenase complex; pyruvate:lipoamide 2-oxidoreductase (decarboxylating and acceptor-acetylating); pyruvic acid dehydrogenase; pyruvic dehydrogenase
Systematic name: pyruvate:[dihydrolipoyllysine-residue acetyltransferase]-lipoyllysine 2-oxidoreductase (decarboxylating, acceptor-acetylating)
Comments: Contains thiamine diphosphate. It is a component (in multiple copies) of the multienzyme pyruvate dehydrogenase complex in which it is bound to a core of molecules of EC 2.3.1.12, dihydrolipoyllysine-residue acetyltransferase, which also binds multiple copies of EC 1.8.1.4, dihydrolipoyl dehydrogenase. It does not act on free lipoamide or lipoyllysine, but only on the lipoyllysine residue in EC 2.3.1.12.
References: [2838, 3419, 2983]

[EC 1.2.4.1 created 1961, modified 2003]

EC 1.2.4.2

- Accepted name:** oxoglutarate dehydrogenase (succinyl-transferring)
Reaction: 2-oxoglutarate + [dihydrolipoyllysine-residue succinyltransferase] lipoyllysine = [dihydrolipoyllysine-residue succinyltransferase] S-succinyldihydrolipoyllysine + CO₂
Other name(s): 2-ketoglutarate dehydrogenase; 2-oxoglutarate dehydrogenase; 2-oxoglutarate:lipoate oxidoreductase; 2-oxoglutarate:lipoamide 2-oxidoreductase (decarboxylating and acceptor-succinylating); α-ketoglutarate dehydrogenase; αketoglutaric acid dehydrogenase; α-ketoglutaric dehydrogenase; α-oxoglutarate dehydrogenase; AKGDH; OGDC; ketoglutaric dehydrogenase; oxoglutarate decarboxylase; oxoglutarate dehydrogenase; oxoglutarate dehydrogenase (lipoamide)
Systematic name: 2-oxoglutarate:[dihydrolipoyllysine-residue succinyltransferase]-lipoyllysine 2-oxidoreductase (decarboxylating, acceptor-succinylating)
Comments: Contains thiamine diphosphate. It is a component of the multienzyme 2-oxoglutarate dehydrogenase complex in which multiple copies of it are bound to a core of molecules of EC 2.3.1.61, dihydrolipoyllysine-residue succinyltransferase, which also binds multiple copies of EC 1.8.1.4, dihydrolipoyl dehydrogenase. It does not act on free lipoamide or lipoyllysine, but only on the lipoyllysine residue in EC 2.3.1.61.
References: [2431, 2838, 3302, 2983]

[EC 1.2.4.2 created 1961, modified 1980, modified 1986, modified 2003]

[1.2.4.3 Deleted entry. 2-oxoisocaproate dehydrogenase. Now included with EC 1.2.4.4, 3-methyl-2-oxobutanoate dehydrogenase (2-methylpropanoyl-transferring)]

[EC 1.2.4.3 created 1972, deleted 1978]

EC 1.2.4.4

- Accepted name:** 3-methyl-2-oxobutanoate dehydrogenase (2-methylpropanoyl-transferring)
- Reaction:** 3-methyl-2-oxobutanoate + [dihydrolipoyllysine-residue (2-methylpropanoyl)transferase] lipoyllysine = [dihydrolipoyllysine-residue (2-methylpropanoyl)transferase] S-(2-methylpropanoyl)dihydrolipoyllysine + CO₂
- Other name(s):** 2-oxoisocaproate dehydrogenase; 2-oxoisovalerate (lipoate) dehydrogenase; 3-methyl-2-oxobutanoate dehydrogenase (lipoamide); 3-methyl-2-oxobutanoate:lipoamide oxidoreductase (decarboxylating and acceptor-2-methylpropanoylating); α -keto- α -methylvalerate dehydrogenase; α -ketoisocaproate dehydrogenase; α -ketoisocaproic dehydrogenase; α -ketoisocaproic- α -keto- α -methylvaleric dehydrogenase; α -ketoisovalerate dehydrogenase; α -oxoisocaproate dehydrogenase; BCKDH; BCOAD; branched chain keto acid dehydrogenase; branched-chain (-2-oxoacid) dehydrogenase (BCD); branched-chain 2-keto acid dehydrogenase; branched-chain 2-oxo acid dehydrogenase; branched-chain α -keto acid dehydrogenase; branched-chain α -oxo acid dehydrogenase; branched-chain keto acid dehydrogenase; branched-chain ketoacid dehydrogenase; dehydrogenase, 2-oxoisovalerate (lipoate); dehydrogenase, branched chain α -keto acid
- Systematic name:** 3-methyl-2-oxobutanoate:[dihydrolipoyllysine-residue (2-methylpropanoyl)transferase]-lipoyllysine 2-oxidoreductase (decarboxylating, acceptor-2-methylpropanoylating)
- Comments:** Contains thiamine diphosphate. It acts not only on 3-methyl-2-oxobutanoate, but also on 4-methyl-2-oxopentanoate and (S)-3-methyl-2-oxopentanoate, so that it acts on the 2-oxo acids that derive from the action of transaminases on valine, leucine and isoleucine. It is a component of the multienzyme 3-methyl-2-oxobutanoate dehydrogenase complex in which multiple copies of it are bound to a core of molecules of EC 2.3.1.168, dihydrolipoyllysine-residue (2-methylpropanoyl)transferase, which also binds multiple copies of EC 1.8.1.4, dihydrolipoyl dehydrogenase. It does not act on free lipoamide or lipoyllysine, but only on the lipoyllysine residue in EC 2.3.1.168.
- References:** [371, 649, 745, 2996, 2983]

[EC 1.2.4.4 created 1972 (EC 1.2.4.3 created 1972, incorporated 1978), modified 2003]

EC 1.2.5 With a quinone or similar compound as acceptor

EC 1.2.5.1

- Accepted name:** pyruvate dehydrogenase (quinone)
- Reaction:** pyruvate + ubiquinone + H₂O = acetate + CO₂ + ubiquinol
- Other name(s):** pyruvate dehydrogenase; pyruvic dehydrogenase; pyruvic (cytochrome *b*₁) dehydrogenase; pyruvate:ubiquinone-8-oxidoreductase; pyruvate oxidase (ambiguous); pyruvate dehydrogenase (cytochrome) (incorrect)
- Systematic name:** pyruvate:ubiquinone oxidoreductase
- Comments:** Flavoprotein (FAD) [3144]. This bacterial enzyme is located on the inner surface of the cytoplasmic membrane and coupled to the respiratory chain via ubiquinone [707, 2013]. Does not accept menaquinone. Activity is greatly enhanced by lipids [4,5,6]. Requires thiamine diphosphate [2837]. The enzyme can also form acetoin [276].
- References:** [3144, 707, 2013, 465, 4102, 4415, 2837, 276]

[EC 1.2.5.1 created 2010]

EC 1.2.5.2

- Accepted name:** aldehyde dehydrogenase (quinone)

Reaction: an aldehyde + a quinone + H₂O = a carboxylate + a quinol
Other name(s): aldehyde dehydrogenase (acceptor)
Systematic name: aldehyde:quinone oxidoreductase
Comments: Wide specificity; acts on straight-chain aldehydes up to C₁₀, aromatic aldehydes, glyoxylate and glyceraldehyde. The enzymes contains a PQQ cofactor and multiple hemes that deliver the electrons to the membrane quinone pool.
References: [70, 74, 2957, 1232]

[EC 1.2.5.2 created 1983 as EC 1.2.99.3, modified 1989, transferred 2015 to EC 1.2.5.2]

EC 1.2.5.3

Accepted name: aerobic carbon monoxide dehydrogenase
Reaction: CO + a quinone + H₂O = CO₂ + a quinol
Other name(s): MoCu-CODH; coxSML (gene names); molybdoenzyme carbon monoxide dehydrogenase
Systematic name: carbon-monoxide:quinone oxidoreductase
Comments: This enzyme, found in carboxydophilic bacteria, catalyses the oxidation of CO to CO₂ under aerobic conditions. The enzyme contains a binuclear Mo-Cu cluster in which the copper is ligated to a molybdopterin center via a sulfur bridge. The enzyme also contains two [2Fe-2S] clusters and FAD, and belongs to the xanthine oxidoreductase family. The CO₂ that is produced is assimilated by the Calvin-Benson-Basham cycle, while the electrons are transferred to a quinone via the FAD site, and continue through the electron transfer chain to a dioxygen terminal acceptor [4213]. *cf.* EC 1.2.7.4, anaerobic carbon monoxide dehydrogenase.
References: [1280, 843, 1226, 3172, 4213, 2978, 1503]

[EC 1.2.5.3 created 2016]

EC 1.2.7 With an iron-sulfur protein as acceptor

EC 1.2.7.1

Accepted name: pyruvate synthase
Reaction: pyruvate + CoA + 2 oxidized ferredoxin = acetyl-CoA + CO₂ + 2 reduced ferredoxin + 2 H⁺
Other name(s): pyruvate oxidoreductase; pyruvate synthetase; pyruvate:ferredoxin oxidoreductase; pyruvic-ferredoxin oxidoreductase; 2-oxobutyrate synthase; α-ketobutyrate-ferredoxin oxidoreductase; 2-ketobutyrate synthase; α-ketobutyrate synthase; 2-oxobutyrate-ferredoxin oxidoreductase; 2-oxobutanoate:ferredoxin 2-oxidoreductase (CoA-propionylating); 2-oxobutanoate:ferredoxin 2-oxidoreductase (CoA-propanoylating)
Systematic name: pyruvate:ferredoxin 2-oxidoreductase (CoA-acetylating)
Comments: Contains thiamine diphosphate and [4Fe-4S] clusters. The enzyme also decarboxylates 2-oxobutyrate with lower efficiency, but shows no activity with 2-oxoglutarate. 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 examples of other members of this family, see EC 1.2.7.3, 2-oxoglutarate synthase and EC 1.2.7.7, 3-methyl-2-oxobutanoate dehydrogenase (ferredoxin).
References: [970, 1177, 3978, 3979, 551]

[EC 1.2.7.1 created 1972, modified 2003, modified 2013]

[1.2.7.2 Deleted entry. 2-oxobutyrate synthase. Now included with EC 1.2.7.1, pyruvate synthase.]

[EC 1.2.7.2 created 1972, deleted 2013]

EC 1.2.7.3

Accepted name: 2-oxoglutarate synthase
Reaction: 2-oxoglutarate + CoA + 2 oxidized ferredoxin = succinyl-CoA + CO₂ + 2 reduced ferredoxin + 2 H⁺

Other name(s): 2-ketoglutarate ferredoxin oxidoreductase; 2-oxoglutarate:ferredoxin oxidoreductase; KGOR; 2-oxoglutarate ferredoxin oxidoreductase; 2-oxoglutarate:ferredoxin 2-oxidoreductase (CoA-succinylating)

Systematic name: 2-oxoglutarate:ferredoxin oxidoreductase (decarboxylating)

Comments: The enzyme contains thiamine diphosphate and two [4Fe-4S] clusters. Highly specific for 2-oxoglutarate. 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 examples of other members of this family, see EC 1.2.7.1, pyruvate synthase and EC 1.2.7.7, 3-methyl-2-oxobutanoate dehydrogenase (ferredoxin).

References: [438, 1177, 858, 2373, 3409]

[EC 1.2.7.3 created 1972, modified 2005]

EC 1.2.7.4

Accepted name: anaerobic carbon-monoxide dehydrogenase

Reaction: $\text{CO} + \text{H}_2\text{O} + 2 \text{ oxidized ferredoxin} = \text{CO}_2 + 2 \text{ reduced ferredoxin} + 2 \text{ H}^+$

Other name(s): Ni-CODH; carbon-monoxide dehydrogenase (ferredoxin)

Systematic name: carbon-monoxide,water:ferredoxin oxidoreductase

Comments: This prokaryotic enzyme catalyses the reversible reduction of CO_2 to CO. The electrons are transferred to redox proteins such as ferredoxin. In purple sulfur bacteria and methanogenic archaea it catalyses the oxidation of CO to CO_2 , which is incorporated by the Calvin-Benson-Basham cycle or released, respectively. In acetogenic and sulfate-reducing microbes it catalyses the reduction of CO_2 to CO, which is incorporated into acetyl CoA by EC 2.3.1.169, CO-methylating acetyl CoA synthase, with which the enzyme forms a tight complex in those organisms. The enzyme contains five metal clusters per homodimeric enzyme: two nickel-iron-sulfur clusters called the C-Clusters, one [4Fe-4S] D-cluster; and two [4Fe-4S] B-clusters. In methanogenic archaea additional [4Fe-4S] clusters exist, presumably as part of the electron transfer chain. In purple sulfur bacteria the enzyme forms complexes with the Ni-Fe-S protein EC 1.12.7.2, ferredoxin hydrogenase, which catalyse the overall reaction: $\text{CO} + \text{H}_2\text{O} = \text{CO}_2 + \text{H}_2$. *cf.* EC 1.2.5.3, aerobic carbon monoxide dehydrogenase.

References: [3101, 820, 342, 870, 845, 865, 491]

[EC 1.2.7.4 created 2003 (EC 1.2.99.2 created 1982, modified 1990, modified 2003, incorporated 2015), modified 2016]

EC 1.2.7.5

Accepted name: aldehyde ferredoxin oxidoreductase

Reaction: an aldehyde + $\text{H}_2\text{O} + 2 \text{ oxidized ferredoxin} = \text{a carboxylate} + 2 \text{ H}^+ + 2 \text{ reduced ferredoxin}$

Other name(s): AOR

Systematic name: aldehyde:ferredoxin oxidoreductase

Comments: This is an oxygen-sensitive enzyme that contains tungsten-molybdopterin and iron-sulfur clusters. Catalyses the oxidation of aldehydes (including crotonaldehyde, acetaldehyde, formaldehyde and glyceraldehyde) to their corresponding acids. However, it does not oxidize glyceraldehyde 3-phosphate [see EC 1.2.7.6, glyceraldehyde-3-phosphate dehydrogenase (ferredoxin)]. Can use ferredoxin or methylviologen but not NAD(P)^+ as electron acceptor.

References: [2649, 1760, 537, 3244]

[EC 1.2.7.5 created 2003]

EC 1.2.7.6

Accepted name: glyceraldehyde-3-phosphate dehydrogenase (ferredoxin)

Reaction: D-glyceraldehyde-3-phosphate + $\text{H}_2\text{O} + 2 \text{ oxidized ferredoxin} = 3\text{-phospho-D-glycerate} + 2 \text{ H}^+ + 2 \text{ reduced ferredoxin}$

Other name(s): GAPOR; glyceraldehyde-3-phosphate Fd oxidoreductase; glyceraldehyde-3-phosphate ferredoxin reductase

Systematic name: D-glyceraldehyde-3-phosphate:ferredoxin oxidoreductase

Comments: Contains tungsten-molybdopterin and iron-sulfur clusters. This enzyme is thought to function in place of glyceralde-3-phosphate dehydrogenase and possibly phosphoglycerate kinase in the novel Embden-Meyerhof-type glycolytic pathway found in *Pyrococcus furiosus* [2650]. It is specific for glyceraldehyde-3-phosphate.

References: [2650, 3244]

[EC 1.2.7.6 created 2003]

EC 1.2.7.7

Accepted name: 3-methyl-2-oxobutanoate dehydrogenase (ferredoxin)

Reaction: 3-methyl-2-oxobutanoate + CoA + 2 oxidized ferredoxin = *S*-(2-methylpropanoyl)-CoA + CO₂ + 2 reduced ferredoxin + H⁺

Other name(s): 2-ketoisovalerate ferredoxin reductase; 3-methyl-2-oxobutanoate synthase (ferredoxin); VOR; branched-chain ketoacid ferredoxin reductase; branched-chain oxo acid ferredoxin reductase; keto-valine-ferredoxin oxidoreductase; ketoisovalerate ferredoxin reductase; 2-oxoisovalerate ferredoxin reductase

Systematic name: 3-methyl-2-oxobutanoate:ferredoxin oxidoreductase (decarboxylating; CoA-2-methylpropanoylating)

Comments: The enzyme is CoA-dependent and contains thiamine diphosphate and iron-sulfur clusters. Preferentially utilizes 2-oxo-acid derivatives of branched chain amino acids, e.g. 3-methyl-2-oxopentanoate, 4-methyl-2-oxo-pentanoate, and 2-oxobutanoate. This enzyme is a member of the 2-oxoacid oxidoreductases, a family of enzymes that reversibly catalyse the oxidative decarboxylation of different 2-oxoacids to form their CoA derivatives, and are differentiated based on their substrate specificity. For examples of other members of this family, see EC 1.2.7.1, pyruvate synthase, and EC 1.2.7.3, 2-oxoglutarate synthase.

References: [436, 1458, 3851, 3409]

[EC 1.2.7.7 created 2003]

EC 1.2.7.8

Accepted name: indolepyruvate ferredoxin oxidoreductase

Reaction: (indol-3-yl)pyruvate + CoA + 2 oxidized ferredoxin = *S*-2-(indol-3-yl)acetyl-CoA + CO₂ + 2 reduced ferredoxin + H⁺

Other name(s): 3-(indol-3-yl)pyruvate synthase (ferredoxin); IOR

Systematic name: 3-(indol-3-yl)pyruvate:ferredoxin oxidoreductase (decarboxylating, CoA-indole-acetylating)

Comments: Contains thiamine diphosphate and [4Fe-4S] clusters. Preferentially utilizes the transaminated forms of aromatic amino acids and can use phenylpyruvate and *p*-hydroxyphenylpyruvate as substrates. This enzyme, which is found in archaea, 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 examples of other members of this family, see EC 1.2.7.3, 2-oxoglutarate synthase and EC 1.2.7.7, 3-methyl-2-oxobutanoate dehydrogenase (ferredoxin).

References: [2374, 3526, 3851, 3409]

[EC 1.2.7.8 created 2003]

[1.2.7.9 Deleted entry. 2-oxoglutarate ferredoxin oxidoreductase. This enzyme is identical to EC 1.2.7.3, 2-oxoglutarate synthase]

[EC 1.2.7.9 created 2003, deleted 2005]

EC 1.2.7.10

Accepted name: oxalate oxidoreductase

Reaction: oxalate + oxidized ferredoxin = 2 CO₂ + reduced ferredoxin

Systematic name: oxalate:ferredoxin oxidoreductase

Comments: Contains thiamine diphosphate and [4Fe-4S] clusters. Acceptors include ferredoxin and the nickel-dependent carbon monoxide dehydrogenase (EC 1.2.7.4)

References: [743, 3005]

[EC 1.2.7.10 created 2011]

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 [4444]. 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: [1883, 4444, 1104, 1105, 2803, 2941]

[EC 1.2.7.11 created 2013]

EC 1.2.7.12

Accepted name: formylmethanofuran dehydrogenase

Reaction: a formylmethanofuran + H₂O + 2 oxidized ferredoxin [iron-sulfur] cluster = CO₂ + a methanofuran + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺

Other name(s): formylmethanofuran:acceptor oxidoreductase

Systematic name: formylmethanofuran:ferredoxin oxidoreductase

Comments: Contains a molybdopterin cofactor. In some organisms an additional subunit enables the incorporation of tungsten when molybdenum availability is low. The enzyme catalyses a reversible reaction in methanogenic archaea, and is involved in methanogenesis from CO₂ as well as the oxidation of coenzyme M to CO₂. The reaction is endergonic, and is driven by coupling with the soluble CoB-CoM heterodisulfide reductase via electron bifurcation.

References: [1819, 283, 282, 4066, 2515, 1826]

[EC 1.2.7.12 created 1992 as EC 1.2.99.5, transferred 2017 to EC 1.2.7.12]

EC 1.2.98 With an iron-sulfur protein as acceptor

EC 1.2.98.1

Accepted name: formaldehyde dismutase

Reaction: 2 formaldehyde + H₂O = formate + methanol

Other name(s): aldehyde dismutase; cannizzanase; nicotinoprotein aldehyde dismutase

Systematic name: formaldehyde:formaldehyde oxidoreductase

Comments: The enzyme contains a tightly but noncovalently bound NADP(H) cofactor, as well as Zn²⁺ and Mg²⁺. Enzyme-bound NADPH formed by oxidation of formaldehyde to formate is oxidized back to NADP⁺ by reaction with a second formaldehyde, yielding methanol. The enzyme from the bacterium *Mycobacterium* sp. DSM 3803 also catalyses the reactions of EC 1.1.99.36, alcohol dehydrogenase (nicotinoprotein) and EC 1.1.99.37, methanol dehydrogenase (nicotinoprotein) [2940]. Formaldehyde and acetaldehyde can act as donors; formaldehyde, acetaldehyde and propanal can act as acceptors [1837, 1840].

References: [1837, 1840, 2940]

[EC 1.2.98.1 created 1986 as EC 1.2.99.4, modified 2012, transferred 2015 to EC 1.2.98.1]

EC 1.2.99 With unknown physiological acceptors

[1.2.99.1 Transferred entry. *uracil dehydrogenase*. Now EC 1.17.99.4, *uracil/thymine dehydrogenase*]

[EC 1.2.99.1 created 1961, deleted 1984]

[1.2.99.2 Transferred entry. *carbon-monoxide dehydrogenase (acceptor)*. Now EC 1.2.7.4, *carbon-monoxide dehydrogenase (ferredoxin)*]

[EC 1.2.99.2 created 1982, modified 1990, modified 2003, deleted 2016]

[1.2.99.3 Transferred entry. *aldehyde dehydrogenase (pyrroloquinoline-quinone)*. Now EC 1.2.5.2, *aldehyde dehydrogenase (quinone)*]

[EC 1.2.99.3 created 1983, modified 1989, deleted 2015]

[1.2.99.4 Transferred entry. *formaldehyde dismutase*. Now EC 1.2.98.1, *formaldehyde dismutase*.]

[EC 1.2.99.4 created 1986, modified 2012, deleted 2015]

[1.2.99.5 Transferred entry. *formylmethanofuran dehydrogenase*. Now EC 1.2.7.12, *formylmethanofuran dehydrogenase*]

[EC 1.2.99.5 created 1992, deleted 2017]

EC 1.2.99.6

Accepted name: carboxylate reductase
Reaction: an aldehyde + acceptor + H₂O = a carboxylate + reduced acceptor
Other name(s): aldehyde:(acceptor) oxidoreductase
Systematic name: aldehyde:acceptor oxidoreductase
Comments: A tungsten protein. Methylviologen can act as acceptor. In the reverse direction, non-activated acids are reduced by reduced viologens to aldehydes, but not to the corresponding alcohols.
References: [4190]

[EC 1.2.99.6 created 1992]

EC 1.2.99.7

Accepted name: aldehyde dehydrogenase (FAD-independent)
Reaction: an aldehyde + H₂O + acceptor = a carboxylate + reduced acceptor
Other name(s): aldehyde oxidase; aldehyde oxidoreductase; Mop; AORDd
Systematic name: aldehyde:acceptor oxidoreductase (FAD-independent)
Comments: Belongs to the xanthine oxidase family of enzymes. The enzyme from *Desulfovibrio* sp. contains a molybdenum-molybdopterin-cytosine dinucleotide (MCD) complex and two types of [2Fe-2S] cluster per monomer, but does not contain FAD.
References: [3955, 880, 86, 3227]

[EC 1.2.99.7 created 2004]

EC 1.2.99.8

Accepted name: glyceraldehyde dehydrogenase (FAD-containing)
Reaction: D-glyceraldehyde + H₂O + acceptor = D-glycerate + reduced acceptor
Other name(s): glyceraldehyde oxidoreductase
Systematic name: D-glyceraldehyde:acceptor oxidoreductase (FAD-containing)
Comments: The enzyme from the archaeon *Sulfolobus acidocaldarius* catalyses the oxidation of D-glyceraldehyde in the nonphosphorylative Entner-Doudoroff pathway. With 2,6-dichlorophenolindophenol as artificial electron acceptor, the enzyme shows a broad substrate range, but is most active with D-glyceraldehyde. It is not known which acceptor is utilized *in vivo*. The iron-sulfur protein contains FAD and molybdopterin guanine dinucleotide.

References: [1813]

[EC 1.2.99.8 created 2013]

[1.2.99.9 Transferred entry. formate dehydrogenase (coenzyme F₄₂₀). Now EC 1.17.98.3, formate dehydrogenase (coenzyme F₄₂₀)]

[EC 1.2.99.9 created 2014, deleted 2017]

EC 1.2.99.10

Accepted name: 4,4'-diapolycopenoate synthase
Reaction: (1) 4,4'-diapolycopen-4-al + H₂O + acceptor = 4,4'-diapolycopen-4-oate + reduced acceptor
(2) 4,4'-diapolycopen-4,4'-dial + 2 H₂O + 2 acceptor = 4,4'-diapolycopen-4,4'-dioate + 2 reduced acceptor
Other name(s): *crtNc*; 4,4'-diapolycopenaldehyde oxidase (misleading)
Systematic name: 4,4'-diapolycopen-4-al, donor:oxygen oxidoreductase (4,4'-diapolycopen-4-oate-forming)
Comments: The enzyme has been described from the bacteria *Methylomonas* sp. 16a and *Bacillus indicus*.
References: [3821, 3633]

[EC 1.2.99.10 created 2017]

EC 1.3 Acting on the CH-CH group of donors

This subclass contains enzymes that introduce a double-bond into the substrate by direct dehydrogenation at a carbon-carbon single bond. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.3.1), a cytochrome (EC 1.3.2), oxygen (EC 1.3.3), a quinone or related compound (EC 1.3.5), an iron-sulfur protein (EC 1.3.7), a flavin (EC 1.3.8) or some other acceptor (EC 1.3.99).

EC 1.3.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.3.1.1

Accepted name: dihydropyrimidine dehydrogenase (NAD⁺)
Reaction: (1) 5,6-dihydrouracil + NAD⁺ = uracil + NADH + H⁺
(2) 5,6-dihydrothymine + NAD⁺ = thymine + NADH + H⁺
Other name(s): dihydropyrimidine dehydrogenase; dihydrothymine dehydrogenase; pyrimidine reductase; thymine reductase; uracil reductase; dihydrouracil dehydrogenase (NAD⁺)
Systematic name: 5,6-dihydropyrimidine:NAD⁺ oxidoreductase
Comments: An iron-sulfur flavoenzyme. The enzyme was originally discovered in the uracil-fermenting bacterium, *Clostridium uracilicum*, which utilizes uracil and thymine as nitrogen and carbon sources for growth [489]. Since then the enzyme was found in additional organisms including *Alcaligenes eutrophus* [3377], *Pseudomonas* strains [1918, 4182] and *Escherichia coli* [4181, 1492].
References: [489, 3377, 1918, 4182, 4181, 1492]

[EC 1.3.1.1 created 1961, modified 2011]

EC 1.3.1.2

Accepted name: dihydropyrimidine dehydrogenase (NADP⁺)
Reaction: 5,6-dihydrouracil + NADP⁺ = uracil + NADPH + H⁺
Other name(s): dihydrothymine dehydrogenase; dihydrouracil dehydrogenase (NADP⁺); 4,5-dihydrothymine: oxidoreductase; DPD; DHPDH; dehydrogenase, dihydrouracil (nicotinamide adenine dinucleotide phosphate); DHU dehydrogenase; hypopyrimidine dehydrogenase; dihydropyrimidine dehydrogenase (NADP)

Systematic name: 5,6-dihydrouracil:NADP⁺ 5-oxidoreductase
Comments: Also acts on dihydrothymine.
References: [1080, 3516]

[EC 1.3.1.2 created 1961, modified 1986]

EC 1.3.1.3

Accepted name: Δ^4 -3-oxosteroid 5 β -reductase
Reaction: (1) 5 β -cholestan-3-one + NADP⁺ = cholest-4-en-3-one + NADPH + H⁺
(2) 17,21-dihydroxy-5 β -pregnane-3,11,20-trione + NADP⁺ = cortisone + NADPH + H⁺
Other name(s): 3-oxo- Δ^4 -steroid 5 β -reductase; 5 β -reductase; androstenedione 5 β -reductase; cholestenone 5 β -reductase; cortisone 5 β -reductase; cortisone β -reductase; cortisone Δ^4 -5 β -reductase; steroid 5 β -reductase; testosterone 5 β -reductase; Δ^4 -3-ketosteroid 5 β -reductase; Δ^4 -5 β -reductase; Δ^4 -hydrogenase; 4,5 β -dihydrocortisone:NADP⁺ Δ^4 -oxidoreductase; 3-oxo-5 β -steroid:NADP⁺ Δ^4 -oxidoreductase
Systematic name: 5 β -cholestan-3-one:NADP⁺ 4,5-oxidoreductase
Comments: The enzyme from human efficiently catalyses the reduction of progesterone, androstenedione, 17 α -hydroxyprogesterone and testosterone to 5 β -reduced metabolites; it can also act on aldosterone, corticosterone and cortisol, but to a lesser extent [546]. The bile acid intermediates 7 α ,12 α -dihydroxy-4-cholesten-3-one and 7 α -hydroxy-4-cholesten-3-one can also act as substrates [2022].
References: [1031, 419, 2216, 3906, 3712, 1121, 2867, 546, 2022]

[EC 1.3.1.3 created 1961 (EC 1.3.1.23 created 1972, incorporated 2005), modified 2005]

[1.3.1.4 Transferred entry. EC 1.3.1.4, cortisone α -reductase, transferred to EC 1.3.1.22, 3-oxo-5 α -steroid 4-dehydrogenase (NADP⁺)]

[EC 1.3.1.4 created 1965, deleted 2012]

EC 1.3.1.5

Accepted name: cucurbitacin Δ^{23} -reductase
Reaction: 23,24-dihydrocucurbitacin B + NAD(P)⁺ = cucurbitacin B + NAD(P)H + H⁺
Other name(s): NAD(P)H: cucurbitacin B Δ^{23} -oxidoreductase
Systematic name: 23,24-dihydrocucurbitacin:NAD(P)⁺ Δ^{23} -oxidoreductase
Comments: Requires Mn²⁺. Fe²⁺ or Zn²⁺ can replace Mn²⁺ to some extent.
References: [3340, 3342]

[EC 1.3.1.5 created 1965, modified 2011]

EC 1.3.1.6

Accepted name: fumarate reductase (NADH)
Reaction: succinate + NAD⁺ = fumarate + NADH + H⁺
Other name(s): NADH-fumarate reductase; NADH-dependent fumarate reductase; fumarate reductase (NADH₂)
Systematic name: succinate:NAD⁺ oxidoreductase
References: [1558]

[EC 1.3.1.6 created 1972]

EC 1.3.1.7

Accepted name: meso-tartrate dehydrogenase
Reaction: meso-tartrate + NAD⁺ = dihydroxyfumarate + NADH + H⁺
Systematic name: meso-tartrate:NAD⁺ oxidoreductase
References: [2004]

[EC 1.3.1.7 created 1972]

EC 1.3.1.8

- Accepted name:** acyl-CoA dehydrogenase (NADP⁺)
Reaction: acyl-CoA + NADP⁺ = 2,3-dehydroacyl-CoA + NADPH + H⁺
Other name(s): 2-enoyl-CoA reductase; dehydrogenase, acyl coenzyme A (nicotinamide adenine dinucleotide phosphate); enoyl coenzyme A reductase; crotonyl coenzyme A reductase; crotonyl-CoA reductase; acyl-CoA dehydrogenase (NADP⁺)
Systematic name: acyl-CoA:NADP⁺ 2-oxidoreductase
Comments: The liver enzyme acts on enoyl-CoA derivatives of carbon chain length 4 to 16, with optimum activity on 2-hexenoyl-CoA. In *Escherichia coli*, *cis*-specific and *trans*-specific enzymes exist [EC 1.3.1.37 *cis*-2-enoyl-CoA reductase (NADPH) and EC 1.3.1.38 *trans*-2-enoyl-CoA reductase (NADPH)].
References: [853, 3449]

[EC 1.3.1.8 created 1972, modified 1986]

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)
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 [4405]. The FAS-I enzyme from the bacterium *Mycobacterium tuberculosis* prefers substrates with carbon chain length from 12 to 24 carbons.
References: [3496, 4157, 4405]

[EC 1.3.1.9 created 1972, modified 2013]

EC 1.3.1.10

- Accepted name:** enoyl-[acyl-carrier-protein] reductase (NADPH, *Si*-specific)
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 acyl-carrier-protein reductase (ambiguous); enoyl-ACP reductase (ambiguous); acyl-[acyl-carrier-protein]:NADP⁺ oxidoreductase (B-specific); acyl-[acyl-carrier protein]:NADP⁺ oxidoreductase (B-specific); enoyl-[acyl-carrier-protein] reductase (NADPH, B-specific)
Systematic name: acyl-[acyl-carrier protein]:NADP⁺ oxidoreductase (*Si*-specific)
Comments: One of the activities of EC 2.3.1.86, fatty-acyl-CoA synthase system, an enzyme found in yeasts (Ascomycota and Basidiomycota). Catalyses the reduction of enoyl-acyl-[acyl-carrier protein] derivatives of carbon chain length from 4 to 16. The yeast enzyme is *Si*-specific with respect to NADP⁺. *cf.* EC 1.3.1.39, enoyl-[acyl-carrier-protein] reductase (NADPH, *Re*-specific) and EC 1.3.1.104, enoyl-[acyl-carrier-protein] reductase (NADPH), which describes enzymes whose stereo-specificity towards NADPH is not known. See also EC 1.3.1.9, enoyl-[acyl-carrier-protein] reductase (NADH).
References: [3455]

[EC 1.3.1.10 created 1972, modified 1986, modified 2013, modified 2014, modified 2018]

EC 1.3.1.11

Accepted name: 2-coumarate reductase
Reaction: 3-(2-hydroxyphenyl)propanoate + NAD⁺ = 2-coumarate + NADH + H⁺
Other name(s): melilotate dehydrogenase
Systematic name: 3-(2-hydroxyphenyl)propanoate:NAD⁺ oxidoreductase
References: [2215]

[EC 1.3.1.11 created 1972]

EC 1.3.1.12

Accepted name: prephenate dehydrogenase
Reaction: prephenate + NAD⁺ = 4-hydroxyphenylpyruvate + CO₂ + NADH
Other name(s): hydroxyphenylpyruvate synthase; chorismate mutase—prephenate dehydrogenase
Systematic name: prephenate:NAD⁺ oxidoreductase (decarboxylating)
Comments: This enzyme in the enteric bacteria also possesses chorismate mutase activity (EC 5.4.99.5 chorismate mutase) and converts chorismate into prephenate.
References: [1985]

[EC 1.3.1.12 created 1972]

EC 1.3.1.13

Accepted name: prephenate dehydrogenase (NADP⁺)
Reaction: prephenate + NADP⁺ = 4-hydroxyphenylpyruvate + CO₂ + NADPH
Other name(s): prephenate dehydrogenase; prephenate (nicotinamide adenine dinucleotide phosphate) dehydrogenase; prephenate dehydrogenase (NADP)
Systematic name: prephenate:NADP⁺ oxidoreductase (decarboxylating)
References: [1149]

[EC 1.3.1.13 created 1972]

EC 1.3.1.14

Accepted name: dihydroorotate dehydrogenase (NAD⁺)
Reaction: (S)-dihydroorotate + NAD⁺ = orotate + NADH + H⁺
Other name(s): orotate reductase (NADH); orotate reductase (NADH₂); DHODEhase (ambiguous); DHOD (ambiguous); DHODase (ambiguous); dihydroorotate oxidase, *pyrD* (gene name)
Systematic name: (S)-dihydroorotate:NAD⁺ oxidoreductase
Comments: Binds FMN, FAD and a [2Fe-2S] cluster. The enzyme consists of two subunits, an FMN binding catalytic subunit and a FAD and iron-sulfur binding electron transfer subunit [2785]. The reaction, which takes place in the cytosol, is the only redox reaction in the *de-novo* biosynthesis of pyrimidine nucleotides. Other class 1 dihydroorotate dehydrogenases use either fumarate (EC 1.3.98.1) or NADP⁺ (EC 1.3.1.15) as electron acceptor. The membrane bound class 2 dihydroorotate dehydrogenase (EC 1.3.5.2) uses quinone as electron acceptor.
References: [1073, 1074, 2248, 2785, 3242, 1799, 2394]

[EC 1.3.1.14 created 1972, modified 2011]

EC 1.3.1.15

Accepted name: dihydroorotate dehydrogenase (NADP⁺)
Reaction: (S)-dihydroorotate + NADP⁺ = orotate + NADPH + H⁺
Other name(s): orotate reductase; dihydro-orotic dehydrogenase; L-5,6-dihydro-orotate:NAD⁺ oxidoreductase; orotate reductase (NADPH)
Systematic name: (S)-dihydroorotate:NADP⁺ oxidoreductase

Comments: Binds FMN and FAD [3957]. Other class 1 dihydroorotate dehydrogenases use either fumarate (EC 1.3.98.1) or NAD⁺ (EC 1.3.1.14) as electron acceptor. The membrane bound class 2 dihydroorotate dehydrogenase (EC 1.3.5.2) uses quinone as electron acceptor .

References: [3835, 3957]

[EC 1.3.1.15 created 1972, modified 2011]

EC 1.3.1.16

Accepted name: β-nitroacrylate reductase
Reaction: 3-nitropropanoate + NADP⁺ = 3-nitroacrylate + NADPH + H⁺
Systematic name: 3-nitropropanoate:NADP⁺ oxidoreductase
References: [3470]

[EC 1.3.1.16 created 1972]

EC 1.3.1.17

Accepted name: 3-methyleneoxindole reductase
Reaction: 3-methyl-1,3-dihydroindol-2-one + NADP⁺ = 3-methylene-1,3-dihydro-2*H*-indol-2-one + NADPH + H⁺
Other name(s): 3-methyloxindole:NADP⁺ oxidoreductase
Systematic name: 3-methyl-1,3-dihydroindol-2-one:NADP⁺ oxidoreductase
References: [2642]

[EC 1.3.1.17 created 1972]

EC 1.3.1.18

Accepted name: kynurenate-7,8-dihydrodiol dehydrogenase
Reaction: 7,8-dihydro-7,8-dihydroxykynurenate + NAD⁺ = 7,8-dihydroxykynurenate + NADH + H⁺
Other name(s): 7,8-dihydro-7,8-dihydroxykynurenate dehydrogenase; 7,8-dihydroxykynurenic acid 7,8-diol dehydrogenase
Systematic name: 7,8-dihydro-7,8-dihydroxykynurenate:NAD⁺ oxidoreductase
References: [3816]

[EC 1.3.1.18 created 1972]

EC 1.3.1.19

Accepted name: *cis*-1,2-dihydrobenzene-1,2-diol dehydrogenase
Reaction: *cis*-1,2-dihydrobenzene-1,2-diol + NAD⁺ = catechol + NADH + H⁺
Other name(s): *cis*-benzene glycol dehydrogenase; *cis*-1,2-dihydrocyclohexa-3,5-diene (nicotinamide adenine dinucleotide) oxidoreductase;
Systematic name: *cis*-1,2-dihydrobenzene-1,2-diol:NAD⁺ oxidoreductase
References: [148, 1200]

[EC 1.3.1.19 created 1972]

EC 1.3.1.20

Accepted name: *trans*-1,2-dihydrobenzene-1,2-diol dehydrogenase
Reaction: *trans*-1,2-dihydrobenzene-1,2-diol + NADP⁺ = catechol + NADPH + H⁺
Other name(s): dihydrodiol dehydrogenase
Systematic name: *trans*-1,2-dihydrobenzene-1,2-diol:NADP⁺ oxidoreductase
References: [150]

[EC 1.3.1.20 created 1972]

EC 1.3.1.21

Accepted name: 7-dehydrocholesterol reductase
Reaction: cholesterol + NADP⁺ = cholesta-5,7-dien-3 β -ol + NADPH + H⁺
Other name(s): DHCR7 (gene name); 7-DHC reductase; 7-dehydrocholesterol dehydrogenase/cholesterol oxidase; Δ^7 -sterol reductase
Systematic name: cholesterol:NADP⁺ Δ^7 -oxidoreductase
Comments: The enzyme is part of the cholesterol biosynthesis pathway.
References: [791, 2586]

[EC 1.3.1.21 created 1972, modified 2013]

EC 1.3.1.22

Accepted name: 3-oxo-5 α -steroid 4-dehydrogenase (NADP⁺)
Reaction: a 3-oxo-5 α -steroid + NADP⁺ = a 3-oxo- Δ^4 -steroid + NADPH + H⁺
Other name(s): cholestenone 5 α -reductase; testosterone Δ^4 -5 α -reductase; steroid 5 α -reductase; 3-oxosteroid Δ^4 -dehydrogenase; 5 α -reductase; steroid 5 α -hydrogenase; 3-oxosteroid 5 α -reductase; testosterone Δ^4 -hydrogenase; 4-ene-3-oxosteroid 5 α -reductase; reduced nicotinamide adenine dinucleotide phosphate: Δ^4 -3-ketosteroid 5 α -oxidoreductase; 4-ene-5 α -reductase; Δ^4 -3-ketosteroid 5 α -oxidoreductase; cholest-4-en-3-one 5 α -reductase; testosterone 5 α -reductase; 3-oxo-5 α -steroid 4-dehydrogenase
Systematic name: 3-oxo-5 α -steroid:NADP⁺ Δ^4 -oxidoreductase
Comments: The enzyme catalyses the conversion of assorted 3-oxo- Δ^4 steroids into their corresponding 5 α form. Substrates for the mammalian enzyme include testosterone, progesterone, and corticosterone. Substrates for the plant enzyme are brassinosteroids such as campest-4-en-3-one and (22 α)-hydroxy-campest-4-en-3-one. *cf.* EC 1.3.99.5, 3-oxo-5 α -steroid 4-dehydrogenase (acceptor).
References: [2217, 3471, 585, 3313, 3093, 3030, 2225, 3231]

[EC 1.3.1.22 created 1972, modified 2012]

[1.3.1.23 Deleted entry. cholestenone β -reductase. The enzyme is identical to EC 1.3.1.3, Δ^4 -3-oxosteroid 5 β -reductase]

[EC 1.3.1.23 created 1972, deleted 2005]

EC 1.3.1.24

Accepted name: biliverdin reductase
Reaction: bilirubin + NAD(P)⁺ = biliverdin + NAD(P)H + H⁺
Systematic name: bilirubin:NAD(P)⁺ oxidoreductase
References: [3539]

[EC 1.3.1.24 created 1972]

EC 1.3.1.25

Accepted name: 1,6-dihydroxycyclohexa-2,4-diene-1-carboxylate dehydrogenase
Reaction: (1R,6S)-1,6-dihydroxycyclohexa-2,4-diene-1-carboxylate + NAD⁺ = catechol + CO₂ + NADH + H⁺
Other name(s): 3,5-cyclohexadiene-1,2-diol-1-carboxylate dehydrogenase; 3,5-cyclohexadiene-1,2-diol-1-carboxylic acid dehydrogenase; dihydrodihydroxybenzoate dehydrogenase; DHBBDH; *cis*-1,2-dihydroxycyclohexa-3,5-diene-1-carboxylate dehydrogenase; 2-hydro-1,2-dihydroxybenzoate dehydrogenase; *cis*-1,2-dihydroxycyclohexa-3,5-diene-1-carboxylate:NAD⁺ oxidoreductase; dihydrodihydroxybenzoate dehydrogenase; (1R,6R)-1,6-dihydroxycyclohexa-2,4-diene-1-carboxylate:NAD⁺ oxidoreductase (decarboxylating)
Systematic name: (1R,6S)-1,6-dihydroxycyclohexa-2,4-diene-1-carboxylate:NAD⁺ oxidoreductase (decarboxylating)
References: [3161, 2759]

[EC 1.3.1.25 created 1976, modified 2004 (EC 1.3.1.55 created 1999, incorporated 2004)]

[1.3.1.26 Transferred entry. dihydrodipicolinate reductase. Now EC 1.17.1.8, 4-hydroxy-tetrahydrodipicolinate reductase.]

[EC 1.3.1.26 created 1976, modified 2011, deleted 2013]

EC 1.3.1.27

Accepted name: 2-hexadecenal reductase
Reaction: hexadecanal + NADP⁺ = 2-*trans*-hexadecenal + NADPH + H⁺
Other name(s): 2-alkenal reductase; hexadecanal: NADP⁺ oxidoreductase
Systematic name: hexadecanal:NADP⁺ Δ²-oxidoreductase
Comments: Specific for long chain 2-*trans*- and 2-*cis*-alkenals, with chain length optimum around 14 to 16 carbon atoms.
References: [3654]

[EC 1.3.1.27 created 1976]

EC 1.3.1.28

Accepted name: 2,3-dihydro-2,3-dihydroxybenzoate dehydrogenase
Reaction: (2*S*,3*S*)-2,3-dihydro-2,3-dihydroxybenzoate + NAD⁺ = 2,3-dihydroxybenzoate + NADH + H⁺
Other name(s): 2,3-DHB dehydrogenase; 2,3-dihydro-2,3-dihydroxybenzoate:NAD⁺ oxidoreductase
Systematic name: (2*S*,3*S*)-2,3-dihydro-2,3-dihydroxybenzoate:NAD⁺ oxidoreductase
References: [4395]

[EC 1.3.1.28 created 1972 as EC 1.1.1.109, transferred 1976 to EC 1.3.1.28]

EC 1.3.1.29

Accepted name: *cis*-1,2-dihydro-1,2-dihydroxynaphthalene dehydrogenase
Reaction: (1*R*,2*S*)-1,2-dihydronaphthalene-1,2-diol + NAD⁺ = naphthalene-1,2-diol + NADH + H⁺
Other name(s): (+)-*cis*-naphthalene dihydrodiol dehydrogenase; naphthalene dihydrodiol dehydrogenase; *cis*-dihydrodiol naphthalene dehydrogenase; *cis*-1,2-dihydronaphthalene-1,2-diol:NAD⁺ 1,2-oxidoreductase
Systematic name: (1*R*,2*S*)-1,2-dihydronaphthalene-1,2-diol:NAD⁺ 1,2-oxidoreductase
Comments: Also acts, at half the rate, on *cis*-anthracene dihydrodiol and *cis*-phenanthrene dihydrodiol.
References: [2959]

[EC 1.3.1.29 created 1976]

[1.3.1.30 Transferred entry. EC 1.3.1.30, progesterone 5α-reductase, transferred to EC 1.3.1.22, 3-oxo-5α-steroid 4-dehydrogenase (NADP⁺).]

[EC 1.3.1.30 created 1978, deleted 2012]

EC 1.3.1.31

Accepted name: 2-enoate reductase
Reaction: butanoate + NAD⁺ = but-2-enoate + NADH + H⁺
Other name(s): enoate reductase
Systematic name: butanoate:NAD⁺ Δ²-oxidoreductase
Comments: An iron-sulfur-flavoprotein (FAD). Acts (in the reverse direction) on a wide range of alkyl and aryl αβ-unsaturated carboxylate ions; but-2-enoate was the best substrate tested.
References: [3896]

[EC 1.3.1.31 created 1982]

EC 1.3.1.32

Accepted name: maleylacetate reductase
Reaction: 3-oxoadipate + NAD(P)⁺ = 2-maleylacetate + NAD(P)H + H⁺
Other name(s): maleolylacetate reductase
Systematic name: 3-oxoadipate:NAD(P)⁺ oxidoreductase
References: [1127, 1128]

[EC 1.3.1.32 created 1983]

EC 1.3.1.33

Accepted name: protochlorophyllide reductase
Reaction: chlorophyllide *a* + NADP⁺ = protochlorophyllide + NADPH + H⁺
Other name(s): NADPH₂-protochlorophyllide oxidoreductase; NADPH-protochlorophyllide oxidoreductase; NADPH-protochlorophyllide reductase; protochlorophyllide oxidoreductase (ambiguous); protochlorophyllide photooxidoreductase; light-dependent protochlorophyllide reductase
Systematic name: chlorophyllide-*a*:NADP⁺ 7,8-oxidoreductase
Comments: The enzyme catalyses a light-dependent *trans*-reduction of the D-ring of protochlorophyllide; the product has the (7*S*,8*S*)-configuration.
References: [105, 1284]

[EC 1.3.1.33 created 1984]

EC 1.3.1.34

Accepted name: 2,4-dienoyl-CoA reductase (NADPH)
Reaction: *trans*-2,3-didehydroacyl-CoA + NADP⁺ = *trans,trans*-2,3,4,5-tetrahydroacyl-CoA + NADPH + H⁺
Other name(s): 4-enoyl-CoA reductase (NADPH₂); 4-enoyl coenzyme A (reduced nicotinamide adenine dinucleotide phosphate) reductase; 4-enoyl-CoA reductase; 2,4-dienoyl-CoA reductase (NADPH₂)
Systematic name: *trans*-2,3-didehydroacyl-CoA:NADP⁺ 4-oxidoreductase
Comments: Best substrates for reduction contain a 2,4-diene structure with a chain-length of 8 or 10
References: [853, 2078]

[EC 1.3.1.34 created 1984, modified 1986]

[1.3.1.35 Transferred entry. phosphatidylcholine desaturase. Now EC 1.14.19.22, microsomal oleoyl-lipid 12-desaturase]

[EC 1.3.1.35 created 1984, deleted 2015]

EC 1.3.1.36

Accepted name: geissoschizine dehydrogenase
Reaction: geissoschizine + NADP⁺ = 4,21-didehydrogeissoschizine + NADPH
Systematic name: geissoschizine:NADP⁺ 4,21-oxidoreductase
Comments: Involved in the interconversion of heteroyohimbine alkaloids in *Catharanthus roseus*.
References: [2998]

[EC 1.3.1.36 created 1986]

EC 1.3.1.37

Accepted name: *cis*-2-enoyl-CoA reductase (NADPH)
Reaction: acyl-CoA + NADP⁺ = *cis*-2,3-dehydroacyl-CoA + NADPH + H⁺
Other name(s): NADPH-dependent *cis*-enoyl-CoA reductase; reductase, *cis*-2-enoyl coenzyme A; *cis*-2-enoyl-coenzyme A reductase; *cis*-2-enoyl-CoA reductase (NADPH)
Systematic name: acyl-CoA:NADP⁺ *cis*-2-oxidoreductase
Comments: Not identical with EC 1.3.1.38 *trans*-2-enoyl-CoA reductase (NADPH) [*cf.* EC 1.3.1.8 acyl-CoA dehydrogenase (NADP⁺)].

References: [2580]

[EC 1.3.1.37 created 1986]

EC 1.3.1.38

Accepted name: *trans*-2-enoyl-CoA reductase (NADPH)
Reaction: acyl-CoA + NADP⁺ = *trans*-2,3-dehydroacyl-CoA + NADPH + H⁺
Other name(s): NADPH-dependent *trans*-2-enoyl-CoA reductase; reductase, *trans*-enoyl coenzyme A; *trans*-2-enoyl-CoA reductase (NADPH₂)
Systematic name: acyl-CoA:NADP⁺ *trans*-2-oxidoreductase
Comments: Not identical with EC 1.3.1.37 *cis*-2-enoyl-CoA reductase (NADPH) [*cf.* EC 1.3.1.8 acyl-CoA dehydrogenase (NADP⁺)].
References: [2580]

[EC 1.3.1.38 created 1986]

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); 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 one of the activities of EC 2.3.1.85, fatty-acid synthase system. The mammalian enzyme is *Re*-specific with respect to NADP⁺. *cf.* EC 1.3.1.10, enoyl-[acyl-carrier-protein] reductase (NADPH, *Si*-specific) and EC 1.3.1.104, enoyl-[acyl-carrier-protein] reductase (NADPH).
References: [883, 506]

[EC 1.3.1.39 created 1986, modified 2013, modified 2018]

EC 1.3.1.40

Accepted name: 2-hydroxy-6-oxo-6-phenylhexa-2,4-dienoate reductase
Reaction: 2,6-dioxo-6-phenylhexanoate + NADP⁺ = 2-hydroxy-6-oxo-6-phenylhexa-2,4-dienoate + NADPH + H⁺
Other name(s): 2-hydroxy-6-oxo-phenylhexa-2,4-dienoate (reduced nicotinamide adenine dinucleotide phosphate) reductase
Systematic name: 2,6-dioxo-6-phenylhexanoate:NADP⁺ Δ²-oxidoreductase
Comments: Broad specificity; reduces a number of compounds produced by *Pseudomonas* from aromatic hydrocarbons by ring fission.
References: [2883]

[EC 1.3.1.40 created 1989]

EC 1.3.1.41

Accepted name: xanthommatin reductase
Reaction: 5,12-dihydroxanthommatin + NAD⁺ = xanthommatin + NADH + H⁺
Systematic name: 5,12-dihydroxanthommatin:NAD⁺ oxidoreductase
Comments: From *Drosophila melanogaster*.
References: [3311]

[EC 1.3.1.41 created 1989]

EC 1.3.1.42

Accepted name: 12-oxophytodienoate reductase
Reaction: 8-[(1*R*,2*R*)-3-oxo-2-(*Z*)-pent-2-enylcyclopentyl]octanoate + NADP⁺ = (15*Z*)-12-oxophyto-10,15-dienoate + NADPH + H⁺
Other name(s): 12-oxo-phytodienoic acid reductase
Systematic name: 8-[(1*R*,2*R*)-3-oxo-2-(*Z*)-pent-2-enylcyclopentyl]octanoate:NADP⁺ 4-oxidoreductase
Comments: Involved in the conversion of linolenate into jasmonate in *Zea mays*.
References: [4039]

[EC 1.3.1.42 created 1989]

EC 1.3.1.43

Accepted name: aroenate dehydrogenase
Reaction: L-aroenate + NAD⁺ = L-tyrosine + NADH + CO₂
Other name(s): arogenic dehydrogenase (ambiguous); cyclohexadienyl dehydrogenase; pretyrosine dehydrogenase (ambiguous); L-aroenate:NAD⁺ oxidoreductase; aroenate dehydrogenase (NAD⁺)
Systematic name: L-aroenate:NAD⁺ oxidoreductase (decarboxylating)
Comments: Aroenate dehydrogenases may utilize NAD⁺ (EC 1.3.1.43), NADP⁺ (EC 1.3.1.78), or both (EC 1.3.1.79). NAD⁺-specific enzymes have been reported from some bacteria [463] and plants [462]. Some enzymes also possess the activity of EC 1.3.1.12, prephenate dehydrogenase.
References: [3640, 463, 462, 2473, 2267, 4425]

[EC 1.3.1.43 created 1989, modified 2003, modified 2005, modified 2015]

EC 1.3.1.44

Accepted name: *trans*-2-enoyl-CoA reductase (NAD⁺)
Reaction: acyl-CoA + NAD⁺ = *trans*-didehydroacyl-CoA + NADH + H⁺
Other name(s): *trans*-2-enoyl-CoA reductase (NAD)
Systematic name: acyl-CoA:NAD⁺ *trans*-2-oxidoreductase
Comments: The enzyme from *Euglena gracilis* acts on crotonoyl-CoA and, more slowly, on *trans*-hex-2-enoyl-CoA and *trans*-oct-2-enoyl-CoA.
References: [1657]

[EC 1.3.1.44 created 1989]

EC 1.3.1.45

Accepted name: 2'-hydroxyisoflavone reductase
Reaction: vestitone + NADP⁺ = 2'-hydroxyformononetin + NADPH + H⁺
Other name(s): NADPH:2'-hydroxyisoflavone oxidoreductase; isoflavone reductase; 2',7-dihydroxy-4',5'-methylenedioxyisoflavone reductase
Systematic name: vestitone:NADP⁺ oxidoreductase
Comments: In the reverse reaction, a 2'-hydroxyisoflavone is reduced to an isoflavanone; 2'-hydroxypseudobaptigenin also acts. Involved in the biosynthesis of the pterocarpin phytoalexins medicarpin and maackiain.
References: [3890]

[EC 1.3.1.45 created 1990]

EC 1.3.1.46

Accepted name: biochanin-A reductase

Reaction: dihydrobiochanin A + NADP⁺ = biochanin A + NADPH + H⁺
Systematic name: dihydrobiochanin-A:NADP⁺ Δ²-oxidoreductase
Comments: Some other isoflavones are reduced to the corresponding isoflavanones.
References: [3890]

[EC 1.3.1.46 created 1990]

EC 1.3.1.47

Accepted name: α-santonin 1,2-reductase
Reaction: 1,2-dihydrosantonin + NAD(P)⁺ = α-santonin + NAD(P)H + H⁺
Systematic name: 1,2-dihydrosantonin:NAD(P)⁺ 1,2-oxidoreductase
References: [2692]

[EC 1.3.1.47 created 1990]

EC 1.3.1.48

Accepted name: 13,14-dehydro-15-oxoprostaglandin 13-reductase
Reaction: 11α-hydroxy-9,15-dioxoprostanoate + NAD(P)⁺ = (13E)-11α-hydroxy-9,15-dioxoprost-13-enoate + NAD(P)H + H⁺
Other name(s): 15-oxo-Δ¹³-prostaglandin reductase; Δ¹³-15-ketoprostaglandin reductase; 15-ketoprostaglandin Δ¹³-reductase; prostaglandin Δ¹³-reductase; prostaglandin 13-reductase; (5Z)-(15S)-11α-hydroxy-9,15-dioxoprostanoate:NAD(P)⁺ Δ¹³-oxidoreductase; (5Z)-11α-hydroxy-9,15-dioxoprost-5-enoate:NAD(P)⁺ Δ¹³-oxidoreductase
Systematic name: 11α-hydroxy-9,15-dioxoprostanoate:NAD(P)⁺ Δ¹³-oxidoreductase
Comments: Reduces 13,14-dehydro-15-oxoprostaglandins to 13,14-dihydro derivatives. The enzyme from placenta is specific for NAD⁺.
References: [1374, 1723]

[EC 1.3.1.48 created 1990, modified 2014]

EC 1.3.1.49

Accepted name: *cis*-3,4-dihydrophenanthrene-3,4-diol dehydrogenase
Reaction: (+)-*cis*-3,4-dihydrophenanthrene-3,4-diol + NAD⁺ = phenanthrene-3,4-diol + NADH + H⁺
Systematic name: (+)-*cis*-3,4-dihydrophenanthrene-3,4-diol:NAD⁺ 3,4-oxidoreductase
References: [2686]

[EC 1.3.1.49 created 1992]

[1.3.1.50 Deleted entry. tetrahydroxynaphthalene reductase. Now EC 1.1.1.252 tetrahydroxynaphthalene reductase]

[EC 1.3.1.50 created 1992, deleted 1999]

EC 1.3.1.51

Accepted name: 2'-hydroxydaidzein reductase
Reaction: 2'-hydroxy-2,3-dihydrodaidzein + NADP⁺ = 2'-hydroxydaidzein + NADPH + H⁺
Other name(s): NADPH:2'-hydroxydaidzein oxidoreductase; HDR; 2'-hydroxydihydrodaidzein:NADP⁺ 2'-oxidoreductase
Systematic name: 2'-hydroxy-2,3-dihydrodaidzein:NADP⁺ 2'-oxidoreductase
Comments: In the reverse reaction, the 2'-hydroxyisoflavone (2'-hydroxydaidzein) is reduced to an isoflavanone. Also acts on 2'-hydroxyformononetin and to a small extent on 2'-hydroxygenistein. Involved in the biosynthesis of the phytoalexin glyceollin. The isoflavones biochanin A, daidzein and genestein as well as the flavonoids apigenin, kaempferol and quercetin do not act as substrates.
References: [1018]

[EC 1.3.1.51 created 1992, modified 2004]

[1.3.1.52 *Transferred entry. 2-methyl-branched-chain-enoyl-CoA reductase. Now EC 1.3.8.5, 2-methyl-branched-chain-enoyl-CoA reductase*]

[EC 1.3.1.52 created 1992, deleted 2012]

EC 1.3.1.53

Accepted name: (3*S*,4*R*)-3,4-dihydroxycyclohexa-1,5-diene-1,4-dicarboxylate dehydrogenase
Reaction: (3*S*,4*R*)-3,4-dihydroxycyclohexa-1,5-diene-1,4-dicarboxylate + NAD⁺ = 3,4-dihydroxybenzoate + CO₂ + NADH
Other name(s): (1*R*,2*S*)-dihydroxy-3,5-cyclohexadiene-1,4-dicarboxylate dehydrogenase; terephthalate 1,2-*cis*-dihydrodiol dehydrogenase; *cis*-4,5-dihydroxycyclohexa-1(6),2-diene-1,4-dicarboxylate:NAD⁺ oxidoreductase (decarboxylating)
Systematic name: (3*S*,4*R*)-3,4-dihydroxycyclohexa-1,5-diene-1,4-dicarboxylate:NAD⁺ oxidoreductase
Comments: Requires Fe^{II}. Involved in the terephthalate degradation pathway in bacteria [4127].
References: [3299, 4127]

[EC 1.3.1.53 created 1999 (EC 1.3.1.61 created 2000, incorporated 2007)]

EC 1.3.1.54

Accepted name: precorrin-6A reductase
Reaction: precorrin-6B + NADP⁺ = precorrin-6A + NADPH + H⁺
Other name(s): precorrin-6X reductase; precorrin-6Y:NADP⁺ oxidoreductase
Systematic name: precorrin-6B:NADP⁺ oxidoreductase
References: [318, 4137]

[EC 1.3.1.54 created 1999, modified 2004]

[1.3.1.55 *Deleted entry. cis-1,2-dihydroxycyclohexa-3,5-diene-1-carboxylate dehydrogenase. Enzyme is identical to EC 1.3.1.25, 1,6-dihydroxycyclohexa-2,4-diene-1-carboxylate dehydrogenase*]

[EC 1.3.1.55 created 1999, deleted 2004]

EC 1.3.1.56

Accepted name: *cis*-2,3-dihydrobiphenyl-2,3-diol dehydrogenase
Reaction: *cis*-3-phenylcyclohexa-3,5-diene-1,2-diol + NAD⁺ = biphenyl-2,3-diol + NADH + H⁺
Other name(s): 2,3-dihydro-2,3-dihydroxybiphenyl dehydrogenase
Systematic name: *cis*-3-phenylcyclohexa-3,5-diene-1,2-diol:NAD⁺ oxidoreductase
Comments: Catalyses the second step in the biphenyl degradation pathway in bacteria.
References: [3766, 1108, 1531]

[EC 1.3.1.56 created 2000]

EC 1.3.1.57

Accepted name: phloroglucinol reductase
Reaction: dihydrophloroglucinol + NADP⁺ = phloroglucinol + NADPH + H⁺
Systematic name: dihydrophloroglucinol:NADP⁺ oxidoreductase
Comments: Involved in the gallate anaerobic degradation pathway in bacteria.
References: [1332]

[EC 1.3.1.57 created 2000]

EC 1.3.1.58

Accepted name: 2,3-dihydroxy-2,3-dihydro-*p*-cumate dehydrogenase
Reaction: *cis*-5,6-dihydroxy-4-isopropylcyclohexa-1,3-dienecarboxylate + NAD⁺ = 2,3-dihydroxy-*p*-cumate + NADH + H⁺
Systematic name: *cis*-2,3-dihydroxy-2,3-dihydro-*p*-cumate:NAD⁺ oxidoreductase
Comments: Involved in the *p*-cymene degradation pathway in *Pseudomonas putida*.
References: [909]

[EC 1.3.1.58 created 2000]

[1.3.1.59 Deleted entry. 1,2-dihydroxy-3-methyl-1,2-dihydrobenzoate dehydrogenase. No evidence in the paper cited that the enzyme exists]

[EC 1.3.1.59 created 2000, deleted 2006]

EC 1.3.1.60

Accepted name: dibenzothiophene dihydrodiol dehydrogenase
Reaction: *cis*-1,2-dihydroxy-1,2-dihydrodibenzothiophene + NAD⁺ = 1,2-dihydroxydibenzothiophene + NADH + H⁺
Systematic name: *cis*-1,2-dihydroxy-1,2-dihydrodibenzothiophene:NAD⁺ oxidoreductase
Comments: Involved in the dibenzothiophene degradation pathway in bacteria.
References: [2110, 798]

[EC 1.3.1.60 created 2000]

[1.3.1.61 Deleted entry. terephthalate 1,2-*cis*-dihydrodiol dehydrogenase. Enzyme is identical to EC 1.3.1.53, (3*S*,4*R*)-3,4-dihydroxycyclohexa-1,5-diene-1,4-dicarboxylate dehydrogenase]

[EC 1.3.1.61 created 2000, deleted 2007]

EC 1.3.1.62

Accepted name: pimeloyl-CoA dehydrogenase
Reaction: pimeloyl-CoA + NAD⁺ = 6-carboxyhex-2-enoyl-CoA + NADH + H⁺
Systematic name: pimeloyl-CoA:NAD⁺ oxidoreductase
Comments: Involved in the benzoate degradation (anaerobic) pathway in bacteria.
References: [1145]

[EC 1.3.1.62 created 2000]

[1.3.1.63 Transferred entry. 2,4-dichlorobenzoyl-CoA reductase. Now EC 1.21.1.2, 2,4-dichlorobenzoyl-CoA reductase]

[EC 1.3.1.63 created 2000, modified 2011, deleted 2015]

EC 1.3.1.64

Accepted name: phthalate 4,5-*cis*-dihydrodiol dehydrogenase
Reaction: *cis*-4,5-dihydroxycyclohexa-1(6),2-diene-1,2-dicarboxylate + NAD⁺ = 4,5-dihydroxyphthalate + NADH + H⁺
Systematic name: *cis*-4,5-dihydroxycyclohexa-1(6),2-diene-1,2-dicarboxylate:NAD⁺ oxidoreductase
Comments: Involved in the phthalate degradation pathway in bacteria.
References: [212]

[EC 1.3.1.64 created 2000]

EC 1.3.1.65

Accepted name: 5,6-dihydroxy-3-methyl-2-oxo-1,2,5,6-tetrahydroquinoline dehydrogenase
Reaction: 5,6-dihydroxy-3-methyl-2-oxo-1,2,5,6-tetrahydroquinoline + NAD⁺ = 5,6-dihydroxy-3-methyl-2-oxo-1,2-dihydroquinoline + NADH + H⁺

Systematic name: 5,6-dihydroxy-3-methyl-2-oxo-1,2,5,6-tetrahydroquinoline:NAD⁺ oxidoreductase
Comments: Acts in the reverse direction to form part of the 3-methylquinoline degradation pathway in bacteria.
References: [3343]

[EC 1.3.1.65 created 2000]

EC 1.3.1.66

Accepted name: *cis*-dihydroethylcatechol dehydrogenase
Reaction: *cis*-1,2-dihydro-3-ethylcatechol + NAD⁺ = 3-ethylcatechol + NADH + H⁺
Systematic name: *cis*-1,2-dihydro-3-ethylcatechol:NAD⁺ oxidoreductase
Comments: Involved in the ethylbenzene degradation pathway in bacteria.
References: [1199]

[EC 1.3.1.66 created 2000]

EC 1.3.1.67

Accepted name: *cis*-1,2-dihydroxy-4-methylcyclohexa-3,5-diene-1-carboxylate dehydrogenase
Reaction: *cis*-1,2-dihydroxy-4-methylcyclohexa-3,5-diene-1-carboxylate + NAD(P)⁺ = 4-methylcatechol + NAD(P)H + CO₂
Systematic name: *cis*-1,2-dihydroxy-4-methylcyclohexa-3,5-diene-1-carboxylate:NAD(P)⁺ oxidoreductase (decarboxylating)
Comments: Involved in the *p*-xylene degradation pathway in bacteria.
References: [4194]

[EC 1.3.1.67 created 2000]

EC 1.3.1.68

Accepted name: 1,2-dihydroxy-6-methylcyclohexa-3,5-dienecarboxylate dehydrogenase
Reaction: 1,2-dihydroxy-6-methylcyclohexa-3,5-dienecarboxylate + NAD⁺ = 3-methylcatechol + NADH + CO₂
Systematic name: 1,2-dihydroxy-6-methylcyclohexa-3,5-dienecarboxylate:NAD⁺ oxidoreductase (decarboxylating)
Comments: Involved in the *o*-xylene degradation pathway in bacteria.
References: [1497]

[EC 1.3.1.68 created 2000]

EC 1.3.1.69

Accepted name: zeatin reductase
Reaction: dihydrozeatin + NADP⁺ = zeatin + NADPH + H⁺
Systematic name: dihydrozeatin:NADP⁺ oxidoreductase
Comments: Previously classified erroneously as EC 1.1.1.242.
References: [2414]

[EC 1.3.1.69 created 1992 as EC 1.1.1.242, transferred 2001 to EC 1.3.1.69]

EC 1.3.1.70

Accepted name: Δ¹⁴-sterol reductase
Reaction: 4,4-dimethyl-5α-cholesta-8,24-dien-3β-ol + NADP⁺ = 4,4-dimethyl-5α-cholesta-8,14,24-trien-3β-ol + NADPH + H⁺
Systematic name: 4,4-dimethyl-5α-cholesta-8,24-dien-3β-ol:NADP⁺ Δ¹⁴-oxidoreductase
Comments: This enzyme acts on a range of steroids with a 14(15)-double bond.
References: [365, 2924]

[EC 1.3.1.70 created 2001]

EC 1.3.1.71

Accepted name: $\Delta^{24(24^1)}$ -sterol reductase
Reaction: ergosterol + NADP⁺ = ergosta-5,7,22,24(24¹)-tetraen-3 β -ol + NADPH + H⁺
Other name(s): sterol $\Delta^{24(28)}$ -methylene reductase; sterol $\Delta^{24(28)}$ -reductase
Systematic name: ergosterol:NADP⁺ $\Delta^{24(24^1)}$ -oxidoreductase
Comments: Acts on a range of steroids with a 24(24¹)-double bond.
References: [2752, 4500]

[EC 1.3.1.71 created 2001, modified 2002]

EC 1.3.1.72

Accepted name: Δ^{24} -sterol reductase
Reaction: 5 α -cholest-7-en-3 β -ol + NADP⁺ = 5 α -cholesta-7,24-dien-3 β -ol + NADPH + H⁺
Other name(s): lanosterol Δ^{24} -reductase
Systematic name: sterol:NADP⁺ Δ^{24} -oxidoreductase
Comments: Acts on a range of steroids with a 24(25)-double bond, including lanosterol, desmosterol and zymosterol.
References: [159]

[EC 1.3.1.72 created 2001]

EC 1.3.1.73

Accepted name: 1,2-dihydrovomilenine reductase
Reaction: 17-*O*-acetylnorajmaline + NADP⁺ = 1,2-dihydrovomilenine + NADPH + H⁺
Systematic name: 17-*O*-acetylnorajmaline:NADP⁺ oxidoreductase
Comments: Forms part of the ajmaline biosynthesis pathway.
References: [1153]

[EC 1.3.1.73 created 2002]

EC 1.3.1.74

Accepted name: 2-alkenal reductase [NAD(P)⁺]
Reaction: a *n*-alkanal + NAD(P)⁺ = an alk-2-enal + NAD(P)H + H⁺
Other name(s): NAD(P)H-dependent alkenal/one oxidoreductase; NADPH:2-alkenal α,β -hydrogenase; 2-alkenal reductase
Systematic name: *n*-alkanal:NAD(P)⁺ 2-oxidoreductase
Comments: Highly specific for 4-hydroxynon-2-enal and non-2-enal. Alk-2-enals of shorter chain have lower affinities. Exhibits high activities also for alk-2-enones such as but-3-en-2-one and pent-3-en-2-one. Inactive with cyclohex-2-en-1-one and 12-oxophytodienoic acid. Involved in the detoxication of α,β -unsaturated aldehydes and ketones [*cf.* EC 1.3.1.102, 2-alkenal reductase (NADP⁺)].
References: [2384, 815]

[EC 1.3.1.74 created 2003, modified 2014]

EC 1.3.1.75

Accepted name: 3,8-divinyl protochlorophyllide *a* 8-vinyl-reductase (NADPH)
Reaction: protochlorophyllide *a* + NADP⁺ = 3,8-divinyl protochlorophyllide *a* + NADPH + H⁺
Other name(s): DVR (gene name); *bciA* (gene name); [4-vinyl]chlorophyllide *a* reductase; 4VCR; chlorophyllide-*a*:NADP⁺ oxidoreductase; divinyl chlorophyllide *a* 8-vinyl-reductase; plant-type divinyl chlorophyllide *a* 8-vinyl-reductase

Systematic name: protochlorophyllide-*a*:NADP⁺ C-8¹-oxidoreductase
Comments: The enzyme, found in higher plants, green algae, and some phototrophic bacteria, is involved in the production of monovinyl versions of (bacterio)chlorophyll pigments from their divinyl precursors. It can also act on 3,8-divinyl chlorophyllide *a*. *cf.* EC 1.3.7.13, 3,8-divinyl protochlorophyllide *a* 8-vinyl-reductase (ferredoxin).
References: [3928, 2938, 2939, 2017, 2687, 587]

[EC 1.3.1.75 created 2003, modified 2016]

EC 1.3.1.76

Accepted name: precorrin-2 dehydrogenase
Reaction: precorrin-2 + NAD⁺ = sirohydrochlorin + NADH + H⁺
Other name(s): Met8p; SirC; CysG
Systematic name: precorrin-2:NAD⁺ oxidoreductase
Comments: This enzyme catalyses the second of three steps leading to the formation of siroheme from uroporphyrinogen III. The first step involves the donation of two *S*-adenosyl-L-methionine-derived methyl groups to carbons 2 and 7 of uroporphyrinogen III to form precorrin-2 (EC 2.1.1.107, uroporphyrin-III *C*-methyltransferase) and the third step involves the chelation of ferrous iron to sirohydrochlorin to form siroheme (EC 4.99.1.4, sirohydrochlorin ferrochelatase). In *Saccharomyces cerevisiae*, the last two steps are carried out by a single bifunctional enzyme, Met8p. In some bacteria, steps 1-3 are catalysed by a single multifunctional protein called CysG, whereas in *Bacillus megaterium*, three separate enzymes carry out each of the steps, with SirC being responsible for the above reaction.
References: [3395, 4137]

[EC 1.3.1.76 created 2004]

EC 1.3.1.77

Accepted name: anthocyanidin reductase [(2*R*,3*R*)-flavan-3-ol-forming]
Reaction: a (2*R*,3*R*)-flavan-3-ol + 2 NAD(P)⁺ = an anthocyanidin with a 3-hydroxy group + 2 NAD(P)H + H⁺
Other name(s): ANR (gene name) (ambiguous); flavan-3-ol:NAD(P)⁺ oxidoreductase; anthocyanidin reductase (ambiguous)
Systematic name: (2*R*,3*R*)-flavan-3-ol:NAD(P)⁺ 3,4-oxidoreductase
Comments: The enzyme participates in the flavonoid biosynthesis pathway found in plants. It catalyses the double reduction of anthocyanidins, producing (2*R*,3*R*)-flavan-3-ol monomers required for the formation of proanthocyanidins. While the enzyme from the legume *Medicago truncatula* (MtANR) can use both NADPH and NADH as reductant, that from the crucifer *Arabidopsis thaliana* (AtANR) uses only NADPH. Also, while the substrate preference of MtANR is cyanidin; pelargonidin; delphinidin, the reverse preference is found with AtANR. *cf.* EC 1.3.1.112, anthocyanidin reductase [(2*S*)-flavan-3-ol-forming].
References: [4278, 4277, 2933]

[EC 1.3.1.77 created 2004, modified 2016]

EC 1.3.1.78

Accepted name: arogenate dehydrogenase (NADP⁺)
Reaction: L-arogenate + NADP⁺ = L-tyrosine + NADPH + CO₂
Other name(s): arogenic dehydrogenase (ambiguous); pretyrosine dehydrogenase (ambiguous); TyrAAT1; TyrAAT2; TyrAa
Systematic name: L-arogenate:NADP⁺ oxidoreductase (decarboxylating)
Comments: Arogenate dehydrogenases may utilize NAD⁺ (EC 1.3.1.43), NADP⁺ (EC 1.3.1.78), or both (EC 1.3.1.79). NADP⁺-dependent enzymes usually predominate in higher plants. The enzyme from the cyanobacterium *Synechocystis* sp. PCC 6803 and the TyrAAT1 isoform of the plant *Arabidopsis thaliana* cannot use prephenate as a substrate, while the *Arabidopsis* isoform TyrAAT2 can use it very poorly [3193, 346].

References: [1140, 3193, 346]

[EC 1.3.1.78 created 2005]

EC 1.3.1.79

Accepted name: aroenate dehydrogenase [NAD(P)⁺]
Reaction: L-aroenate + NAD(P)⁺ = L-tyrosine + NAD(P)H + CO₂
Other name(s): aroenic dehydrogenase (ambiguous); cyclohexadienyl dehydrogenase; pretyrosine dehydrogenase (ambiguous)
Systematic name: L-aroenate:NAD(P)⁺ oxidoreductase (decarboxylating)
Comments: Aroenate dehydrogenases may utilize NAD⁺ (EC 1.3.1.43), NADP⁺ (EC 1.3.1.78), or both (EC 1.3.1.79). Enzymes that can utilize both cofactors have been reported from some Proteobacteria, including *Burkholderia caryophylli*, *Burkholderia cepacia*, *Pseudomonas marginata* and *Delftia acidovorans*.
References: [463]

[EC 1.3.1.79 created 2005]

[1.3.1.80 Transferred entry. red chlorophyll catabolite reductase. Now classified as EC 1.3.7.12, red chlorophyll catabolite reductase]

[EC 1.3.1.80 created 2007, deleted 2016]

EC 1.3.1.81

Accepted name: (+)-pulegone reductase
Reaction: (1) (-)-menthone + NADP⁺ = (+)-pulegone + NADPH + H⁺
(2) (+)-isomenthone + NADP⁺ = (+)-pulegone + NADPH + H⁺
Systematic name: (-)-menthone:NADP⁺ oxidoreductase
Comments: NADH cannot replace NADPH as reductant. The Δ^{8,9}-double bond of (+)-*cis*-isopulegone and the Δ^{1,2}-double bond of (±)-piperitone are not substrates. The enzyme from peppermint (*Mentha × piperita*) converts (+)-pulegone into both (-)-menthone and (+)-isomenthone at a ratio of 70:30 for native enzyme but it does not catalyse the reverse reaction. This enzyme is a member of the medium-chain dehydrogenase/reductase superfamily.
References: [3191]

[EC 1.3.1.81 created 2008]

EC 1.3.1.82

Accepted name: (-)-isopiperitenone reductase
Reaction: (+)-*cis*-isopulegone + NADP⁺ = (-)-isopiperitenone + NADPH + H⁺
Systematic name: (+)-*cis*-isopulegone:NADP⁺ oxidoreductase
Comments: The reaction occurs in the opposite direction to that shown above. The enzyme participates in the menthol-biosynthesis pathway of *Mentha* plants. (+)-Pulegone, (+)-*cis*-isopulegone and (-)-menthone are not substrates. The enzyme has a preference for NADPH as the reductant, with NADH being a poor substitute [3191]. The enzyme is highly regioselective for the reduction of the endocyclic 1,2-double bond, and is stereoselective, producing only the 1*R*-configured product. It is a member of the short-chain dehydrogenase/reductase superfamily.
References: [697, 3191]

[EC 1.3.1.82 created 2008]

EC 1.3.1.83

Accepted name: geranylgeranyl diphosphate reductase
Reaction: phytyl diphosphate + 3 NADP⁺ = geranylgeranyl diphosphate + 3 NADPH + 3 H⁺

Other name(s): geranylgeranyl reductase; CHL P
Systematic name: geranylgeranyl-diphosphate:NADP⁺ oxidoreductase
Comments: This enzyme also acts on geranylgeranyl-chlorophyll *a*. The reaction occurs in three steps. Which order the three double bonds are reduced is not known.
References: [3574, 3805, 1876]

[EC 1.3.1.83 created 2009]

EC 1.3.1.84

Accepted name: acrylyl-CoA reductase (NADPH)
Reaction: propanoyl-CoA + NADP⁺ = acryloyl-CoA + NADPH + H⁺
Systematic name: propanoyl-CoA:NADP⁺ oxidoreductase
Comments: Catalyses a step in the 3-hydroxypropanoate/4-hydroxybutanoate cycle, an autotrophic CO₂ fixation pathway found in some thermoacidophilic archaea [265]. The enzyme from *Sulfolobus tokodaii* does not act on either NADH or crotonyl-CoA [3852]. Different from EC 1.3.1.8, which acts only on enoyl-CoA derivatives of carbon chain length 4 to 16. Contains Zn²⁺.
References: [265, 3852]

[EC 1.3.1.84 created 2009, modified 2014]

EC 1.3.1.85

Accepted name: crotonyl-CoA carboxylase/reductase
Reaction: (2*S*)-ethylmalonyl-CoA + NADP⁺ = (*E*)-but-2-enoyl-CoA + CO₂ + NADPH + H⁺
Other name(s): CCR; crotonyl-CoA reductase (carboxylating)
Systematic name: (2*S*)-ethylmalonyl-CoA:NADP⁺ oxidoreductase (decarboxylating)
Comments: The reaction is catalysed in the reverse direction. This enzyme, isolated from the bacterium *Rhodobacter sphaeroides*, catalyses (*E*)-but-2-enoyl-CoA-dependent oxidation of NADPH in the presence of CO₂. When CO₂ is absent, the enzyme catalyses the reduction of (*E*)-but-2-enoyl-CoA to butanoyl-CoA, but with only 10% of maximal activity (relative to (*E*)-but-2-enoyl-CoA carboxylation).
References: [961, 962]

[EC 1.3.1.85 created 2011]

EC 1.3.1.86

Accepted name: crotonyl-CoA reductase
Reaction: butanoyl-CoA + NADP⁺ = (*E*)-but-2-enoyl-CoA + NADPH + H⁺
Other name(s): butyryl-CoA dehydrogenase; butyryl dehydrogenase; unsaturated acyl-CoA reductase; ethylene reductase; enoyl-coenzyme A reductase; unsaturated acyl coenzyme A reductase; butyryl coenzyme A dehydrogenase; short-chain acyl CoA dehydrogenase; short-chain acyl-coenzyme A dehydrogenase; 3-hydroxyacyl CoA reductase; butanoyl-CoA:(acceptor) 2,3-oxidoreductase; CCR
Systematic name: butanoyl-CoA:NADP⁺ 2,3-oxidoreductase
Comments: Catalyses the reaction in the reverse direction. This enzyme from *Streptomyces collinus* is specific for (*E*)-but-2-enoyl-CoA, and is proposed to provide butanoyl-CoA as a starter unit for straight-chain fatty acid biosynthesis.
References: [4092]

[EC 1.3.1.86 created 2011]

EC 1.3.1.87

Accepted name: 3-(*cis*-5,6-dihydroxycyclohexa-1,3-dien-1-yl)propanoate dehydrogenase
Reaction: (1) 3-(*cis*-5,6-dihydroxycyclohexa-1,3-dien-1-yl)propanoate + NAD⁺ = 3-(2,3-dihydroxyphenyl)propanoate + NADH + H⁺

(2) (2E)-3-(*cis*-5,6-dihydroxycyclohexa-1,3-dien-1-yl)prop-2-enoate + NAD⁺ = (2E)-3-(2,3-dihydroxyphenyl)prop-2-enoate + NADH + H⁺

Other name(s): *hcaB* (gene name); *cis*-dihydrodiol dehydrogenase; 2,3-dihydroxy-2,3-dihydro-phenylpropionate dehydrogenase
Systematic name: 3-(*cis*-5,6-dihydroxycyclohexa-1,3-dien-1-yl)propanoate:NAD⁺ oxidoreductase
Comments: This enzyme catalyses a step in the pathway of phenylpropanoid compounds degradation.
References: [813]

[EC 1.3.1.87 created 2011]

EC 1.3.1.88

Accepted name: tRNA-dihydrouridine^{16/17} synthase [NAD(P)⁺]
Reaction: (1) 5,6-dihydrouracil¹⁶ in tRNA + NAD(P)⁺ = uracil¹⁶ in tRNA + NAD(P)H + H⁺
(2) 5,6-dihydrouracil¹⁷ in tRNA + NAD(P)⁺ = uracil¹⁷ in tRNA + NAD(P)H + H⁺
Other name(s): Dus1p; tRNA-dihydrouridine synthase 1
Systematic name: tRNA-5,6-dihydrouracil^{16/17}:NAD(P)⁺ oxidoreductase
Comments: A flavoprotein. The enzyme specifically modifies uracil¹⁶ and uracil¹⁷ in tRNA.
References: [4280, 4281]

[EC 1.3.1.88 created 2011]

EC 1.3.1.89

Accepted name: tRNA-dihydrouridine⁴⁷ synthase [NAD(P)⁺]
Reaction: 5,6-dihydrouracil⁴⁷ in tRNA + NAD(P)⁺ = uracil⁴⁷ in tRNA + NAD(P)H + H⁺
Other name(s): Dus3p; tRNA-dihydrouridine synthase 3
Systematic name: tRNA-5,6-dihydrouracil⁴⁷:NAD(P)⁺ oxidoreductase
Comments: A flavoenzyme. The enzyme specifically modifies uracil⁴⁷ in tRNA.
References: [4280]

[EC 1.3.1.89 created 2011]

EC 1.3.1.90

Accepted name: tRNA-dihydrouridine^{20a/20b} synthase [NAD(P)⁺]
Reaction: (1) 5,6-dihydrouracil^{20a} in tRNA + NAD(P)⁺ = uracil^{20a} in tRNA + NAD(P)H + H⁺
(2) 5,6-dihydrouracil^{20b} in tRNA + NAD(P)⁺ = uracil^{20b} in tRNA + NAD(P)H + H⁺
Other name(s): Dus4p
Systematic name: tRNA-5,6-dihydrouracil^{20a/20b}:NAD(P)⁺ oxidoreductase
Comments: A flavoenzyme. The enzyme specifically modifies uracil^{20a} and uracil^{20b} in tRNA.
References: [4280]

[EC 1.3.1.90 created 2011]

EC 1.3.1.91

Accepted name: tRNA-dihydrouridine²⁰ synthase [NAD(P)⁺]
Reaction: 5,6-dihydrouracil²⁰ in tRNA + NAD(P)⁺ = uracil²⁰ in tRNA + NAD(P)H + H⁺
Other name(s): Dus2p; tRNA-dihydrouridine synthase 2
Systematic name: tRNA-5,6-dihydrouracil²⁰:NAD(P)⁺ oxidoreductase
Comments: A flavoenzyme [3184]. The enzyme specifically modifies uracil²⁰ in tRNA.
References: [4280, 4281, 3184, 1841]

[EC 1.3.1.91 created 2011]

EC 1.3.1.92

- Accepted name:** artemisinic aldehyde $\Delta^{11(13)}$ -reductase
Reaction: (11*R*)-dihydroartemisinic aldehyde + NADP⁺ = artemisinic aldehyde + NADPH + H⁺
Other name(s): Dbr2
Systematic name: artemisinic aldehyde:NADP⁺ oxidoreductase
Comments: Cloned from *Artemisia annua*. In addition to the reduction of artemisinic aldehyde it is also able to a lesser extent to reduce artemisinic alcohol and artemisinic acid. Part of the biosynthesis of artemisinin.
References: [277, 4448]

[EC 1.3.1.92 created 2012]

EC 1.3.1.93

- Accepted name:** very-long-chain enoyl-CoA reductase
Reaction: a very-long-chain acyl-CoA + NADP⁺ = a very-long-chain *trans*-2,3-dehydroacyl-CoA + NADPH + H⁺
Other name(s): TSC13 (gene name); CER10 (gene name)
Systematic name: very-long-chain acyl-CoA:NADP⁺ oxidoreductase
Comments: This is the fourth component of the elongase, a microsomal protein complex responsible for extending palmitoyl-CoA and stearoyl-CoA (and modified forms thereof) to very-long-chain acyl CoAs. *cf.* EC 2.3.1.199, very-long-chain 3-oxoacyl-CoA synthase, EC 1.1.1.330, very-long-chain 3-oxoacyl-CoA reductase, and EC 4.2.1.134, very-long-chain (3*R*)-3-hydroxyacyl-[acyl-carrier protein] dehydratase.
References: [2003, 1131, 2104, 4468]

[EC 1.3.1.93 created 2012]

EC 1.3.1.94

- Accepted name:** polyprenol reductase
Reaction: *ditrans, polycis*-dolichol + NADP⁺ = *ditrans, polycis*-polyprenol + NADPH + H⁺
Other name(s): SRD5A3 (gene name); DFG10 (gene name)
Systematic name: *ditrans, polycis*-dolichol:NADP⁺ 2,3-oxidoreductase
Comments: The reaction occurs in the reverse direction with reduction of the terminal double bond next to the alcohol group. Isolated from human fetal brain tissue but present in all eukaryotes. In mammalian cells dolichols are predominantly 18-21 isoprene units in length.
References: [3279, 493]

[EC 1.3.1.94 created 2012]

EC 1.3.1.95

- Accepted name:** acrylyl-CoA reductase (NADH)
Reaction: propanoyl-CoA + NAD⁺ = acryloyl-CoA + NADH + H⁺
Systematic name: propanoyl-CoA:NAD⁺ oxidoreductase
Comments: Contains FAD. The reaction is catalysed in the opposite direction to that shown. The enzyme from the bacterium *Clostridium propionicum* is a complex that includes an electron-transfer flavoprotein (ETF). The ETF is reduced by NADH and transfers the electrons to the active site. Catalyses a step in a pathway for L-alanine fermentation to propanoate [1483]. *cf.* EC 1.3.1.84, acrylyl-CoA reductase (NADPH).
References: [1483, 1809]

[EC 1.3.1.95 created 2012]

EC 1.3.1.96

- Accepted name:** *Botryococcus* squalene synthase
Reaction: squalene + diphosphate + NADP⁺ = presqualene diphosphate + NADPH + H⁺

Other name(s): SSL-2 (gene name)
Systematic name: squalene:NADP⁺ oxidoreductase
Comments: Isolated from the green alga *Botryococcus braunii* BOT22. Acts in the reverse direction. *cf.* EC 2.5.1.21, squalene synthase, where squalene is formed directly from farnesyl diphosphate.
References: [2784]

[EC 1.3.1.96 created 2012]

EC 1.3.1.97

Accepted name: botryococcene synthase
Reaction: C₃₀ botryococcene + NADP⁺ + diphosphate = presqualene diphosphate + NADPH + H⁺
Other name(s): SSL-3 (gene name)
Systematic name: C₃₀ botryococcene:NADP⁺ oxidoreductase
Comments: Isolated from the green alga *Botryococcus braunii* BOT22. Acts in the reverse direction. Involved in the production of botryococcenes, which are triterpenoid hydrocarbons of isoprenoid origin produced in large amount by this alga.
References: [2784]

[EC 1.3.1.97 created 2012]

EC 1.3.1.98

Accepted name: UDP-*N*-acetylmuramate dehydrogenase
Reaction: UDP-*N*-acetyl- α -D-muramate + NADP⁺ = UDP-*N*-acetyl-3-*O*-(1-carboxyvinyl)- α -D-glucosamine + NADPH + H⁺
Other name(s): MurB reductase; UDP-*N*-acetylenolpyruvoylglucosamine reductase; UDP-*N*-acetylglucosamine-enoylpyruvate reductase; UDP-GlcNAc-enoylpyruvate reductase; uridine diphosphoacetylpyruvoylglucosamine reductase; uridine diphospho-*N*-acetylglucosamine-enolpyruvate reductase; uridine-5'-diphospho-*N*-acetyl-2-amino-2-deoxy-3-*O*-lactylglucose:NADP-oxidoreductase
Systematic name: UDP-*N*-acetyl- α -D-muramate:NADP⁺ oxidoreductase
Comments: A flavoprotein (FAD). NADH can to a lesser extent replace NADPH.
References: [3795, 3796, 4003]

[EC 1.3.1.98 created 1976 as EC 1.1.1.158, modified 1983, modified 2002, transferred 2013 to EC 1.3.1.98]

EC 1.3.1.99

Accepted name: iridoid synthase
Reaction: (6*E*)-8-oxogeranial + NAD(P)H + H⁺ = *cis-trans*-nepetalactol + NAD(P)⁺
Systematic name: 8-oxogeranial:NAD(P)⁺ oxidoreductase (cyclizing, *cis-trans*-nepetalactol forming)
Comments: Isolated from the plant *Catharanthus roseus*. The reaction may involve cyclization via a Diels-Alder or Michael reaction. Iridoids are involved in the biosynthesis of many indole alkaloids. The cyclic hemiacetal is readily hydrolysed to the corresponding dial.
References: [1192]

[EC 1.3.1.99 created 2013]

EC 1.3.1.100

Accepted name: chanoclavine-I aldehyde reductase
Reaction: dihydrochanoclavine-I aldehyde + NADP⁺ = chanoclavine-I aldehyde + NADPH + H⁺
Other name(s): FgaOx3; *easA* (gene name)
Systematic name: chanoclavine-I aldehyde:NAD⁺ oxidoreductase

Comments: Contains FMN. The enzyme participates in the biosynthesis of fumigaclavine C, an ergot alkaloid produced by some fungi of the *Trichocomaceae* family. The enzyme catalyses the reduction of chanoclavine-I aldehyde to dihydrochanoclavine-I aldehyde. This hydrolyses spontaneously to form 6,8-dimethyl-6,7-didehydroergoline, which is converted to festuclavine by EC 1.5.1.44, festuclavine dehydrogenase.

References: [682, 582, 4097, 4279]

[EC 1.3.1.100 created 2013]

EC 1.3.1.101

Accepted name: 2,3-bis-*O*-geranylgeranyl-*sn*-glycerol 1-phosphate reductase [NAD(P)H]
Reaction: 2,3-bis-(*O*-phytanyl)-*sn*-glycerol 1-phosphate + 8 NAD(P)⁺ = 2,3-bis-(*O*-geranylgeranyl)-*sn*-glycerol 1-phosphate + 8 NAD(P)H + 8 H⁺
Other name(s): digeranylgeranyl-glycerophospholipid reductase; Ta0516m (gene name); DGGGPL reductase; 2,3-digeranylgeranyl-glycerophospholipid reductase
Systematic name: 2,3-bis-(*O*-phytanyl)-*sn*-glycerol 1-phosphate:NAD(P)⁺ oxidoreductase
Comments: A flavoprotein (FAD). The enzyme from the archaeon *Thermoplasma acidophilum* is involved in the biosynthesis of membrane lipids. *In vivo* the reaction occurs in the reverse direction with the formation of 2,3-bis-*O*-phytanyl-*sn*-glycerol 1-phosphate. *cf.* EC 1.3.7.11, 2,3-bis-*O*-geranylgeranyl-*sn*-glycero-phospholipid reductase.
References: [2795, 2796, 4286]

[EC 1.3.1.101 created 2013]

EC 1.3.1.102

Accepted name: 2-alkenal reductase (NADP⁺)
Reaction: an *n*-alkanal + NADP⁺ = an alk-2-enal + NADPH + H⁺
Other name(s): NADPH-dependent alkenal/one oxidoreductase; NADPH:2-alkenal α,β-hydrogenase
Systematic name: *n*-alkanal:NADP⁺ 2-oxidoreductase
Comments: Shows highest activity with 1-nitrocyclohexene but also has significant activity with 2-methylpentenal and *trans*-cinnamaldehyde [2387]. Involved in the detoxication of α,β-unsaturated aldehydes and ketones. Has very low activity with NAD as reductant (*cf.* EC 1.3.1.74, 2-alkenal reductase [NAD(P)⁺]).
References: [1518, 2454, 2387]

[EC 1.3.1.102 created 2013]

EC 1.3.1.103

Accepted name: 2-haloacrylate reductase
Reaction: (*S*)-2-chloropropanoate + NADP⁺ = 2-chloroacrylate + NADPH + H⁺
Other name(s): CAA43 (gene name)
Systematic name: (*S*)-2-chloropropanoate:NADP⁺ oxidoreductase
Comments: The enzyme acts in the degradation pathway of unsaturated organohalogen compounds by the bacterium *Burkholderia* sp. WS.
References: [2087]

[EC 1.3.1.103 created 2013]

EC 1.3.1.104

Accepted name: enoyl-[acyl-carrier-protein] reductase (NADPH)
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: [1448, 1914, 1912]

[EC 1.3.1.104 created 2013]

EC 1.3.1.105

Accepted name: 2-methylene-furan-3-one reductase

Reaction: 4-hydroxy-2,5-dimethylfuran-3(2*H*)-one + NADP⁺ = 4-hydroxy-5-methyl-2-methylenefuran-3(2*H*)-one + NADPH + H⁺

Other name(s): FaEO; SIEO; enone oxidoreductase; 4-hydroxy-2,5-dimethylfuran-3(2*H*)-one:NAD(P)⁺ oxidoreductase

Systematic name: 4-hydroxy-2,5-dimethylfuran-3(2*H*)-one:NADP⁺ oxidoreductase

Comments: The enzyme was discovered in strawberry (*Fragaria x ananassa*), where it produces furaneol, one of the major aroma compounds in the fruits. It has also been detected in tomato (*Solanum lycopersicum*) and pineapple (*Ananas comosus*). The enzyme can also act on derivatives substituted at the methylene functional group. The enzyme from the yeast *Saccharomyces cerevisiae* acts on (2*E*)-2-ethylidene-4-hydroxy-5-methylfuran-3(2*H*)-one and produces homofuraneol, an important aroma compound in soy sauce and miso. NADPH is the preferred cofactor.

References: [3095, 1964, 3364, 3965]

[EC 1.3.1.105 created 2013]

EC 1.3.1.106

Accepted name: cobalt-precorrin-6A reductase

Reaction: cobalt-precorrin-6B + NAD⁺ = cobalt-precorrin-6A + NADH + H⁺

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

Systematic name: cobalt-precorrin-6B:NAD⁺ oxidoreductase

Comments: The enzyme catalyses a step in the anaerobic (early cobalt insertion) pathway of adenosylcobalamin biosynthesis. The enzyme from the bacterium *Bacillus megaterium* has no activity with NADPH. The equivalent enzyme in the aerobic pathway is EC 1.3.1.54, precorrin-6A reductase.

References: [1922, 2609]

[EC 1.3.1.106 created 2014]

EC 1.3.1.107

Accepted name: sanguinarine reductase

Reaction: (1) dihydrosanguinarine + NAD(P)⁺ = sanguinarine + NAD(P)H + H⁺
(2) dihydrochelirubine + NAD(P)⁺ = chelirubine + NAD(P)H + H⁺

Systematic name: dihydrosanguinarine:NAD(P)⁺ oxidoreductase

Comments: The enzyme, purified from the California poppy (*Eschscholzia californica*), is involved in detoxifying the phytoalexin sanguinarine produced by poppy itself (*cf.* EC 1.5.3.12, dihydrobenzophenanthridine oxidase), when it binds to the cell wall of the poppy cell. The reaction with NADPH is up to three times faster than that with NADH at low concentrations (¡10 µM) of the dinucleotide. At higher concentrations the reaction with NADPH is inhibited but not that with NADH [4166].

References: [4166, 4050]

[EC 1.3.1.107 created 2014]

EC 1.3.1.108

Accepted name: caffeoyl-CoA reductase
Reaction: 3-(3,4-dihydroxyphenyl)propanoyl-CoA + 2 NAD⁺ + 2 reduced ferredoxin [iron-sulfur] cluster = (2E)-3-(3,4-dihydroxyphenyl)prop-2-enoyl-CoA + 2 NADH + 2 oxidized ferredoxin [iron-sulfur] cluster
Other name(s): electron-bifurcating caffeoyl-CoA reductase; caffeoyl-CoA reductase-Etf complex; hydrocaffeoyl-CoA:NAD⁺,ferredoxin oxidoreductase
Systematic name: 3-(3,4-dihydroxyphenyl)propanoyl-CoA:NAD⁺,ferredoxin oxidoreductase
Comments: The enzyme, characterized from the bacterium *Acetobacterium woodii*, contains two [4Fe-4S] clusters and FAD. The enzyme couples the endergonic ferredoxin reduction with NADH as reductant to the exergonic reduction of caffeoyl-CoA with the same reductant. It uses the mechanism of electron bifurcation to overcome the steep energy barrier in ferredoxin reduction. It also reduces 4-coumaroyl-CoA and feruloyl-CoA.
References: [285]

[EC 1.3.1.108 created 2015]

EC 1.3.1.109

Accepted name: butanoyl-CoA dehydrogenase (NAD⁺, ferredoxin)
Reaction: butanoyl-CoA + 2 NAD⁺ + 2 reduced ferredoxin [iron-sulfur] cluster = (E)-but-2-enoyl-CoA + 2 NADH + 2 oxidized ferredoxin [iron-sulfur] cluster
Other name(s): bifurcating butyryl-CoA dehydrogenase; butyryl-CoA dehydrogenase/Etf complex; Etf-Bcd complex; bifurcating butanoyl-CoA dehydrogenase; butanoyl-CoA dehydrogenase/Etf complex
Systematic name: butanoyl-CoA:NAD⁺, ferredoxin oxidoreductase
Comments: This flavin containing enzyme, isolated from the bacteria *Acidaminococcus fermentans* and butanoate-producing *Clostridia* species, couples the exergonic reduction of (E)-but-2-enoyl-CoA to butanoyl-CoA with NADH to the endergonic reduction of ferredoxin by NADH, using electron bifurcation to overcome the steep energy barrier in ferredoxin reduction.
References: [2223, 3014, 617]

[EC 1.3.1.109 created 2015]

EC 1.3.1.110

Accepted name: lactate dehydrogenase (NAD⁺,ferredoxin)
Reaction: lactate + 2 NAD⁺ + 2 reduced ferredoxin [iron-sulfur] cluster = pyruvate + 2 NADH + 2 oxidized ferredoxin [iron-sulfur] cluster
Other name(s): electron bifurcating LDH/Etf complex
Systematic name: lactate:NAD⁺,ferredoxin oxidoreductase
Comments: The enzyme, isolated from the bacterium *Acetobacterium woodii*, uses flavin-based electron bifurcation to drive endergonic lactate oxidation with NAD⁺ as oxidant at the expense of simultaneous exergonic electron flow from reduced ferredoxin to NAD⁺.
References: [4159]

[EC 1.3.1.110 created 2015]

EC 1.3.1.111

Accepted name: geranylgeranyl-bacteriochlorophyllide *a* reductase
Reaction: bacteriochlorophyll *a* + 3 NADP⁺ = geranylgeranyl bacteriochlorophyllide *a* + 3 NADPH + 3 H⁺
Other name(s): geranylgeranyl-bacteriopheophytin reductase; *bchP* (gene name)
Systematic name: bacteriochlorophyll-*a*:NADP⁺ oxidoreductase (geranylgeranyl-reducing)

Comments: The enzyme catalyses the successive reduction of the geranylgeraniol esterifying group to phytol, reducing three out of four double bonds, and transforming geranylgeranyl bacteriochlorophyllide *a* via dihydrogeranylgeranyl bacteriochlorophyllide *a* and tetrahydrogeranylgeranyl bacteriochlorophyllide *a* to bacteriochlorophyll *a*. The enzyme can also accept the pheophytin derivative geranylgeranyl bacteriopheophytin, converting it to bacteriopheophytin *a*.

References: [341, 25, 26, 1388]

[EC 1.3.1.111 created 2016]

EC 1.3.1.112

Accepted name: anthocyanidin reductase [(2*S*)-flavan-3-ol-forming]

Reaction: (1) a (2*S*,3*R*)-flavan-3-ol + 2 NADP⁺ = an anthocyanidin with a 3-hydroxy group + 2 NADPH + H⁺
(2) a (2*S*,3*S*)-flavan-3-ol + 2 NADP⁺ = an anthocyanidin with a 3-hydroxy group + 2 NADPH + H⁺

Systematic name: (2*S*)-flavan-3-ol:NAD(P)⁺ oxidoreductase

Comments: The enzyme, characterized from *Vitis vinifera* (grape), participates in the flavonoid biosynthesis pathway. It catalyses the double reduction of anthocyanidins, producing a mixture of (2*S*,3*S*)- and (2*S*,3*R*)-flavan-3-ols. The enzyme catalyses sequential hydride transfers to C-2 and C-4, respectively. Epimerization at C-3 is achieved by tautomerization that occurs between the two hydride transfers. *cf.* EC 1.3.1.77, anthocyanidin reductase [(2*R*,3*R*)-flavan-3-ol-forming].

References: [1158, 1157]

[EC 1.3.1.112 created 2016]

EC 1.3.1.113

Accepted name: (4-alkanoyl-5-oxo-2,5-dihydrofuran-3-yl)methyl phosphate reductase

Reaction: a [(3*S*)-4-alkanoyl-5-oxoxolan-3-yl]methyl phosphate + NADP⁺ = a (4-alkanoyl-5-oxo-2,5-dihydrofuran-3-yl)methyl phosphate + NADPH + H⁺

Other name(s): *bprA* (gene name); *scbB* (gene name)

Systematic name: [(3*S*)-4-alkanoyl-5-oxoxolan-3-yl]methyl phosphate:NADP⁺ oxidoreductase

Comments: The enzyme, characterized from the bacteria *Streptomyces griseus* and *Streptomyces coelicolor*, is involved in the biosynthesis of γ -butyrolactone autoregulators that control secondary metabolism and morphological development in *Streptomyces* bacteria.

References: [1835]

[EC 1.3.1.113 created 2017]

EC 1.3.1.114

Accepted name: 3-dehydro-bile acid $\Delta^{4,6}$ -reductase

Reaction: (1) 3-oxocholan-24-oyl-CoA + NAD⁺ = 3-oxochol-4-en-24-oyl-CoA + NADH + H⁺
(2) 3-oxochol-4-en-24-oyl-CoA + NAD⁺ = 3-oxochol-4,6-dien-24-oyl-CoA + NADH + H⁺
(3) 12 α -hydroxy-3-oxocholan-24-oyl-CoA + NAD⁺ = 12 α -hydroxy-3-oxochol-4-en-24-oyl-CoA + NADH + H⁺
(4) 12 α -hydroxy-3-oxochol-4-en-24-oyl-CoA + NAD⁺ = 12 α -hydroxy-3-oxochol-4,6-dien-24-oyl-CoA + NADH + H⁺

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

Systematic name: 3-oxocholan-24-oyl-CoA $\Delta^{4,6}$ -oxidoreductase

Comments: Contains flavin. The enzyme, characterized from the bacterium *Clostridium scindens*, participates in the bile acid 7 α -dehydroxylation pathway. The enzyme catalyses two subsequent reductions of the double bonds within the bile acid A/B rings, following 7 α -dehydration.

References: [1399]

[EC 1.3.1.114 created 2018]

EC 1.3.1.115

- Accepted name:** 3-oxocholoyl-CoA 4-desaturase
- Reaction:** (1) $7\alpha,12\alpha$ -dihydroxy-3-oxochol-24-oyl-CoA + NAD⁺ = $7\alpha,12\alpha$ -dihydroxy-3-oxochol-4-en-24-oyl-CoA + NADH + H⁺
(2) 7α -hydroxy-3-oxochol-24-oyl-CoA + NAD⁺ = 7α -hydroxy-3-oxochol-4-en-24-oyl-CoA + NADH + H⁺
- Other name(s):** *baiCD* (gene name); 3-oxo-choloyl-CoA dehydrogenase
- Systematic name:** 3-oxocholoyl-CoA Δ^4 -oxidoreductase
- Comments:** Contains flavin. The enzyme, characterized from the bacterium *Clostridium scindens*, participates in the bile acid 7α -dehydroxylation pathway. The enzyme catalyses the stereo-specific oxidation of its substrates and has no activity with the 7β anomers. *cf.* EC 1.3.1.116, 7β -hydroxy-3-oxochol-24-oyl-CoA 4-desaturase.
- References:** [1810]

[EC 1.3.1.115 created 2018]

EC 1.3.1.116

- Accepted name:** 7β -hydroxy-3-oxochol-24-oyl-CoA 4-desaturase
- Reaction:** 7β -hydroxy-3-oxochol-24-oyl-CoA + NAD⁺ = 7β -hydroxy-3-oxochol-4-en-24-oyl-CoA + NADH + H⁺
- Other name(s):** *baiH* (gene name)
- Systematic name:** 7β -hydroxy-3-oxochol-24-oyl-CoA Δ^4 -oxidoreductase
- Comments:** Contains FAD and FMN. The enzyme, characterized from the bacterium *Clostridium scindens*, participates in the bile acid 7α -dehydroxylation pathway. The enzyme catalyses the stereo-specific oxidation of its substrate and has no activity with the 7α anomer. *cf.* EC 1.3.1.115, 3-oxocholoyl-CoA 4-desaturase.
- References:** [203, 1056, 1810]

[EC 1.3.1.116 created 2018]

EC 1.3.1.117

- Accepted name:** hydroxycinnamoyl-CoA reductase
- Reaction:** (1) dihydro-4-coumaroyl-CoA + NADP⁺ = *trans*-4-coumaroyl-CoA + NADPH + H⁺
(2) dihydroferuloyl-CoA + NADP⁺ = *trans*-feruloyl-CoA + NADPH + H⁺
- Other name(s):** MdHCDBR; hydroxycinnamoyl-CoA double bond reductase
- Systematic name:** dihydro-4-coumaroyl-CoA:NADP⁺ 2,3-oxidoreductase
- Comments:** Isolated from *Malus X domestica* (apple). Involved in dihydrochalcone biosynthesis.
- References:** [1623]

[EC 1.3.1.117 created 2018]

EC 1.3.1.118

- Accepted name:** meromycolic acid enoyl-[acyl-carrier-protein] reductase
- Reaction:** a meromycolyl-[acyl-carrier protein] + NAD⁺ = a *trans*- Δ^2 -meromycolyl-[acyl-carrier protein] + NADH + H⁺
- Other name(s):** *inhA* (gene name)
- Systematic name:** meromycolyl-[acyl-carrier protein]:NAD⁺ oxidoreductase
- Comments:** InhA is a component of the fatty acid synthase (FAS) II system of *Mycobacterium tuberculosis*, catalysing an enoyl-[acyl-carrier-protein] reductase step. The enzyme acts on very long and unsaturated fatty acids that form the meromycolic component of mycolic acids. It extends FASI-derived C₂₀ fatty acids to form C₆₀ to C₉₀ mycolic acids. The enzyme, which forms a homotetramer, is the target of the preferred antitubercular drug isoniazid.
- References:** [3092, 3247, 2405, 4045, 1321, 612]

[EC 1.3.1.118 created 2018]

EC 1.3.1.119

- Accepted name:** chlorobenzene dihydrodiol dehydrogenase
Reaction: (1*R*,2*R*)-3-chlorocyclohexa-3,5-diene-1,2-diol + NAD⁺ = 3-chlorocatechol + NADH + H⁺
Other name(s): *tecB* (gene name)
Systematic name: (1*R*,2*R*)-3-chlorocyclohexa-3,5-diene-1,2-diol:NAD⁺ oxidoreductase
Comments: This bacterial enzyme can transform various dihydrodiols of chlorobenzenes into the respective catechols, including the dihydrodiols of mono-, di-, tri-, and tetra-chlorinated benzenes. It also accepts the dihydrodiols of various chlorotoluenes. Substrates for the enzyme are generated by the broad spectrum EC 1.14.12.26, chlorobenzene dioxygenase.
References: [3603, 3032, 3033]

[EC 1.3.1.119 created 2018]

EC 1.3.2 With a cytochrome as acceptor

[1.3.2.1 *Transferred entry. butyryl-CoA dehydrogenase. Now EC 1.3.99.2, butyryl-CoA dehydrogenase*]

[EC 1.3.2.1 created 1961, deleted 1964]

[1.3.2.2 *Transferred entry. acyl-CoA dehydrogenase. Now EC 1.3.99.3, acyl-CoA dehydrogenase*]

[EC 1.3.2.2 created 1961, deleted 1964]

EC 1.3.2.3

- Accepted name:** L-galactonolactone dehydrogenase
Reaction: L-galactono-1,4-lactone + 4 ferricytochrome *c* = L-dehydroascorbate + 4 ferrocyclochrome *c* + 4 H⁺ (overall reaction)
(1a) L-galactono-1,4-lactone + 2 ferricytochrome *c* = L-ascorbate + 2 ferrocyclochrome *c* + 2 H⁺
(1b) L-ascorbate + 2 ferricytochrome *c* = L-dehydroascorbate + 2 ferrocyclochrome *c* + 2 H⁺ (spontaneous)
Other name(s): galactonolactone dehydrogenase; L-galactono- γ -lactone dehydrogenase; L-galactono- γ -lactone:ferricytochrome-*c* oxidoreductase; GLDHase; GLDase
Systematic name: L-galactono-1,4-lactone:ferricytochrome-*c* oxidoreductase
Comments: This enzyme catalyses the final step in the biosynthesis of L-ascorbic acid in higher plants and in nearly all higher animals with the exception of primates and some birds [2904]. The enzyme is very specific for its substrate L-galactono-1,4-lactone as D-galactono- γ -lactone, D-gulono- γ -lactone, L-gulono- γ -lactone, D-erythronic- γ -lactone, D-xylonic- γ -lactone, L-mannono- γ -lactone, D-galactonate, D-glucuronate and D-gluconate are not substrates [2904]. FAD, NAD⁺, NADP⁺ and O₂ (*cf.* EC 1.3.3.12, L-galactonolactone oxidase) cannot act as electron acceptor [2904].
References: [2390, 2391, 1662, 2832, 2904]

[EC 1.3.2.3 created 1961, modified 2006]

EC 1.3.3 With oxygen as acceptor

[1.3.3.1 *Transferred entry. dihydroorotate oxidase. Now EC 1.3.98.1 [dihydroorotate dehydrogenase (fumarate)]*]

[EC 1.3.3.1 created 1961, deleted 2011]

[1.3.3.2 *Transferred entry. now EC 1.14.21.6, lathosterol oxidase. NAD(P)H had not been included previously, so enzyme had to be reclassified*]

[EC 1.3.3.2 created 1972, deleted 2005]

EC 1.3.3.3

Accepted name: coproporphyrinogen oxidase
Reaction: coproporphyrinogen III + O₂ + 2 H⁺ = protoporphyrinogen-IX + 2 CO₂ + 2 H₂O
Other name(s): coproporphyrinogen III oxidase; coproporphyrinogenase
Systematic name: coproporphyrinogen:oxygen oxidoreductase (decarboxylating)
References: [214, 2495, 2010]

[EC 1.3.3.3 created 1972, modified 2003]

EC 1.3.3.4

Accepted name: protoporphyrinogen oxidase
Reaction: protoporphyrinogen IX + 3 O₂ = protoporphyrin IX + 3 H₂O₂
Other name(s): protoporphyrinogen IX oxidase; protoporphyrinogenase; PPO; Protox; HemG; HemY
Systematic name: protoporphyrinogen-IX:oxygen oxidoreductase
Comments: This is the last common enzyme in the biosynthesis of chlorophylls and heme [561]. Two isoenzymes exist in plants: one in plastids and the other in mitochondria. This is the target enzyme of phthalimide-type and diphenylether-type herbicides [561]. The enzyme from oxygen-dependent species contains FAD [727]. Also slowly oxidizes mesoporphyrinogen IX.
References: [3046, 3047, 724, 4108, 665, 1003, 726, 561, 727]

[EC 1.3.3.4 created 1978, modified 2003]

EC 1.3.3.5

Accepted name: bilirubin oxidase
Reaction: 2 bilirubin + O₂ = 2 biliverdin + 2 H₂O
Other name(s): bilirubin oxidase M-1
Systematic name: bilirubin:oxygen oxidoreductase
References: [2668, 3804]

[EC 1.3.3.5 created 1984]

EC 1.3.3.6

Accepted name: acyl-CoA oxidase
Reaction: acyl-CoA + O₂ = *trans*-2,3-dehydroacyl-CoA + H₂O₂
Other name(s): fatty acyl-CoA oxidase; acyl coenzyme A oxidase; fatty acyl-coenzyme A oxidase
Systematic name: acyl-CoA:oxygen 2-oxidoreductase
Comments: A flavoprotein (FAD). Acts on CoA derivatives of fatty acids with chain lengths from 8 to 18.
References: [1857, 2907]

[EC 1.3.3.6 created 1986]

EC 1.3.3.7

Accepted name: dihydrouracil oxidase
Reaction: 5,6-dihyrouracil + O₂ = uracil + H₂O₂
Systematic name: 5,6-dihyrouracil:oxygen oxidoreductase
Comments: Also oxidizes dihydrothymine to thymine. A flavoprotein (FMN).
References: [2920]

[EC 1.3.3.7 created 1989]

EC 1.3.3.8

Accepted name: tetrahydroberberine oxidase

Reaction: (S)-tetrahydroberberine + 2 O₂ = berberine + 2 H₂O₂
Other name(s): (S)-THB oxidase
Systematic name: (S)-tetrahydroberberine:oxygen oxidoreductase
Comments: The enzyme from *Berberis* sp. is a flavoprotein; that from *Coptis japonica* is not. (R)-Tetrahydroberberines are not oxidized.
References: [68, 2860]

[EC 1.3.3.8 created 1990 (EC 1.5.3.8 created 1989, incorporated 1992)]

[1.3.3.9 Transferred entry. secologanin synthase. Now EC 1.14.19.62, secologanin synthase]

[EC 1.3.3.9 created 2002, deleted 2018]

EC 1.3.3.10

Accepted name: tryptophan α,β -oxidase
Reaction: L-tryptophan + O₂ = α,β -didehydrotryptophan + H₂O₂
Other name(s): L-tryptophan 2',3'-oxidase; L-tryptophan α,β -dehydrogenase
Systematic name: L-tryptophan:oxygen α,β -oxidoreductase
Comments: Requires heme. The enzyme from *Chromobacterium violaceum* is specific for tryptophan derivatives possessing its carboxyl group free or as an amide or ester, and an unsubstituted indole ring. Also catalyses the α,β dehydrogenation of L-tryptophan side chains in peptides. The product of the reaction can hydrolyse spontaneously to form (indol-3-yl)pyruvate.
References: [1180, 1179]

[EC 1.3.3.10 created 2000 as EC 1.4.3.17, transferred 2003 to EC 1.3.3.10]

EC 1.3.3.11

Accepted name: pyrroloquinoline-quinone synthase
Reaction: 6-(2-amino-2-carboxyethyl)-7,8-dioxo-1,2,3,4,7,8-hexahydroquinoline-2,4-dicarboxylate + 3 O₂ = 4,5-dioxo-4,5-dihydro-1H-pyrrolo[2,3-f]quinoline-2,7,9-tricarboxylate + 2 H₂O₂ + 2 H₂O
Other name(s): PqqC; 6-(2-amino-2-carboxyethyl)-7,8-dioxo-1,2,3,4,5,6,7,8-octahydroquinoline-2,4-dicarboxylate:oxygen oxidoreductase (cyclizing) [incorrect]
Systematic name: 6-(2-amino-2-carboxyethyl)-7,8-dioxo-1,2,3,4,7,8-hexahydroquinoline-2,4-dicarboxylate:oxygen oxidoreductase (cyclizing)
Comments: So far only a single turnover of the enzyme has been observed, and the pyrroloquinoline quinone remains bound to it. It is not yet known what releases the product in the bacterium.
References: [2363, 2362, 3919, 3921, 3414]

[EC 1.3.3.11 created 2005]

EC 1.3.3.12

Accepted name: L-galactonolactone oxidase
Reaction: L-galactono-1,4-lactone + O₂ = L-ascorbate + H₂O₂
Other name(s): L-galactono-1,4-lactone oxidase
Systematic name: L-galactono-1,4-lactone:oxygen 3-oxidoreductase
Comments: A flavoprotein. Acts on the 1,4-lactones of L-galactonic, D-altronic, L-fuconic, D-arabinic and D-threonic acids; not identical with EC 1.1.3.8 L-gulonolactone oxidase. (cf. EC 1.3.2.3 galactonolactone dehydrogenase).
References: [321]

[EC 1.3.3.12 created 1984 as EC 1.1.3.24, transferred 2006 to EC 1.3.3.12]

EC 1.3.3.13

Accepted name: albonoursin synthase

Reaction: cyclo(L-leucyl-L-phenylalanyl) + 2 O₂ = albonoursin + 2 H₂O₂ (overall reaction)
(1a) cyclo(L-leucyl-L-phenylalanyl) + O₂ = cyclo[(Z)-α,β-didehydrophenylalanyl-L-leucyl] + H₂O₂
(1b) cyclo[(Z)-α,β-didehydrophenylalanyl-L-leucyl] + O₂ = albonoursin + H₂O₂

Other name(s): cyclo(dipeptide):oxygen oxidoreductase; cyclic dipeptide oxidase; AlbA

Systematic name: cyclo(L-leucyl-L-phenylalanyl):oxygen oxidoreductase

Comments: A flavoprotein from the bacterium *Streptomyces noursei*. The enzyme can also oxidize several other cyclo dipeptides, the best being cyclo(L-tryptophyl-L-tryptophyl) and cyclo(L-phenylalanyl-L-phenylalanyl) [1237, 2152].

References: [1237, 2152]

[EC 1.3.3.13 created 2013]

EC 1.3.3.14

Accepted name: aclacinomycin-A oxidase

Reaction: aclacinomycin A + O₂ = aclacinomycin Y + H₂O₂

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 rhodnose 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: [4385, 60, 3725]

[EC 1.3.3.14 created 2013]

EC 1.3.3.15

Accepted name: coproporphyrinogen III oxidase (coproporphyrin-forming)

Reaction: coproporphyrinogen III + 3 O₂ = coproporphyrin III + 3 H₂O₂

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

Systematic name: coproporphyrinogen-III:oxygen oxidoreductase (coproporphyrin-forming)

Comments: Contains FAD. The enzyme, present in Gram-positive bacteria, participates in heme biosynthesis. It can also catalyse the reaction of EC 1.3.3.4, protoporphyrinogen oxidase, at a lower level.

References: [1376, 665, 3078, 725]

[EC 1.3.3.15 created 2016]

EC 1.3.4 With a disulfide as acceptor

EC 1.3.4.1

Accepted name: fumarate reductase (CoM/CoB)

Reaction: fumarate + CoM + CoB = succinate + CoM-S-S-CoB

Other name(s): thiol:fumarate reductase; Tfr

Systematic name: fumarate CoM:CoB oxidoreductase (succinate-forming)

Comments: The enzyme, isolated from the archaeon *Methanobacterium thermoautotrophicum*, is very oxygen sensitive. It cannot use reduced flavins, reduced coenzyme F₄₂₀, or NAD(P)H as an electron donor. Distinct from EC 1.3.1.6 [fumarate reductase (NADH)], EC 1.3.5.1 [succinate dehydrogenase (ubiquinone)], and EC 1.3.5.4 [fumarate reductase (quinol)].

References: [1894, 1462]

[EC 1.3.4.1 created 2014 as EC 1.3.98.2, transferred 2014 to EC 1.3.4.1]

EC 1.3.5 With a quinone or related compound as acceptor

EC 1.3.5.1

- Accepted name:** succinate dehydrogenase
Reaction: succinate + a quinone = fumarate + a quinol
Other name(s): succinate dehydrogenase (quinone); succinate dehydrogenase (ubiquinone); succinic dehydrogenase; complex II (ambiguous); succinate dehydrogenase complex; SDH; succinate:ubiquinone oxidoreductase
- Systematic name:** succinate:quinone oxidoreductase
Comments: A flavoprotein (FAD) complex containing iron-sulfur centres. The enzyme is found in the inner mitochondrial membrane in eukaryotes and the plasma membrane of many aerobic or facultative bacteria and archaea. It catalyses succinate oxidation in the citric acid cycle and transfers the electrons to quinones in the membrane, thus constituting a part of the aerobic respiratory chain (known as complex II). *In vivo* the enzyme uses the quinone found in the organism - eukaryotic enzymes utilize ubiquinone, bacterial enzymes utilize ubiquinone or menaquinone, and archaeobacterial enzymes from the *Sulfolobus* genus use caldariellaquinone. *cf.* EC 1.3.5.4, fumarate reductase (quinone).
References: [1942, 1420, 2595, 1014, 528, 2921, 2092]

[EC 1.3.5.1 created 1983 (EC 1.3.99.1 created 1961, incorporated 2014)]

EC 1.3.5.2

- Accepted name:** dihydroorotate dehydrogenase (quinone)
Reaction: (S)-dihydroorotate + a quinone = orotate + a quinol
Other name(s): dihydroorotate:ubiquinone oxidoreductase; (S)-dihydroorotate:(acceptor) oxidoreductase; (S)-dihydroorotate:acceptor oxidoreductase; DHODEhase (ambiguous); DHOD (ambiguous); DHODase (ambiguous); DHODH
- Systematic name:** (S)-dihydroorotate:quinone oxidoreductase
Comments: This Class 2 dihydroorotate dehydrogenase enzyme contains FMN [978]. The enzyme is found in eukaryotes in the mitochondrial membrane, in cyanobacteria, and in some Gram-negative and Gram-positive bacteria associated with the cytoplasmic membrane [2,5,6]. The reaction is the only redox reaction in the *de-novo* biosynthesis of pyrimidine nucleotides [1510, 978]. The best quinone electron acceptors for the enzyme from bovine liver are ubiquinone-6 and ubiquinone-7, although simple quinones, such as benzoquinone, can also act as acceptor at lower rates [1510]. Methyl-, ethyl-, *tert*-butyl and benzyl (S)-dihydroorotates are also substrates, but methyl esters of (S)-1-methyl and (S)-3-methyl and (S)-1,3-dimethyldihydroorotates are not [1510]. Class 1 dihydroorotate dehydrogenases use either fumarate (EC 1.3.98.1), NAD⁺ (EC 1.3.1.14) or NADP⁺ (EC 1.3.1.15) as electron acceptor.
References: [1035, 1510, 157, 978, 305, 2732]

[EC 1.3.5.2 created 1983 as EC 1.3.99.11, transferred 2009 to EC 1.3.5.2, modified 2011]

EC 1.3.5.3

- Accepted name:** protoporphyrinogen IX dehydrogenase (menaquinone)
Reaction: protoporphyrinogen IX + 3 menaquinone = protoporphyrin IX + 3 menaquinol
Other name(s): HemG
Systematic name: protoporphyrinogen IX:menaquinone oxidoreductase
Comments: This enzyme enables *Escherichia coli* to synthesize heme in both aerobic and anaerobic environments.
References: [374]

[EC 1.3.5.3 created 2010]

EC 1.3.5.4

Accepted name: fumarate reductase (quinol)
Reaction: succinate + a quinone = fumarate + a quinol
Other name(s): FRD; menaquinol-fumarate oxidoreductase; succinate dehydrogenase (menaquinone); succinate:menaquinone oxidoreductase; fumarate reductase (menaquinone); complex II (ambiguous)
Systematic name: succinate:quinone oxidoreductase
Comments: The enzyme, which is found in anaerobic and facultative organisms such as bacteria, parasitic helminthes, and lower marine organisms, utilizes low potential quinols, such as menaquinol and rhodoquinol, to reduce fumarate as the final step of an anaerobic respiratory chain. The enzyme is known as complex II of the electron transfer chain, similarly to EC 1.3.5.1, succinate dehydrogenase (quinone), to which it is closely related.
References: [1468, 1689, 529, 1690, 4004]

[EC 1.3.5.4 created 2010, modified 2013]

EC 1.3.5.5

Accepted name: 15-*cis*-phytoene desaturase
Reaction: 15-*cis*-phytoene + 2 plastoquinone = 9,15,9'-*tricus*- ζ -carotene + 2 plastoquinol (overall reaction)
(1a) 15-*cis*-phytoene + plastoquinone = 15,9'-*dicis*-phytofluene + plastoquinol
(1b) 15,9'-*dicis*-phytofluene + plastoquinone = 9,15,9'-*tricus*- ζ -carotene + plastoquinol
Other name(s): phytoene desaturase (ambiguous); PDS; plant-type phytoene desaturase
Systematic name: 15-*cis*-phytoene:plastoquinone oxidoreductase
Comments: This enzyme is involved in carotenoid biosynthesis in plants and cyanobacteria. The enzyme from *Synechococcus* can also use NAD⁺ and NADP⁺ as electron acceptor under anaerobic conditions. The enzyme from *Gentiana lutea* shows no activity with NAD⁺ or NADP⁺ [397].
References: [397, 3381, 1057, 396]

[EC 1.3.5.5 created 2011]

EC 1.3.5.6

Accepted name: 9,9'-*dicis*- ζ -carotene desaturase
Reaction: 9,9'-*dicis*- ζ -carotene + 2 quinone = 7,9,7',9'-*tetracis*-lycopene + 2 quinol (overall reaction)
(1a) 9,9'-*dicis*- ζ -carotene + a quinone = 7,9,9'-*tricus*-neurosporene + a quinol
(1b) 7,9,9'-*tricus*-neurosporene + a quinone = 7,9,7',9'-*tetracis*-lycopene + a quinol
Other name(s): ζ -carotene desaturase; ZDS
Systematic name: 9,9'-*dicis*- ζ -carotene:quinone oxidoreductase
Comments: This enzyme is involved in carotenoid biosynthesis in plants and cyanobacteria.
References: [55, 1778, 394, 396]

[EC 1.3.5.6 created 1999 as EC 1.14.99.30, transferred 2011 to EC 1.3.5.6]

EC 1.3.7 With an iron-sulfur protein as acceptor

EC 1.3.7.1

Accepted name: 6-hydroxynicotinate reductase
Reaction: 6-oxo-1,4,5,6-tetrahydronicotinate + oxidized ferredoxin = 6-hydroxynicotinate + reduced ferredoxin
Other name(s): 6-oxotetrahydronicotinate dehydrogenase; 6-hydroxynicotinic reductase; HNA reductase; 1,4,5,6-tetrahydro-6-oxonicotinate:ferredoxin oxidoreductase
Systematic name: 6-oxo-1,4,5,6-tetrahydronicotinate:ferredoxin oxidoreductase
References: [1538]

[EC 1.3.7.1 created 1972]

EC 1.3.7.2

- Accepted name:** 15,16-dihydrobiliverdin:ferredoxin oxidoreductase
Reaction: 15,16-dihydrobiliverdin + oxidized ferredoxin = biliverdin IX α + reduced ferredoxin
Other name(s): PebA
Systematic name: 15,16-dihydrobiliverdin:ferredoxin oxidoreductase
Comments: Catalyses the two-electron reduction of biliverdin IX α at the C15 methine bridge. It has been proposed that this enzyme and EC 1.3.7.3, phycoerythrobilin:ferredoxin oxidoreductase, function as a dual enzyme complex in the conversion of biliverdin IX α into phycoerythrobilin.
References: [1055]

[EC 1.3.7.2 created 2002]

EC 1.3.7.3

- Accepted name:** phycoerythrobilin:ferredoxin oxidoreductase
Reaction: (3Z)-phycoerythrobilin + oxidized ferredoxin = 15,16-dihydrobiliverdin + reduced ferredoxin
Other name(s): PebB
Systematic name: (3Z)-phycoerythrobilin:ferredoxin oxidoreductase
Comments: Catalyses the two-electron reduction of the C2 and C3¹ diene system of 15,16-dihydrobiliverdin. Specific for 15,16-dihydrobiliverdin. It has been proposed that this enzyme and EC 1.3.7.2, 15,16-dihydrobiliverdin:ferredoxin oxidoreductase, function as a dual enzyme complex in the conversion of biliverdin IX α to phycoerythrobilin.
References: [1055]

[EC 1.3.7.3 created 2002]

EC 1.3.7.4

- Accepted name:** phytochromobilin:ferredoxin oxidoreductase
Reaction: (3Z)-phytochromobilin + 2 oxidized ferredoxin = biliverdin IX α + 2 reduced ferredoxin
Other name(s): HY2; PPhi B synthase; phytochromobilin synthase
Systematic name: (3Z)-phytochromobilin:ferredoxin oxidoreductase
Comments: Catalyses the two-electron reduction of biliverdin IX α . Can use [2Fe-2S] ferredoxins from a number of sources as acceptor but not the [4Fe-4S] ferredoxin from *Clostridium pasteurianum*. The isomerization of (3Z)-phytochromobilin to (3E)-phytochromobilin is thought to occur prior to covalent attachment to apophytochrome in the plant cell cytoplasm. Flavodoxins can be used instead of ferredoxin.
References: [1055, 2483, 3850]

[EC 1.3.7.4 created 2002]

EC 1.3.7.5

- Accepted name:** phycocyanobilin:ferredoxin oxidoreductase
Reaction: (3Z)-phycocyanobilin + 4 oxidized ferredoxin = biliverdin IX α + 4 reduced ferredoxin
Systematic name: (3Z)-phycocyanobilin:ferredoxin oxidoreductase
Comments: Catalyses the four-electron reduction of biliverdin IX α (2-electron reduction at both the A and D rings). Reaction proceeds via an isolatable 2-electron intermediate, 18¹,18²-dihydrobiliverdin. Flavodoxins can be used instead of ferredoxin. The direct conversion of biliverdin IX α (BV) to (3Z)-phycocyanobilin (PCB) in the cyanobacteria *Synechocystis* sp. PCC 6803, *Anabaena* sp. PCC7120 and *Nostoc punctiforme* is in contrast to the proposed pathways of PCB biosynthesis in the red alga *Cyanidium caldarium*, which involves (3Z)-phycoerythrobilin (PEB) as an intermediate [227] and in the green alga *Mesotaenium caldariorum*, in which PCB is an isolable intermediate.
References: [1055, 227, 4261]

[EC 1.3.7.5 created 2002, modified 2014]

EC 1.3.7.6

- Accepted name:** phycoerythrobilin synthase
Reaction: (3Z)-phycoerythrobilin + 2 oxidized ferredoxin = biliverdin IX α + 2 reduced ferredoxin
Other name(s): PebS
Systematic name: (3Z)-phycoerythrobilin:ferredoxin oxidoreductase (from biliverdin IX α)
Comments: This enzyme, from a cyanophage infecting oceanic cyanobacteria of the *Prochlorococcus* genus, uses a four-electron reduction to carry out the reactions catalysed by EC 1.3.7.2 (15,16-dihydrobiliverdin:ferredoxin oxidoreductase) and EC 1.3.7.3 (phycoerythrobilin:ferredoxin oxidoreductase). 15,16-Dihydrobiliverdin is formed as a bound intermediate. Free 15,16-dihydrobiliverdin can also act as a substrate to form phycoerythrobilin.
References: [733]

[EC 1.3.7.6 created 2008]

EC 1.3.7.7

- Accepted name:** ferredoxin:protochlorophyllide reductase (ATP-dependent)
Reaction: chlorophyllide *a* + oxidized ferredoxin + 2 ADP + 2 phosphate = protochlorophyllide *a* + reduced ferredoxin + 2 ATP + 2 H₂O
Other name(s): light-independent protochlorophyllide reductase
Systematic name: ATP-dependent ferredoxin:protochlorophyllide-*a* 7,8-oxidoreductase
Comments: Occurs in photosynthetic bacteria, cyanobacteria, green algae and gymnosperms. The enzyme catalyses *trans*-reduction of the D-ring of protochlorophyllide; the product has the (7*S*,8*S*)-configuration. Unlike EC 1.3.1.33 (protochlorophyllide reductase), light is not required. The enzyme contains a [4Fe-4S] cluster, and structurally resembles the Fe protein/MoFe protein complex of nitrogenase (EC 1.18.6.1), which catalyses an ATP-driven reduction.
References: [1100, 2815, 2666]

[EC 1.3.7.7 created 2011, modified 2013]

EC 1.3.7.8

- Accepted name:** benzoyl-CoA reductase
Reaction: cyclohexa-1,5-diene-1-carbonyl-CoA + oxidized ferredoxin + 2 ADP + 2 phosphate = benzoyl-CoA + reduced ferredoxin + 2 ATP + 2 H₂O
Other name(s): benzoyl-CoA reductase (dearomatizing)
Systematic name: cyclohexa-1,5-diene-1-carbonyl-CoA:ferredoxin oxidoreductase (aromatizing, ATP-forming)
Comments: An iron-sulfur protein. Requires Mg²⁺ or Mn²⁺. Inactive towards aromatic acids that are not CoA esters but will also catalyse the reaction: ammonia + acceptor + 2 ADP + 2 phosphate = hydroxylamine + reduced acceptor + 2 ATP + H₂O. In the presence of reduced acceptor, but in the absence of oxidizable substrate, the enzyme catalyses the hydrolysis of ATP to ADP plus phosphate.
References: [339, 2079]

[EC 1.3.7.8 created 1999 as EC 1.3.99.15, transferred 2011 to EC 1.3.7.8, modified 2011]

EC 1.3.7.9

- Accepted name:** 4-hydroxybenzoyl-CoA reductase
Reaction: benzoyl-CoA + oxidized ferredoxin + H₂O = 4-hydroxybenzoyl-CoA + reduced ferredoxin
Other name(s): 4-hydroxybenzoyl-CoA reductase (dehydroxylating); 4-hydroxybenzoyl-CoA:(acceptor) oxidoreductase
Systematic name: benzoyl-CoA:acceptor oxidoreductase
Comments: A molybdenum-flavin-iron-sulfur protein that is involved in the anaerobic pathway of phenol metabolism in bacteria. A ferredoxin with two [4Fe-4S] clusters functions as the natural electron donor [392].
References: [1223, 1456, 392, 378, 1457]

[EC 1.3.7.9 created 2000 as EC 1.3.99.20, transferred 2011 to EC 1.3.7.9]

[1.3.7.10 Transferred entry. pentalenolactone synthase. Now EC 1.14.19.8, pentalenolactone synthase]

[EC 1.3.7.10 created 2012, deleted 2013]

EC 1.3.7.11

Accepted name: 2,3-bis-*O*-geranylgeranyl-*sn*-glycero-phospholipid reductase
Reaction: a 2,3-bis-(*O*-phytanyl)-*sn*-glycero-phospholipid + **16** oxidized ferredoxin [iron-sulfur] cluster = a 2,3-bis-(*O*-geranylgeranyl)-*sn*-glycero-phospholipid + **16** reduced ferredoxin [iron-sulfur] cluster + **16** H⁺
Other name(s): AF0464 (gene name); 2,3-bis-*O*-geranylgeranyl-*sn*-glycerol 1-phosphate reductase (donor)
Systematic name: 2,3-bis-(*O*-phytanyl)-*sn*-glycero-phospholipid:ferredoxin oxidoreductase
Comments: A flavoprotein (FAD). The enzyme is involved in the biosynthesis of archaeal membrane lipids. It catalyses the reduction of all 8 double bonds in 2,3-bis-*O*-geranylgeranyl-*sn*-glycero-phospholipids and all 4 double bonds in 3-*O*-geranylgeranyl-*sn*-glycerol phospholipids with comparable activity. Unlike EC 1.3.1.101, 2,3-bis-*O*-geranylgeranyl-*sn*-glycerol 1-phosphate reductase [NAD(P)H], this enzyme shows no activity with NADPH, and requires a dedicated ferredoxin [1674].
References: [2665, 3319, 3316, 1674]

[EC 1.3.7.11 created 2013 as EC 1.3.99.34, transferred 2015 to EC 1.3.7.11]

EC 1.3.7.12

Accepted name: red chlorophyll catabolite reductase
Reaction: primary fluorescent chlorophyll catabolite + **2** oxidized ferredoxin [iron-sulfur] cluster = red chlorophyll catabolite + **2** reduced ferredoxin [iron-sulfur] cluster + **2** H⁺
Other name(s): RCCR; RCC reductase; red Chl catabolite reductase
Systematic name: primary fluorescent chlorophyll catabolite:ferredoxin oxidoreductase
Comments: The enzyme participates in chlorophyll degradation, which occurs during leaf senescence and fruit ripening in higher plants. The reaction requires reduced ferredoxin, which is generated from NADPH produced either through the pentose-phosphate pathway or by the action of photosystem I [3209, 4270]. This reaction takes place while red chlorophyll catabolite is still bound to EC 1.14.15.17, pheophorbide *a* oxygenase [3070]. Depending on the plant species used as the source of enzyme, one of two possible C-1 epimers of primary fluorescent chlorophyll catabolite (pFCC), pFCC-1 or pFCC-2, is normally formed, with all genera or species within a family producing the same isomer [3070, 1575]. After modification and export, pFCCs are eventually imported into the vacuole, where the acidic environment causes their non-enzymic conversion into colourless breakdown products called non-fluorescent chlorophyll catabolites (NCCs) [4270].
References: [3209, 4270, 3070, 1575, 3210]

[EC 1.3.7.12 created 2007 as EC 1.3.1.80, transferred 2016 to EC 1.3.7.12]

EC 1.3.7.13

Accepted name: 3,8-divinyl protochlorophyllide *a* 8-vinyl-reductase (ferredoxin)
Reaction: protochlorophyllide *a* + **2** oxidized ferredoxin [iron-sulfur] cluster = 3,8-divinyl protochlorophyllide *a* + **2** reduced ferredoxin [iron-sulfur] cluster + **2** H⁺
Other name(s): *bciB* (gene name); cyano-type divinyl chlorophyllide *a* 8-vinyl-reductase
Systematic name: protochlorophyllide-*a*:ferredoxin C-8¹-oxidoreductase
Comments: The enzyme, found in many phototrophic bacteria, land plants, and some green and red algae, is involved in the production of monovinyl versions of (bacterio)chlorophyll pigments from their divinyl precursors. Binds two [4Fe-4S] clusters and an FAD cofactor. It can also act on 3,8-divinyl chlorophyllide *a*, 3,8-divinyl chlorophyll *a*, and chlorophyll *c*₂. *cf.* EC 1.3.1.75, 3,8-divinyl protochlorophyllide *a* 8-vinyl-reductase (NADPH).
References: [587, 3325, 1682]

[EC 1.3.7.13 created 2016]

EC 1.3.7.14

- Accepted name:** 3,8-divinyl chlorophyllide *a* reductase
Reaction: bacteriochlorophyllide *g* + 2 oxidized ferredoxin [iron-sulfur] cluster + ADP + phosphate = 3,8-divinyl chlorophyllide *a* + 2 reduced ferredoxin [iron-sulfur] cluster + ATP + H₂O + 2 H⁺
Systematic name: bacteriochlorophyllide-*g*:ferredoxin C-8¹-oxidoreductase
Comments: The enzyme, found only in bacteriochlorophyll *b*-producing bacteria, catalyses the introduction of a C-8 ethylidene group. The enzyme contains a [4Fe-4S] cluster, and structurally resembles the Fe protein/MoFe protein complex of nitrogenase. It is very similar to EC 1.3.7.15, chlorophyllide *a* reductase, and is composed of three subunits. Two of them form the catalytic component, while the third one functions as an ATP-dependent reductase component that catalyses the electron transfer from ferredoxin to the catalytic component.
References: [3943, 3942]

[EC 1.3.7.14 created 2016]

EC 1.3.7.15

- Accepted name:** chlorophyllide *a* reductase
Reaction: (1) 3-deacetyl-3-vinylbacteriochlorophyllide *a* + 2 oxidized ferredoxin [iron-sulfur] cluster + ADP + phosphate = chlorophyllide *a* + 2 reduced ferredoxin [iron-sulfur] cluster + ATP + H₂O + 2 H⁺
(2) bacteriochlorophyllide *a* + 2 oxidized ferredoxin [iron-sulfur] cluster + ADP + phosphate = 3-acetyl-3-devinylchlorophyllide *a* + 2 reduced ferredoxin [iron-sulfur] cluster + ATP + H₂O + 2 H⁺
(3) 3-deacetyl-3-(1-hydroxyethyl)bacteriochlorophyllide *a* + 2 oxidized ferredoxin [iron-sulfur] cluster + ADP + phosphate = 3-devinyl-3-(1-hydroxyethyl)chlorophyllide *a* + 2 reduced ferredoxin [iron-sulfur] cluster + ATP + H₂O + 2 H⁺
Other name(s): *bchX* (gene name); *bchY* (gene name); *bchZ* (gene name); COR
Systematic name: bacteriochlorophyllide-*a*:ferredoxin 7,8-oxidoreductase
Comments: The enzyme, together with EC 1.1.1.396, bacteriochlorophyllide-*a* dehydrogenase, and EC 4.2.1.165, chlorophyllide-*a* 3¹-hydratase, is involved in the conversion of chlorophyllide *a* to bacteriochlorophyllide *a*. These enzymes can act in multiple orders, resulting in the formation of different intermediates, but the final product of the cumulative action of the three enzymes is always bacteriochlorophyllide *a*. This enzyme catalyses a *trans*-reduction of the B-ring; the product has the (7*R*,8*R*)-configuration. In addition, the enzyme has a latent activity of EC 1.3.7.13, 3,8-divinyl protochlorophyllide *a* 8-vinyl-reductase (ferredoxin) [1390]. The enzyme contains a [4Fe-4S] cluster, and structurally resembles the Fe protein/MoFe protein complex of nitrogenase (EC 1.18.6.1), which catalyses an ATP-driven reduction.
References: [2814, 3943, 2131, 1390]

[EC 1.3.7.15 created 1965 as EC 1.3.99.35, modified 2012, transferred 2016 to EC 1.3.7.15]

EC 1.3.8 With a flavin as acceptor

EC 1.3.8.1

- Accepted name:** short-chain acyl-CoA dehydrogenase
Reaction: a short-chain acyl-CoA + electron-transfer flavoprotein = a short-chain *trans*-2,3-dehydroacyl-CoA + reduced electron-transfer flavoprotein
Other name(s): butyryl-CoA dehydrogenase; butanoyl-CoA dehydrogenase; butyryl dehydrogenase; unsaturated acyl-CoA reductase; ethylene reductase; enoyl-coenzyme A reductase; unsaturated acyl coenzyme A reductase; butyryl coenzyme A dehydrogenase; short-chain acyl CoA dehydrogenase; short-chain acyl-coenzyme A dehydrogenase; 3-hydroxyacyl CoA reductase; butanoyl-CoA:(acceptor) 2,3-oxidoreductase; ACADS (gene name).

Systematic name: short-chain acyl-CoA:electron-transfer flavoprotein 2,3-oxidoreductase
Comments: Contains FAD as prosthetic group. One of several enzymes that catalyse the first step in fatty acids β -oxidation. The enzyme catalyses the oxidation of saturated short-chain acyl-CoA thioesters to give a *trans* 2,3-unsaturated product by removal of the two *pro-R*-hydrogen atoms. The enzyme from beef liver accepts substrates with acyl chain lengths of 3 to 8 carbon atoms. The highest activity was reported with either butanoyl-CoA [1271] or pentanoyl-CoA [3468]. The enzyme from rat has only 10% activity with hexanoyl-CoA (compared to butanoyl-CoA) and no activity with octanoyl-CoA [1634]. *cf.* EC 1.3.8.7, medium-chain acyl-CoA dehydrogenase, EC 1.3.8.8, long-chain acyl-CoA dehydrogenase, and EC 1.3.8.9, very-long-chain acyl-CoA dehydrogenase.
References: [2366, 1271, 249, 3468, 3879, 1634, 2490]

[EC 1.3.8.1 created 1961 as EC 1.3.2.1, transferred 1964 to EC 1.3.99.2, transferred 2011 to EC 1.3.8.1, modified 2012]

EC 1.3.8.2

Accepted name: 4,4'-diapophytoene desaturase (4,4'-diapolycopene-forming)
Reaction: 15-*cis*-4,4'-diapophytoene + 4 FAD = *all-trans*-4,4'-diapolycopene + 4 FADH₂ (overall reaction)
(1a) 15-*cis*-4,4'-diapophytoene + FAD = *all-trans*-4,4'-diapophytofluene + FADH₂
(1b) *all-trans*-4,4'-diapophytofluene + FAD = *all-trans*-4,4'-diapo- ζ -carotene + FADH₂
(1c) *all-trans*-4,4'-diapo- ζ -carotene + FAD = *all-trans*-4,4'-diaponeurosporene + FADH₂
(1d) *all-trans*-4,4'-diaponeurosporene + FAD = *all-trans*-4,4'-diapolycopene + FADH₂
Other name(s): dehydrosqualene desaturase (ambiguous); CrtN (ambiguous); 4,4'-diapophytoene:FAD oxidoreductase (ambiguous); 15-*cis*-4,4'-diapophytoene:FAD oxidoreductase; 4,4'-diapophytoene desaturase (ambiguous)
Systematic name: 15-*cis*-4,4'-diapophytoene:FAD oxidoreductase (4,4'-diapolycopene-forming)
Comments: The enzyme catalyses four successive dehydrogenations, resulting in production of 4,4'-diapolycopene. While the enzyme from *Staphylococcus aureus* was only shown to produce 4,4'-diaponeurosporene *in vivo* [3821], it is able to catalyse the last reaction *in vitro* [4375].
References: [4208, 3107, 3108, 3821, 4375]

[EC 1.3.8.2 created 2011, modified 2011]

EC 1.3.8.3

Accepted name: (*R*)-benzylsuccinyl-CoA dehydrogenase
Reaction: (*R*)-2-benzylsuccinyl-CoA + electron-transfer flavoprotein = (*E*)-2-benzylidenesuccinyl-CoA + reduced electron-transfer flavoprotein
Other name(s): BbsG; (*R*)-benzylsuccinyl-CoA:(acceptor) oxidoreductase
Systematic name: (*R*)-benzylsuccinyl-CoA:electron transfer flavoprotein oxidoreductase
Comments: Requires FAD as prosthetic group. Unlike other acyl-CoA dehydrogenases, this enzyme exhibits high substrate- and enantiomer specificity; it is highly specific for (*R*)-benzylsuccinyl-CoA and is inhibited by (*S*)-benzylsuccinyl-CoA. Forms the third step in the anaerobic toluene metabolic pathway in *Thauera aromatica*. Ferricenium ion is an effective artificial electron acceptor.
References: [2208, 2209]

[EC 1.3.8.3 created 2003 as EC 1.3.99.21, transferred 2012 to EC 1.3.8.3]

EC 1.3.8.4

Accepted name: isovaleryl-CoA dehydrogenase
Reaction: isovaleryl-CoA + electron-transfer flavoprotein = 3-methylcrotonyl-CoA + reduced electron-transfer flavoprotein
Other name(s): isovaleryl-coenzyme A dehydrogenase; isovaleroyl-coenzyme A dehydrogenase; 3-methylbutanoyl-CoA:(acceptor) oxidoreductase
Systematic name: 3-methylbutanoyl-CoA:electron-transfer flavoprotein oxidoreductase
Comments: Contains FAD as prosthetic group. Pentanoate can act as donor.
References: [155, 1635, 3802]

[EC 1.3.8.4 created 1978 as EC 1.3.99.10, modified 1986, transferred 2012 to EC 1.3.8.4]

EC 1.3.8.5

- Accepted name:** 2-methyl-branched-chain-enoyl-CoA reductase
Reaction: 2-methylbutanoyl-CoA + electron-transfer flavoprotein = (*E*)-2-methylbut-2-enoyl-CoA + reduced electron-transfer flavoprotein + H⁺
Systematic name: 2-methyl-branched-chain-acyl-CoA:electron-transfer flavoprotein 2-oxidoreductase
Comments: A flavoprotein (FAD) from *Ascaris suum*. The enzyme functions in shuttling reducing power from the electron-transport chain to 2-methyl branched-chain enoyl CoA
References: [2019, 2020]

[EC 1.3.8.5 created 1992 as EC 1.3.1.52, transferred 2012 to EC 1.3.8.5]

EC 1.3.8.6

- Accepted name:** glutaryl-CoA dehydrogenase (ETF)
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
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).
References: [286, 1401, 897, 3124]

[EC 1.3.8.6 created 1972 as EC 1.3.99.7, transferred 2012 to EC 1.3.8.6, modified 2013]

EC 1.3.8.7

- Accepted name:** medium-chain acyl-CoA dehydrogenase
Reaction: a medium-chain acyl-CoA + electron-transfer flavoprotein = a medium-chain *trans*-2,3-dehydroacyl-CoA + reduced electron-transfer flavoprotein
Other name(s): fatty acyl coenzyme A dehydrogenase (ambiguous); acyl coenzyme A dehydrogenase (ambiguous); acyl dehydrogenase (ambiguous); fatty-acyl-CoA dehydrogenase (ambiguous); acyl CoA dehydrogenase (ambiguous); general acyl CoA dehydrogenase (ambiguous); medium-chain acyl-coenzyme A dehydrogenase; acyl-CoA:(acceptor) 2,3-oxidoreductase (ambiguous); ACADM (gene name).
Systematic name: medium-chain acyl-CoA:electron-transfer flavoprotein 2,3-oxidoreductase
Comments: Contains FAD as prosthetic group. One of several enzymes that catalyse the first step in fatty acids β-oxidation. The enzyme from pig liver can accept substrates with acyl chain lengths of 4 to 16 carbon atoms, but is most active with C₈ to C₁₂ compounds [691]. The enzyme from rat does not accept C₁₆ at all and is most active with C₆-C₈ compounds [1634]. *cf.* EC 1.3.8.1, short-chain acyl-CoA dehydrogenase, EC 1.3.8.8, long-chain acyl-CoA dehydrogenase, and EC 1.3.8.9, very-long-chain acyl-CoA dehydrogenase.
References: [690, 691, 249, 1634, 3879, 1911, 2990, 3912]

[EC 1.3.8.7 created 1961 as EC 1.3.2.2, transferred 1964 to EC 1.3.99.3, part transferred 2012 to EC 1.3.8.7]

EC 1.3.8.8

- Accepted name:** long-chain acyl-CoA dehydrogenase
Reaction: a long-chain acyl-CoA + electron-transfer flavoprotein = a long-chain *trans*-2,3-dehydroacyl-CoA + reduced electron-transfer flavoprotein
Other name(s): palmitoyl-CoA dehydrogenase; palmitoyl-coenzyme A dehydrogenase; long-chain acyl-coenzyme A dehydrogenase; long-chain-acyl-CoA:(acceptor) 2,3-oxidoreductase; ACADL (gene name).
Systematic name: long-chain acyl-CoA:electron-transfer flavoprotein 2,3-oxidoreductase
Comments: Contains FAD as prosthetic group. One of several enzymes that catalyse the first step in fatty acids β -oxidation. The enzyme from pig liver can accept substrates with acyl chain lengths of 6 to at least 16 carbon atoms. The highest activity was found with C₁₂, and the rates with C₈ and C₁₆ were 80 and 70%, respectively [1424]. The enzyme from rat can accept substrates with C₈-C₂₂. It is most active with C₁₄ and C₁₆, and has no activity with C₄, C₆ or C₂₄ [1634]. *cf.* EC 1.3.8.1, short-chain acyl-CoA dehydrogenase, EC 1.3.8.8, medium-chain acyl-CoA dehydrogenase, and EC 1.3.8.9, very-long-chain acyl-CoA dehydrogenase.
References: [690, 1424, 1346, 1634, 840]

[EC 1.3.8.8 created 1989 as EC 1.3.99.13, part transferred 2012 to EC 1.3.8.8]

EC 1.3.8.9

- Accepted name:** very-long-chain acyl-CoA dehydrogenase
Reaction: a very-long-chain acyl-CoA + electron-transfer flavoprotein = a very-long-chain *trans*-2,3-dehydroacyl-CoA + reduced electron-transfer flavoprotein
Other name(s): ACADVL (gene name).
Systematic name: very-long-chain acyl-CoA:electron-transfer flavoprotein 2,3-oxidoreductase
Comments: Contains FAD as prosthetic group. One of several enzymes that catalyse the first step in fatty acids β -oxidation. The enzyme is most active toward long-chain acyl-CoAs such as C₁₄, C₁₆ and C₁₈, but is also active with very-long-chain acyl-CoAs up to 24 carbons. It shows no activity for substrates of less than 12 carbons. Its specific activity towards palmitoyl-CoA is more than 10-fold that of the long-chain acyl-CoA dehydrogenase [1698]. *cf.* EC 1.3.8.1, short-chain acyl-CoA dehydrogenase, EC 1.3.8.7, medium-chain acyl-CoA dehydrogenase, and EC 1.3.8.8, long-chain acyl-CoA dehydrogenase.
References: [1698, 101, 2476]

[EC 1.3.8.9 created 1961 as EC 1.3.2.2, transferred 1964 to EC 1.3.99.3, part transferred 2012 to EC 1.3.8.9]

EC 1.3.8.10

- Accepted name:** cyclohex-1-ene-1-carbonyl-CoA dehydrogenase
Reaction: cyclohex-1-ene-1-carbonyl-CoA + electron-transfer flavoprotein = cyclohex-1,5-diene-1-carbonyl-CoA + reduced electron-transfer flavoprotein
Systematic name: cyclohex-1-ene-1-carbonyl-CoA:electron transfer flavoprotein oxidoreductase
Comments: Contains FAD. The enzyme, characterized from the strict anaerobic bacterium *Syntrophus aciditrophicus*, is involved in production of cyclohexane-1-carboxylate, a byproduct produced by that organism during fermentation of benzoate and crotonate to acetate.
References: [2080]

[EC 1.3.8.10 created 2013]

EC 1.3.8.11

- Accepted name:** cyclohexane-1-carbonyl-CoA dehydrogenase
Reaction: cyclohexane-1-carbonyl-CoA + electron-transfer flavoprotein = cyclohex-1-ene-1-carbonyl-CoA + reduced electron-transfer flavoprotein
Systematic name: cyclohexane-1-carbonyl-CoA:electron transfer flavoprotein oxidoreductase
Comments: Contains FAD. The enzyme, characterized from the strict anaerobic bacterium *Syntrophus aciditrophicus*, is involved in production of cyclohexane-1-carboxylate, a byproduct produced by that organism during fermentation of benzoate and crotonate to acetate.

References: [2080]

[EC 1.3.8.11 created 2013]

EC 1.3.8.12

Accepted name: (2*S*)-methylsuccinyl-CoA dehydrogenase
Reaction: (2*S*)-methylsuccinyl-CoA + electron-transfer flavoprotein = 2-methylfumaryl-CoA + reduced electron-transfer flavoprotein
Other name(s): Mcd
Systematic name: (2*S*)-methylsuccinyl-CoA:electron-transfer flavoprotein oxidoreductase
Comments: The enzyme, characterized from the bacterium *Rhodobacter sphaeroides*, is involved in the ethylmalonyl-CoA pathway for acetyl-CoA assimilation. The enzyme contains FAD.
References: [963]

[EC 1.3.8.12 created 2015]

EC 1.3.8.13

Accepted name: crotonobetainyl-CoA reductase
Reaction: γ -butyrobetainyl-CoA + electron-transfer flavoprotein = crotonobetainyl-CoA + reduced electron-transfer flavoprotein
Other name(s): *caiA* (gene name)
Systematic name: γ -butyrobetainyl-CoA:electron-transfer flavoprotein 2,3-oxidoreductase
Comments: The enzyme has been purified from the bacterium *Escherichia coli* O44 K74, in which it forms a complex with EC 2.8.3.21, L-carnitine CoA-transferase. The electron donor is believed to be an electron-transfer flavoprotein (ETF) encoded by the *fixA* and *fixB* genes.
References: [3238, 3059, 943, 4099]

[EC 1.3.8.13 created 2017]

EC 1.3.8.14

Accepted name: L-prolyl-[peptidyl-carrier protein] dehydrogenase
Reaction: L-prolyl-[peptidyl-carrier protein] + 2 electron-transfer flavoprotein = 1*H*-pyrrole-2-carbonyl-[peptidyl-carrier protein] + 2 reduced electron-transfer flavoprotein
Other name(s): *pigA* (gene name); *bmp3* (gene name); *pltE* (gene name); *redW* (gene name); (L-prolyl)-[peptidyl-carrier protein]:electron-transfer flavoprotein oxidoreductase
Systematic name: L-prolyl-[peptidyl-carrier protein]:electron-transfer flavoprotein oxidoreductase
Comments: Contains FAD. The enzyme participates in the biosynthesis of several pyrrole-containing compounds, such as undecylprodigiosin, prodigiosin, pyoluteorin, and coumermycin A1. It is believed to catalyse the formation of a Δ^2 -pyrrolin-2-carbonyl-[peptidyl-carrier protein] intermediate, followed by a two-electron oxidation to 1*H*-pyrrol-2-carbonyl-[peptidyl-carrier protein].
References: [3867, 1396]

[EC 1.3.8.14 created 2017]

EC 1.3.98 With other, known, physiological acceptors

EC 1.3.98.1

Accepted name: dihydroorotate dehydrogenase (fumarate)
Reaction: (*S*)-dihydroorotate + fumarate = orotate + succinate
Other name(s): DHodehase (ambiguous); dihydroorotate dehydrogenase (ambiguous); dihydroorotic acid dehydrogenase (ambiguous); DHOD (ambiguous); DHODase (ambiguous); dihydroorotate oxidase, *pyr4* (gene name)

Systematic name: (S)-dihydroorotate:fumarate oxidoreductase
Comments: Binds FMN. The reaction, which takes place in the cytosol, is the only redox reaction in the *de novo* biosynthesis of pyrimidine nucleotides. Molecular oxygen can replace fumarate *in vitro*. Other class 1 dihydroorotate dehydrogenases use either NAD⁺ (EC 1.3.1.14) or NADP⁺ (EC 1.3.1.15) as electron acceptor. The membrane bound class 2 dihydroorotate dehydrogenase (EC 1.3.5.2) uses quinone as electron acceptor.
References: [306, 3241, 2816, 4424, 1647, 565]

[EC 1.3.98.1 created 1961 as EC 1.3.3.1, transferred 2011 to EC 1.3.98.1]

[1.3.98.2 Transferred entry. fumarate reductase (CoM/CoB). Now EC 1.3.4.1, fumarate reductase (CoM/CoB)]

[EC 1.3.98.2 created 2014, deleted 2014]

EC 1.3.98.3

Accepted name: coproporphyrinogen dehydrogenase
Reaction: coproporphyrinogen III + 2 S-adenosyl-L-methionine = protoporphyrinogen IX + 2 CO₂ + 2 L-methionine + 2 5'-deoxyadenosine
Other name(s): oxygen-independent coproporphyrinogen-III oxidase; HemN; coproporphyrinogen III oxidase
Systematic name: coproporphyrinogen-III:S-adenosyl-L-methionine oxidoreductase (decarboxylating)
Comments: This enzyme differs from EC 1.3.3.3, coproporphyrinogen oxidase, by using S-adenosyl-L-methionine (AdoMet) instead of oxygen as oxidant. It occurs mainly in bacteria, whereas eukaryotes use the oxygen-dependent oxidase. The reaction starts by using an electron from the reduced form of the enzyme's [4Fe-4S] cluster to split AdoMet into methionine and the radical 5'-deoxyadenosin-5'-yl. This radical initiates attack on the 2-carboxyethyl groups, leading to their conversion into vinyl groups. This conversion, —CH-CH₂-COO⁻ → —CH=CH₂ + CO₂ + e⁻ replaces the electron initially used.
References: [2158, 2157]

[EC 1.3.98.3 created 2004 as EC 1.3.99.22, transferred 2016 to EC 1.3.98.3]

EC 1.3.98.4

Accepted name: 5a,11a-dehydrotetracycline reductase
Reaction: tetracycline + oxidized coenzyme F₄₂₀ = 5a,11a-dehydrotetracycline + reduced coenzyme F₄₂₀
Other name(s): oxyR (gene name); 12-dehydrotetracycline dehydrogenase; dehydroxytetracycline dehydrogenase; 12-dehydrotetracycline reductase
Systematic name: tetracycline:coenzyme F₄₂₀ dehydrogenase
Comments: The enzyme, characterized from the bacteria *Streptomyces aureofaciens* and *Streptomyces rimosus*, catalyses the last step in the biosynthesis of the tetracycline antibiotics tetracycline and oxytetracycline.
References: [2479, 2545, 2480, 4112]

[EC 1.3.98.4 created 2016]

EC 1.3.99 With unknown physiological acceptors

[1.3.99.1 Deleted entry. succinate dehydrogenase. The activity is included in EC 1.3.5.1, succinate dehydrogenase (quinone).]

[EC 1.3.99.1 created 1961, deleted 2014]

[1.3.99.2 Transferred entry. butyryl-CoA dehydrogenase. Now EC 1.3.8.1, butyryl-CoA dehydrogenase.]

[EC 1.3.99.2 created 1961 as EC 1.3.2.1, transferred 1964 to EC 1.3.99.2, deleted 2011]

[1.3.99.3 Transferred entry. acyl-CoA dehydrogenase, now EC 1.3.8.7, medium-chain acyl-CoA dehydrogenase, EC 1.3.8.8, long-chain acyl-CoA dehydrogenase and EC 1.3.8.9, very-long-chain acyl-CoA dehydrogenase]

[EC 1.3.99.3 created 1961 as EC 1.3.2.2, transferred 1964 to EC 1.3.99.3, deleted 2012]

EC 1.3.99.4

Accepted name: 3-oxosteroid 1-dehydrogenase
Reaction: a 3-oxosteroid + acceptor = a 3-oxo- Δ^1 -steroid + reduced acceptor
Other name(s): 3-oxosteroid Δ^1 -dehydrogenase; Δ^1 -dehydrogenase; 3-ketosteroid-1-en-dehydrogenase; 3-ketosteroid- Δ^1 -dehydrogenase; 1-ene-dehydrogenase; 3-oxosteroid:(2,6-dichlorphenolindophenol) Δ^1 -oxidoreductase; 4-en-3-oxosteroid:(acceptor)-1-en-oxido-reductase; Δ^1 -steroid reductase; 3-oxosteroid:(acceptor) Δ^1 -oxidoreductase
Systematic name: 3-oxosteroid:acceptor Δ^1 -oxidoreductase
References: [2217]

[EC 1.3.99.4 created 1965]

EC 1.3.99.5

Accepted name: 3-oxo-5 α -steroid 4-dehydrogenase (acceptor)
Reaction: a 3-oxo-5 α -steroid + acceptor = a 3-oxo- Δ^4 -steroid + reduced acceptor
Other name(s): steroid 5 α -reductase; 3-oxosteroid Δ^4 -dehydrogenase; 3-oxo-5 α -steroid Δ^4 -dehydrogenase; steroid Δ^4 -5 α -reductase; Δ^4 -3-keto steroid 5 α -reductase; Δ^4 -3-oxo steroid reductase; Δ^4 -3-ketosteroid5 α -oxidoreductase; Δ^4 -3-oxosteroid-5 α -reductase; 3-keto- Δ^4 -steroid-5 α -reductase; 5 α -reductase; testosterone 5 α -reductase; 4-ene-3-ketosteroid-5 α -oxidoreductase; Δ^4 -5 α -dehydrogenase; 3-oxo-5 α -steroid:(acceptor) Δ^4 -oxidoreductase; *tesI* (gene name)
Systematic name: 3-oxo-5 α -steroid:acceptor Δ^4 -oxidoreductase
Comments: A flavoprotein. This bacterial enzyme, characterized from *Comamonas testosteroni*, is involved in androsterone degradation. cf. EC 1.3.1.22, 3-oxo-5 α -steroid 4-dehydrogenase (NADP⁺).
References: [2217, 1026, 1568]

[EC 1.3.99.5 created 1965, modified 2012]

EC 1.3.99.6

Accepted name: 3-oxo-5 β -steroid 4-dehydrogenase
Reaction: a 3-oxo-5 β -steroid + acceptor = a 3-oxo- Δ^4 -steroid + reduced acceptor
Other name(s): 3-oxo-5 β -steroid:(acceptor) Δ^4 -oxidoreductase
Systematic name: 3-oxo-5 β -steroid:acceptor Δ^4 -oxidoreductase
References: [753]

[EC 1.3.99.6 created 1972]

[1.3.99.7 Transferred entry. glutaryl-CoA dehydrogenase. Now EC 1.3.8.6, glutaryl-CoA dehydrogenase]

[EC 1.3.99.7 created 1972, deleted 2012]

EC 1.3.99.8

Accepted name: 2-furoyl-CoA dehydrogenase
Reaction: 2-furoyl-CoA + H₂O + acceptor = S-(5-hydroxy-2-furoyl)-CoA + reduced acceptor
Other name(s): furoyl-CoA hydroxylase; 2-furoyl coenzyme A hydroxylase; 2-furoyl coenzyme A dehydrogenase; 2-furoyl-CoA:(acceptor) 5-oxidoreductase (hydroxylating)
Systematic name: 2-furoyl-CoA:acceptor 5-oxidoreductase (hydroxylating)
Comments: A copper protein. The oxygen atom of the -OH produced is derived from water, not O₂; the actual oxidative step is probably dehydrogenation of a hydrated form -CHOH-CH₂- to -C(OH)=CH-, which tautomerizes non-enzymically to -CO-CH₂-, giving (5-oxo-4,5-dihydro-2-furoyl)-CoA. Methylene blue, nitro blue, tetrazolium and a membrane fraction from *Pseudomonas putida* can act as acceptors.
References: [1948]

[EC 1.3.99.8 created 1976]

[1.3.99.9 Transferred entry. β -cyclopiazonate dehydrogenase. Now EC 1.21.99.1, β -cyclopiazonate dehydrogenase]

[EC 1.3.99.9 created 1976, deleted 2002]

[1.3.99.10 Transferred entry. *isovaleryl-CoA dehydrogenase*. Now EC 1.3.8.4, *isovaleryl-CoA dehydrogenase*]

[EC 1.3.99.10 created 1978, modified 1986, deleted 2012]

[1.3.99.11 Transferred entry. *dihydroorotate dehydrogenase*. As the acceptor is now known, the enzyme has been transferred to EC 1.3.5.2, *dihydroorotate dehydrogenase*]

[EC 1.3.99.11 created 1983, deleted 2009]

EC 1.3.99.12

Accepted name: 2-methylacyl-CoA dehydrogenase
Reaction: 2-methylbutanoyl-CoA + acceptor = 2-methylbut-2-enoyl-CoA + reduced acceptor
Other name(s): branched-chain acyl-CoA dehydrogenase; 2-methyl branched chain acyl-CoA dehydrogenase; 2-methylbutanoyl-CoA:(acceptor) oxidoreductase
Systematic name: 2-methylbutanoyl-CoA:acceptor oxidoreductase
Comments: Also oxidizes 2-methylpropanoyl-CoA. Not identical with EC 1.3.8.1 (butyryl-CoA dehydrogenase), EC 1.3.8.7 (medium-chain acyl-CoA dehydrogenase), EC 1.3.8.8 (long-chain acyl-CoA dehydrogenase), EC 1.3.8.9 (very-long-chain acyl-CoA dehydrogenase) or EC 1.3.99.10 (isovaleryl-CoA dehydrogenase).
References: [1633]

[EC 1.3.99.12 created 1986]

[1.3.99.13 Transferred entry. *long-chain-acyl-CoA dehydrogenase*. Now EC 1.3.8.8, *long-chain-acyl-CoA dehydrogenase*]

[EC 1.3.99.13 created 1989, deleted 2012]

EC 1.3.99.14

Accepted name: cyclohexanone dehydrogenase
Reaction: cyclohexanone + acceptor = cyclohex-2-enone + reduced acceptor
Other name(s): cyclohexanone:(acceptor) 2-oxidoreductase
Systematic name: cyclohexanone:acceptor 2-oxidoreductase
Comments: 2,6-Dichloroindophenol can act as acceptor. The corresponding ketones of cyclopentane and cycloheptane cannot act as donors.
References: [741]

[EC 1.3.99.14 created 1992]

[1.3.99.15 Transferred entry. *benzoyl-CoA reductase*. Now EC 1.3.7.8.]

[EC 1.3.99.15 created 1999, deleted 2011]

EC 1.3.99.16

Accepted name: isoquinoline 1-oxidoreductase
Reaction: isoquinoline + acceptor + H₂O = isoquinolin-1(2H)-one + reduced acceptor
Systematic name: isoquinoline:acceptor 1-oxidoreductase (hydroxylating)
Comments: The enzyme from *Pseudomonas diminuta* is specific towards *N*-containing *N*-heterocyclic substrates, including isoquinoline, isoquinolin-5-ol, phthalazine and quinazoline. Electron acceptors include 1,2-benzoquinone, cytochrome *c*, ferricyanide, iodinitrotetrazolium chloride, nitroblue tetrazolium, Meldola blue and phenazine methosulfate.
References: [2187, 2186]

[EC 1.3.99.16 created 1999]

EC 1.3.99.17

Accepted name: quinoline 2-oxidoreductase
Reaction: quinoline + acceptor + H₂O = quinolin-2(1*H*)-one + reduced acceptor
Systematic name: quinoline:acceptor 2-oxidoreductase (hydroxylating)
Comments: Quinolin-2-ol, quinolin-7-ol, quinolin-8-ol, 3-, 4- and 8-methylquinolines and 8-chloroquinoline are substrates. Iodonitrotetrazolium chloride can act as an electron acceptor.
References: [215, 3935, 2984, 3344]

[EC 1.3.99.17 created 1999]

EC 1.3.99.18

Accepted name: quinaldate 4-oxidoreductase
Reaction: quinaldate + acceptor + H₂O = kynurenate + reduced acceptor
Other name(s): quinaldic acid 4-oxidoreductase
Systematic name: quinoline-2-carboxylate:acceptor 4-oxidoreductase (hydroxylating)
Comments: The enzyme from *Pseudomonas* sp. AK2 also acts on quinoline-8-carboxylate, whereas that from *Serratia marcescens* 2CC-1 will oxidize nicotinate; quinaldate is a substrate for both of these enzymes. 2,4,6-Trinitrobenzene sulfonate, 1,4-benzoquinone, 1,2-naphthoquinone, nitroblue tetrazolium, thionine and menadione will serve as an electron acceptor for the former enzyme and ferricyanide for the latter; Meldola blue, iodonitrotetrazolium chloride, phenazine methosulfate, 2,6-dichlorophenolindophenol and cytochrome *c* will act as electron acceptors for both.
References: [3327, 1005]

[EC 1.3.99.18 created 1999]

EC 1.3.99.19

Accepted name: quinoline-4-carboxylate 2-oxidoreductase
Reaction: quinoline-4-carboxylate + acceptor + H₂O = 2-oxo-1,2-dihydroquinoline-4-carboxylate + reduced acceptor
Other name(s): quinaldic acid 4-oxidoreductase; quinoline-4-carboxylate:acceptor 2-oxidoreductase (hydroxylating)
Systematic name: quinoline-4-carboxylate:acceptor 2-oxidoreductase (hydroxylating)
Comments: A molybdenum—iron—sulfur flavoprotein with molybdopterin cytosine dinucleotide as the molybdenum cofactor. Quinoline, 4-methylquinoline and 4-chloroquinoline can also serve as substrates for the enzyme from *Agrobacterium* sp. 1B. Iodonitrotetrazolium chloride, thionine, menadione and 2,6-dichlorophenolindophenol can act as electron acceptors.
References: [216]

[EC 1.3.99.19 created 1999, modified 2006]

[1.3.99.20 Transferred entry. EC 1.3.99.20, 4-hydroxybenzoyl-CoA reductase. Now EC 1.3.7.9, 4-hydroxybenzoyl-CoA reductase.]

[EC 1.3.99.20 created 2000, deleted 2011]

[1.3.99.21 Transferred entry. (R)-benzylsuccinyl-CoA dehydrogenase. Now EC 1.3.8.3, (R)-benzylsuccinyl-CoA dehydrogenase]

[EC 1.3.99.21 created 2003 as EC 1.3.99.21, deleted 2012]

[1.3.99.22 Transferred entry. coproporphyrinogen dehydrogenase. Now EC 1.3.98.3, coproporphyrinogen dehydrogenase]

[EC 1.3.99.22 created 2004, deleted 2016]

EC 1.3.99.23

Accepted name: all-trans-retinol 13,14-reductase
Reaction: all-trans-13,14-dihydroretinol + acceptor = all-trans-retinol + reduced acceptor

Other name(s): retinol saturase; RetSat; (13,14)-*all-trans*-retinol saturase; *all-trans*-retinol:*all-trans*-13,14-dihydroretinol saturase
Systematic name: *all-trans*-13,14-dihydroretinol:acceptor 13,14-oxidoreductase
Comments: The reaction is only known to occur in the opposite direction to that given above, with the enzyme being specific for *all-trans*-retinol as substrate. Neither *all-trans*-retinoic acid nor 9-*cis*, 11-*cis* or 13-*cis*-retinol isomers are substrates. May play a role in the metabolism of vitamin A.
References: [2593]

[EC 1.3.99.23 created 2005]

EC 1.3.99.24

Accepted name: 2-amino-4-deoxychorismate dehydrogenase
Reaction: (2*S*)-2-amino-4-deoxychorismate + FMN = 3-(1-carboxyvinyl)anthranilate + FMNH₂
Other name(s): ADIC dehydrogenase; 2-amino-2-deoxyisochorismate dehydrogenase; SgcG
Systematic name: (2*S*)-2-amino-4-deoxychorismate:FMN oxidoreductase
Comments: The sequential action of EC 2.6.1.86, 2-amino-4-deoxychorismate synthase and this enzyme leads to the formation of the benzoxazolinone moiety of the enediyne antitumour antibiotic C-1027 [2126, 4404].
References: [2126, 4404]

[EC 1.3.99.24 created 2008]

EC 1.3.99.25

Accepted name: carvone reductase
Reaction: (1) (+)-dihydrocarvone + acceptor = (-)-carvone + reduced acceptor
(2) (-)-isodihydrocarvone + acceptor = (+)-carvone + reduced acceptor
Systematic name: (+)-dihydrocarvone:acceptor 1,6-oxidoreductase
Comments: This enzyme participates in the carveol and dihydrocarveol degradation pathway of the Gram-positive bacterium *Rhodococcus erythropolis* DCL14. The enzyme has not been purified, and requires an unknown cofactor, which is different from NAD⁺, NADP⁺ or a flavin.
References: [3999]

[EC 1.3.99.25 created 2008]

EC 1.3.99.26

Accepted name: *all-trans*- ζ -carotene desaturase
Reaction: *all-trans*- ζ -carotene + 2 acceptor = *all-trans*-lycopene + 2 reduced acceptor (overall reaction)
(1a) *all-trans*- ζ -carotene + acceptor = *all-trans*-neurosporene + reduced acceptor
(1b) *all-trans*-neurosporene + acceptor = *all-trans*-lycopene + reduced acceptor
Other name(s): CrtIb; phytoene desaturase (ambiguous); 2-step phytoene desaturase (ambiguous); two-step phytoene desaturase (ambiguous); CrtI (ambiguous)
Systematic name: *all-trans*- ζ -carotene:acceptor oxidoreductase
Comments: This enzyme is involved in carotenoid biosynthesis.
References: [1649]

[EC 1.3.99.26 created 2011]

EC 1.3.99.27

Accepted name: 1-hydroxycarotenoid 3,4-desaturase
Reaction: 1-hydroxy-1,2-dihydrolycopene + acceptor = 1-hydroxy-3,4-didehydro-1,2-dihydrolycopene + reduced acceptor
Other name(s): CrtD; hydroxyneurosporene desaturase; carotenoid 3,4-dehydrogenase; 1-hydroxy-carotenoid 3,4-dehydrogenase

Systematic name: 1-hydroxy-1,2-dihydrolycopene:acceptor oxidoreductase
Comments: The enzymes from *Rubrivivax gelatinosus* and *Rhodobacter sphaeroides* prefer the acyclic carotenoids (e.g. 1-hydroxy-1,2-dihydroneurosporene, 1-hydroxy-1,2-dihydrolycopene) as substrates. The conversion rate for the 3,4-desaturation of the monocyclic 1'-hydroxy-1',2'-dihydro- γ -carotene is lower [3632, 56]. The enzyme from the marine bacterium strain P99-3 shows high activity with the monocyclic carotenoid 1'-hydroxy-1',2'-dihydro- γ -carotene [3848]. The enzyme from *Rhodobacter sphaeroides* utilizes molecular oxygen as the electron acceptor *in vitro* [56]. However, oxygen is unlikely to be the natural electron acceptor under anaerobic conditions.
References: [3848, 3632, 56]

[EC 1.3.99.27 created 2011]

EC 1.3.99.28

Accepted name: phytoene desaturase (neurosporene-forming)
Reaction: 15-*cis*-phytoene + 3 acceptor = *all-trans*-neurosporene + 3 reduced acceptor (overall reaction)
(1a) 15-*cis*-phytoene + acceptor = *all-trans*-phytofluene + reduced acceptor
(1b) *all-trans*-phytofluene + acceptor = *all-trans*- ζ -carotene + reduced acceptor
(1c) *all-trans*- ζ -carotene + acceptor = *all-trans*-neurosporene + reduced acceptor
Other name(s): 3-step phytoene desaturase; three-step phytoene desaturase; phytoene desaturase (ambiguous); CrtI (ambiguous)
Systematic name: 15-*cis*-phytoene:acceptor oxidoreductase (neurosporene-forming)
Comments: This enzyme is involved in carotenoid biosynthesis and catalyses up to three desaturation steps (*cf.* EC 1.3.99.29 [phytoene desaturase (ζ -carotene-forming)], EC 1.3.99.30 [phytoene desaturase (3,4-didehydrolycopene-forming)], EC 1.3.99.31 [phytoene desaturase (lycopene-forming)]). The enzyme is activated by FAD. NAD⁺, NADP⁺ or ATP show no activating effect [3106].
References: [3106, 4104]

[EC 1.3.99.28 created 2011]

EC 1.3.99.29

Accepted name: phytoene desaturase (ζ -carotene-forming)
Reaction: 15-*cis*-phytoene + 2 acceptor = *all-trans*- ζ -carotene + 2 reduced acceptor (overall reaction)
(1a) 15-*cis*-phytoene + acceptor = *all-trans*-phytofluene + reduced acceptor
(1b) *all-trans*-phytofluene + acceptor = *all-trans*- ζ -carotene + reduced acceptor
Other name(s): CrtIa; 2-step phytoene desaturase (ambiguous); two-step phytoene desaturase (ambiguous)
Systematic name: 15-*cis*-phytoene:acceptor oxidoreductase (ζ -carotene-forming)
Comments: The enzyme is involved in carotenoid biosynthesis and catalyses up to two desaturation steps (*cf.* EC 1.3.99.28 [phytoene desaturase (neurosporene-forming)], EC 1.3.99.30 [phytoene desaturase (3,4-didehydrolycopene-forming)] and EC 1.3.99.31 [phytoene desaturase (lycopene-forming)]).
References: [1649]

[EC 1.3.99.29 created 2011]

EC 1.3.99.30

Accepted name: phytoene desaturase (3,4-didehydrolycopene-forming)
Reaction: 15-*cis*-phytoene + 5 acceptor = *all-trans*-3,4-didehydrolycopene + 5 reduced acceptor (overall reaction)
(1a) 15-*cis*-phytoene + acceptor = *all-trans*-phytofluene + reduced acceptor
(1b) *all-trans*-phytofluene + acceptor = *all-trans*- ζ -carotene + reduced acceptor
(1c) *all-trans*- ζ -carotene + acceptor = *all-trans*-neurosporene + reduced acceptor
(1d) *all-trans*-neurosporene + acceptor = *all-trans*-lycopene + reduced acceptor
(1e) *all-trans*-lycopene + acceptor = *all-trans*-3,4-didehydrolycopene + reduced acceptor
Other name(s): 5-step phytoene desaturase; five-step phytoene desaturase; phytoene desaturase (ambiguous); Al-1
Systematic name: 15-*cis*-phytoene:acceptor oxidoreductase (3,4-didehydrolycopene-forming)

Comments: This enzyme is involved in carotenoid biosynthesis and catalyses up to five desaturation steps (*cf.* EC 1.3.99.28 [phytoene desaturase (neurosporene-forming)], EC 1.3.99.29 [phytoene desaturase (ζ -carotene-forming)] and EC 1.3.99.31 [phytoene desaturase (lycopene-forming)]).

References: [1427, 967]

[EC 1.3.99.30 created 2011]

EC 1.3.99.31

Accepted name: phytoene desaturase (lycopene-forming)

Reaction: 15-*cis*-phytoene + 4 acceptor = *all-trans*-lycopene + 4 reduced acceptor (overall reaction)

(1a) 15-*cis*-phytoene + acceptor = *all-trans*-phytofluene + reduced acceptor

(1b) *all-trans*-phytofluene + acceptor = *all-trans*- ζ -carotene + reduced acceptor

(1c) *all-trans*- ζ -carotene + acceptor = *all-trans*-neurosporene + reduced acceptor

(1d) *all-trans*-neurosporene + acceptor = *all-trans*-lycopene + reduced acceptor

Other name(s): 4-step phytoene desaturase; four-step phytoene desaturase; phytoene desaturase (ambiguous); CrtI (ambiguous)

Systematic name: 15-*cis*-phytoene:acceptor oxidoreductase (lycopene-forming)

Comments: Requires FAD. The enzyme is involved in carotenoid biosynthesis and catalyses up to four desaturation steps (*cf.* EC 1.3.99.28 [phytoene desaturase (neurosporene-forming)], EC 1.3.99.29 [phytoene desaturase (ζ -carotene-forming)] and EC 1.3.99.30 [phytoene desaturase (3,4-didehydrolycopene-forming)]).

References: [1058]

[EC 1.3.99.31 created 2011]

EC 1.3.99.32

Accepted name: glutaryl-CoA dehydrogenase (acceptor)

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

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

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.

References: [4229, 4228]

[EC 1.3.99.32 created 2012, modified 2013]

EC 1.3.99.33

Accepted name: urocanate reductase

Reaction: dihydrourocanate + acceptor = urocanate + reduced acceptor

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

Systematic name: dihydrourocanate:acceptor oxidoreductase

Comments: The enzyme from the bacterium *Shewanella oneidensis* MR-1 contains a noncovalently-bound FAD and a covalently-bound FMN. It functions as part of an anaerobic electron transfer chain that utilizes urocanate as the terminal electron acceptor. The activity has been demonstrated with the artificial donor reduced methylviologen.

References: [332]

[EC 1.3.99.33 created 2013]

[1.3.99.34 Transferred entry. 2,3-bis-*O*-geranylgeranyl-*sn*-glycerol 1-phosphate reductase (donor). Now classified as EC

1.3.7.11, 2,3-bis-*O*-geranylgeranyl-*sn*-glycero-phospholipid reductase.]

[EC 1.3.99.34 created 2013, deleted 2015]

[1.3.99.35 Transferred entry. chlorophyllide *a* reductase. Now EC 1.3.7.15, chlorophyllide *a* reductase]

[EC 1.3.99.35 created 2014, deleted 2016]

EC 1.3.99.36

Accepted name: cypemycin cysteine dehydrogenase (decarboxylating)
Reaction: cypemycin(1-18)-L-Cys-L-Leu-L-Val-L-Cys + acceptor = C^{3,19},S²¹-cyclocypemycin(1-18)-L-Ala-L-Leu-*N*-thioethenyl-L-valinamide + CO₂ + H₂S + reduced acceptor
Other name(s): cypemycin decarboxylase; CypD
Systematic name: cypemycin(1-18)-L-Cys-L-Leu-L-Val-L-Cys:acceptor oxidoreductase (decarboxylating, cyclizing)
Comments: Cypemycin, isolated from the bacterium *Streptomyces* sp. OH-4156, is a peptide antibiotic, member of the linaridins, a class of posttranslationally modified ribosomally synthesized peptides. The enzyme decarboxylates and reduces the C-terminal L-cysteine residue, producing a reactive ethenethiol group that reacts with a dethiolated cysteine upstream to form an aminovinyl-methyl-cysteine loop that is important for the antibiotic activity of the mature peptide.
References: [625]

[EC 1.3.99.36 created 2014]

EC 1.3.99.37

Accepted name: 1-hydroxy-2-isopentenylcarotenoid 3,4-desaturase
Reaction: (1) dihydroisopentenyldehydrorhodopin + acceptor = isopentenyldehydrorhodopin + reduced acceptor
(2) dihydrobisanhydrobacterioruberin + acceptor = bisanhydrobacterioruberin + reduced acceptor
Other name(s): *crtD* (gene name)
Systematic name: dihydroisopentenyldehydrorhodopin:acceptor 3,4-oxidoreductase
Comments: The enzyme, isolated from the archaeon *Haloarcula japonica*, is involved in the biosynthesis of the C₅₀ carotenoid bacterioruberin. In this pathway it catalyses the desaturation of the C-3,4 double bond in dihydroisopentenyldehydrorhodopin and the desaturation of the C-3',4' double bond in dihydrobisanhydrobacterioruberin.
References: [4339]

[EC 1.3.99.37 created 2015]

EC 1.3.99.38

Accepted name: menaquinone-9 β-reductase
Reaction: menaquinone-9 + reduced acceptor = β-dihydromenaquinone-9 + acceptor
Other name(s): MenJ
Systematic name: menaquinone-9 oxidoreductase (β-dihydromenaquinone-9-forming)
Comments: The enzyme from the bacterium *Mycobacterium tuberculosis* reduces the β-isoprene unit of menaquinone-9, forming the predominant form of menaquinone found in mycobacteria. Contains FAD.
References: [3973]

[EC 1.3.99.38 created 2017]

EC 1.3.99.39

Accepted name: carotenoid φ-ring synthase
Reaction: carotenoid β-end group + 2 acceptor = carotenoid φ-end group + 2 reduced acceptor
Other name(s): *crtU* (gene name)

Systematic name: carotenoid β -ring:acceptor oxidoreductase/methyltransferase (ϕ -ring forming)
Comments: The enzyme, found in green sulfur bacteria, some cyanobacteria and some actinobacteria, introduces additional double bonds to the carotenoid β -end group, leading to aromatization of the ionone ring. As a result, one of the methyl groups at C-1 is transferred to position C-2. It is involved in the biosynthesis of carotenoids with ϕ -type aromatic end groups such as chlorobactene, β -isorenieratene, and isorenieratene.

References: [2638, 2062, 1076]

[EC 1.3.99.39 created 2018]

EC 1.3.99.40

Accepted name: carotenoid χ -ring synthase
Reaction: carotenoid β -end group + 2 acceptor = carotenoid χ -end group + 2 reduced acceptor
Other name(s): *crtU* (gene name); *cruE* (gene name)
Systematic name: carotenoid β -ring:acceptor oxidoreductase/methyltransferase (χ -ring forming)
Comments: The enzyme, found in purple sulfur bacteria (*Chromatiaceae*) and some cyanobacteria, is involved in the biosynthesis of carotenoids that contain χ -type end groups, such as okenone, renierapurpurin, and synechoxanthin.

References: [1257, 4051]

[EC 1.3.99.40 created 2018]

EC 1.4 Acting on the CH-NH₂ group of donors

This subclass contains the amino-acid dehydrogenases and the amine oxidases. In most cases, the imine formed is hydrolysed to give an oxo-group and NH₃. This is indicated as "(deaminating)". Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.4.1), a cytochrome (EC 1.4.2), oxygen (EC 1.4.3), a disulfide (EC 1.4.4), an iron-sulfur protein (EC 1.4.7), or some other acceptor (EC 1.4.99).

EC 1.4.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.4.1.1

Accepted name: alanine dehydrogenase
Reaction: L-alanine + H₂O + NAD⁺ = pyruvate + NH₃ + NADH + H⁺
Other name(s): AlaDH; L-alanine dehydrogenase; NAD-linked alanine dehydrogenase; α -alanine dehydrogenase; NAD-dependent alanine dehydrogenase; alanine oxidoreductase; NADH-dependent alanine dehydrogenase
Systematic name: L-alanine:NAD⁺ oxidoreductase (deaminating)
References: [2840, 3004, 4374]

[EC 1.4.1.1 created 1961]

EC 1.4.1.2

Accepted name: glutamate dehydrogenase
Reaction: L-glutamate + H₂O + NAD⁺ = 2-oxoglutarate + NH₃ + NADH + H⁺
Other name(s): glutamic dehydrogenase; glutamate dehydrogenase (NAD); glutamate oxidoreductase; glutamic acid dehydrogenase; L-glutamate dehydrogenase; NAD-dependent glutamate dehydrogenase; NAD-dependent glutamic dehydrogenase; NAD-glutamate dehydrogenase; NAD-linked glutamate dehydrogenase; NAD-linked glutamic dehydrogenase; NAD-specific glutamic dehydrogenase; NAD-specific glutamate dehydrogenase; NAD:glutamate oxidoreductase; NADH-linked glutamate dehydrogenase
Systematic name: L-glutamate:NAD⁺ oxidoreductase (deaminating)
References: [1068, 2804, 2922, 3556]

[EC 1.4.1.2 created 1961]

EC 1.4.1.3

Accepted name: glutamate dehydrogenase [NAD(P)⁺]
Reaction: L-glutamate + H₂O + NAD(P)⁺ = 2-oxoglutarate + NH₃ + NAD(P)H + H⁺
Other name(s): glutamic dehydrogenase; glutamate dehydrogenase [NAD(P)]
Systematic name: L-glutamate:NAD(P)⁺ oxidoreductase (deaminating)
References: [2880, 3556, 3672]

[EC 1.4.1.3 created 1961]

EC 1.4.1.4

Accepted name: glutamate dehydrogenase (NADP⁺)
Reaction: L-glutamate + H₂O + NADP⁺ = 2-oxoglutarate + NH₃ + NADPH + H⁺
Other name(s): glutamic dehydrogenase; dehydrogenase, glutamate (nicotinamide adenine dinucleotide (phosphate)); glutamic acid dehydrogenase; L-glutamate dehydrogenase; L-glutamic acid dehydrogenase; NAD(P)-glutamate dehydrogenase; NAD(P)H-dependent glutamate dehydrogenase; glutamate dehydrogenase (NADP)
Systematic name: L-glutamate:NADP⁺ oxidoreductase (deaminating)
References: [676, 1289, 3490, 3556]

[EC 1.4.1.4 created 1961]

EC 1.4.1.5

Accepted name: L-amino-acid dehydrogenase
Reaction: an L-amino acid + H₂O + NAD⁺ = a 2-oxo carboxylate + NH₃ + NADH + H⁺
Systematic name: L-amino-acid:NAD⁺ oxidoreductase (deaminating)
Comments: Acts on aliphatic amino acids.
References: [2805]

[EC 1.4.1.5 created 1961]

[1.4.1.6 Deleted entry. D-proline reductase. Now included with EC 1.21.4.1, D-proline reductase (dithiol)]

[EC 1.4.1.6 created 1961, deleted 1982]

EC 1.4.1.7

Accepted name: serine 2-dehydrogenase
Reaction: L-serine + H₂O + NAD⁺ = 3-hydroxypyruvate + NH₃ + NADH + H⁺
Other name(s): L-serine:NAD oxidoreductase (deaminating); serine dehydrogenase
Systematic name: L-serine:NAD⁺ 2-oxidoreductase (deaminating)
References: [2058]

[EC 1.4.1.7 created 1972, modified 2003]

EC 1.4.1.8

Accepted name: valine dehydrogenase (NADP⁺)
Reaction: L-valine + H₂O + NADP⁺ = 3-methyl-2-oxobutanoate + NH₃ + NADPH + H⁺
Other name(s): valine dehydrogenase (nicotinamide adenine dinucleotide phosphate); valine dehydrogenase (NADP)
Systematic name: L-valine:NADP⁺ oxidoreductase (deaminating)
References: [1796, 1797, 1798]

[EC 1.4.1.8 created 1972]

EC 1.4.1.9

Accepted name: leucine dehydrogenase
Reaction: L-leucine + H₂O + NAD⁺ = 4-methyl-2-oxopentanoate + NH₃ + NADH + H⁺
Other name(s): L-leucine dehydrogenase; L-leucine:NAD⁺ oxidoreductase, deaminating; LeuDH
Systematic name: L-leucine:NAD⁺ oxidoreductase (deaminating)
Comments: Also acts on isoleucine, valine, norvaline and norleucine.
References: [3312, 4489]

[EC 1.4.1.9 created 1972]

EC 1.4.1.10

Accepted name: glycine dehydrogenase
Reaction: glycine + H₂O + NAD⁺ = glyoxylate + NH₃ + NADH + H⁺
Systematic name: glycine:NAD⁺ oxidoreductase (deaminating)
References: [1230]

[EC 1.4.1.10 created 1972]

EC 1.4.1.11

Accepted name: L-erythro-3,5-diaminohexanoate dehydrogenase
Reaction: L-erythro-3,5-diaminohexanoate + H₂O + NAD⁺ = (S)-5-amino-3-oxohexanoate + NH₃ + NADH + H⁺
Other name(s): L-3,5-diaminohexanoate dehydrogenase
Systematic name: L-erythro-3,5-diaminohexanoate:NAD⁺ oxidoreductase (deaminating)
References: [176]

[EC 1.4.1.11 created 1976]

EC 1.4.1.12

Accepted name: 2,4-diaminopentanoate dehydrogenase
Reaction: (2R,4S)-2,4-diaminopentanoate + H₂O + NAD(P)⁺ = (2R)-2-amino-4-oxopentanoate + NH₃ + NAD(P)H + H⁺
Other name(s): 2,4-diaminopentanoic acid C₄ dehydrogenase
Systematic name: (2R,4S)-2,4-diaminopentanoate:NAD(P)⁺ oxidoreductase (deaminating)
Comments: Also acts, more slowly, on 2,5-diaminohexanoate forming 2-amino-5-oxohexanoate, which then cyclizes non-enzymically to 1-pyrroline-2-methyl-5-carboxylate. It has equal activity with NAD⁺ and NADP⁺ [cf. EC 1.4.1.26, 2,4-diaminopentanoate dehydrogenase (NAD⁺)].
References: [3575, 3614, 3937]

[EC 1.4.1.12 created 1976, modified 2017]

EC 1.4.1.13

Accepted name: glutamate synthase (NADPH)
Reaction: 2 L-glutamate + NADP⁺ = L-glutamine + 2-oxoglutarate + NADPH + H⁺ (overall reaction)
(1a) L-glutamate + NH₃ = L-glutamine + H₂O
(1b) L-glutamate + NADP⁺ + H₂O = NH₃ + 2-oxoglutarate + NADPH + H⁺
Other name(s): glutamate (reduced nicotinamide adenine dinucleotide phosphate) synthase; L-glutamate synthase; L-glutamate synthetase; glutamate synthetase (NADP); NADPH-dependent glutamate synthase; glutamine-ketoglutaric aminotransferase; NADPH-glutamate synthase; NADPH-linked glutamate synthase; glutamine amide-2-oxoglutarate aminotransferase (oxidoreductase, NADP); L-glutamine:2-oxoglutarate aminotransferase, NADPH oxidizing; GOGAT
Systematic name: L-glutamate:NADP⁺ oxidoreductase (transaminating)

Comments: Binds FMN, FAD, 2 [4Fe-4S] clusters and 1 [3Fe-4S] cluster. The reaction takes place in the direction of L-glutamate production. The protein is composed of two subunits, α and β . The α subunit is composed of two domains, one hydrolysing L-glutamine to NH_3 and L-glutamate (*cf.* EC 3.5.1.2, glutaminase), the other combining the produced NH_3 with 2-oxoglutarate to produce a second molecule of L-glutamate (*cf.* EC 1.4.1.4, glutamate dehydrogenase [NADP^+]). The β subunit transfers electrons to the cosubstrate. The NH_3 is channeled through a 31 Å channel in the active protein. In the absence of the β subunit, coupling between the two domains of the α subunit is compromised and some ammonium can be produced. In the intact $\alpha\beta$ complex, ammonia production only takes place as part of the overall reaction.

References: [2546, 3844, 4022, 3133]

[EC 1.4.1.13 created 1972 as EC 2.6.1.53, transferred 1976 to EC 1.4.1.13, modified 2001, modified 2012]

EC 1.4.1.14

Accepted name: glutamate synthase (NADH)
Reaction: 2 L-glutamate + NAD^+ = L-glutamine + 2-oxoglutarate + NADH + H^+
Other name(s): glutamate (reduced nicotinamide adenine dinucleotide) synthase; NADH: GOGAT; L-glutamate synthase (NADH); L-glutamate synthetase; NADH-glutamate synthase; NADH-dependent glutamate synthase; glutamate synthase (NADH_2)
Systematic name: L-glutamate: NAD^+ oxidoreductase (transaminating)
Comments: A flavoprotein (FMN).
References: [337]

[EC 1.4.1.14 created 1978]

EC 1.4.1.15

Accepted name: lysine dehydrogenase
Reaction: L-lysine + NAD^+ = 1,2-didehydropiperidine-2-carboxylate + NH_3 + NADH + H^+
Systematic name: L-lysine: NAD^+ oxidoreductase (deaminating, cyclizing)
References: [446]

[EC 1.4.1.15 created 1978]

EC 1.4.1.16

Accepted name: diaminopimelate dehydrogenase
Reaction: *meso*-2,6-diaminoheptanedioate + H_2O + NADP^+ = L-2-amino-6-oxoheptanedioate + NH_3 + NADPH + H^+
Other name(s): *meso*- α,ϵ -diaminopimelate dehydrogenase; *meso*-diaminopimelate dehydrogenase
Systematic name: *meso*-2,6-diaminoheptanedioate: NADP^+ oxidoreductase (deaminating)
References: [2557, 2558]

[EC 1.4.1.16 created 1981]

EC 1.4.1.17

Accepted name: N-methylalanine dehydrogenase
Reaction: N-methyl-L-alanine + H_2O + NADP^+ = pyruvate + methylamine + NADPH + H^+
Systematic name: N-methyl-L-alanine: NADP^+ oxidoreductase (demethylating, deaminating)
References: [2256]

[EC 1.4.1.17 created 1984]

EC 1.4.1.18

Accepted name: lysine 6-dehydrogenase
Reaction: L-lysine + NAD⁺ = (S)-2,3,4,5-tetrahydropyridine-2-carboxylate + NADH + H⁺ + NH₃ (overall reaction)
(1a) L-lysine + NAD⁺ + H₂O = (S)-2-amino-6-oxohexanoate + NADH + H⁺ + NH₃
(1b) (S)-2-amino-6-oxohexanoate = (S)-2,3,4,5-tetrahydropyridine-2-carboxylate + H₂O (spontaneous)
Other name(s): L-lysine ε-dehydrogenase; L-lysine 6-dehydrogenase; LysDH
Systematic name: L-lysine:NAD⁺ 6-oxidoreductase (deaminating)
Comments: The enzyme is highly specific for L-lysine as substrate, although S-(2-aminoethyl)-L-cysteine can act as a substrate, but more slowly. While the enzyme from *Agrobacterium tumefaciens* can use only NAD⁺, that from the thermophilic bacterium *Geobacillus stearothermophilus* can also use NADP⁺, but more slowly [2556, 1486].
References: [2556, 2559, 2555, 1486]

[EC 1.4.1.18 created 1989, modified 2006, modified 2011]

EC 1.4.1.19

Accepted name: tryptophan dehydrogenase
Reaction: L-tryptophan + NAD(P)⁺ + H₂O = (indol-3-yl)pyruvate + NH₃ + NAD(P)H + H⁺
Other name(s): NAD(P)⁺-L-tryptophan dehydrogenase; L-tryptophan dehydrogenase; L-Trp-dehydrogenase; TDH
Systematic name: L-tryptophan:NAD(P)⁺ oxidoreductase (deaminating)
Comments: Activated by Ca²⁺.
References: [3982]

[EC 1.4.1.19 created 1989]

EC 1.4.1.20

Accepted name: phenylalanine dehydrogenase
Reaction: L-phenylalanine + H₂O + NAD⁺ = phenylpyruvate + NH₃ + NADH + H⁺
Other name(s): L-phenylalanine dehydrogenase; PHD
Systematic name: L-phenylalanine:NAD⁺ oxidoreductase (deaminating)
Comments: The enzymes from *Bacillus badius* and *Sporosarcina ureae* are highly specific for L-phenylalanine; that from *Bacillus sphaericus* also acts on L-tyrosine.
References: [126, 127]

[EC 1.4.1.20 created 1989]

EC 1.4.1.21

Accepted name: aspartate dehydrogenase
Reaction: L-aspartate + H₂O + NAD(P)⁺ = oxaloacetate + NH₃ + NAD(P)H + H⁺
Other name(s): NAD-dependent aspartate dehydrogenase; NADH₂-dependent aspartate dehydrogenase; NADP⁺-dependent aspartate dehydrogenase
Systematic name: L-aspartate:NAD(P)⁺ oxidoreductase (deaminating)
Comments: The enzyme is strictly specific for L-aspartate as substrate. Catalyses the first step in NAD biosynthesis from aspartate. The enzyme has a higher affinity for NAD⁺ than NADP⁺ [4344].
References: [4344, 2864, 2059]

[EC 1.4.1.21 created 2005]

[1.4.1.22 Deleted entry. ornithine cyclodeaminase. It was pointed out during the public-review process that there is no overall consumption of NAD⁺ during the reaction. As a result, transfer of the enzyme from EC 4.3.1.12 was not necessary and EC 1.4.1.22 was withdrawn before being made official]

[EC 1.4.1.22 created 2006, deleted 2006]

EC 1.4.1.23

- Accepted name:** valine dehydrogenase (NAD⁺)
Reaction: L-valine + H₂O + NAD⁺ = 3-methyl-2-oxobutanoate + NH₃ + NADH + H⁺
Systematic name: L-valine:NAD⁺ oxidoreductase (deaminating)
Comments: The enzyme from *Streptomyces* spp. has no activity with NADP⁺ [*cf.* EC 1.4.1.8, valine dehydrogenase (NADP⁺)].
References: [4015, 2746]

[EC 1.4.1.23 created 2012]

EC 1.4.1.24

- Accepted name:** 3-dehydroquininate synthase II
Reaction: 2-amino-3,7-dideoxy-D-threo-hept-6-ulosonate + H₂O + NAD⁺ = 3-dehydroquininate + NH₃ + NADH + H⁺
Other name(s): DHQ synthase II; MJ1249 (gene name); *aroB'* (gene name)
Systematic name: 2-amino-3,7-dideoxy-D-threo-hept-6-ulosonate:NAD⁺ oxidoreductase (deaminating)
Comments: The enzyme, which was isolated from the archaeon *Methanocaldococcus jannaschii*, plays a key role in an alternative pathway for the biosynthesis of 3-dehydroquininate (DHQ), an intermediate of the canonical pathway for the biosynthesis of aromatic amino acids. The enzyme catalyses a two-step reaction - an oxidative deamination, followed by cyclization.
References: [4191]

[EC 1.4.1.24 created 2012]

EC 1.4.1.25

- Accepted name:** L-arginine dehydrogenase
Reaction: L-arginine + H₂O + NAD(P)⁺ = 5-guanidino-2-oxopentanoate + NH₃ + NAD(P)H + H⁺
Other name(s): *dauB* (gene name); anabolic L-arginine dehydrogenase
Systematic name: L-arginine:NAD(P)⁺ oxidoreductase (deaminating)
Comments: The enzyme, which has been isolated from the bacterium *Pseudomonas aeruginosa* PAO1, forms with EC 1.4.99.6, D-arginine dehydrogenase, a two-enzyme complex involved in the racemization of D- and L-arginine.
References: [2221]

[EC 1.4.1.25 created 2017]

EC 1.4.1.26

- Accepted name:** 2,4-diaminopentanoate dehydrogenase (NAD⁺)
Reaction: (2*R*,4*S*)-2,4-diaminopentanoate + H₂O + NAD⁺ = (2*R*)-2-amino-4-oxopentanoate + NH₃ + NADH + H⁺
Other name(s): DAPDH (ambiguous)
Systematic name: (2*R*,4*S*)-2,4-diaminopentanoate:NADP⁺ oxidoreductase (deaminating)
Comments: The enzyme, characterized from an unknown bacterium in an environmental sample, has some activity with (2*R*,4*R*)-2,4-diaminopentanoate. It has very low activity with NADP⁺ (*cf.* EC 1.4.1.12, 2,4-diaminopentanoate dehydrogenase).
References: [1028]

[EC 1.4.1.26 created 2017]

EC 1.4.2 With a cytochrome as acceptor

EC 1.4.2.1

Accepted name: glycine dehydrogenase (cytochrome)
Reaction: glycine + H₂O + 2 ferricytochrome *c* = glyoxylate + NH₃ + 2 ferrocycytochrome *c* + 2 H⁺
Other name(s): glycine—cytochrome *c* reductase
Systematic name: glycine:ferricytochrome-*c* oxidoreductase (deaminating)
References: [3306]

[EC 1.4.2.1 created 1976]

EC 1.4.3 With oxygen as acceptor

EC 1.4.3.1

Accepted name: D-aspartate oxidase
Reaction: D-aspartate + H₂O + O₂ = oxaloacetate + NH₃ + H₂O₂
Other name(s): aspartic oxidase; D-aspartic oxidase
Systematic name: D-aspartate:oxygen oxidoreductase (deaminating)
Comments: A flavoprotein (FAD).
References: [836, 3648, 3649]

[EC 1.4.3.1 created 1961]

EC 1.4.3.2

Accepted name: L-amino-acid oxidase
Reaction: an L-amino acid + H₂O + O₂ = a 2-oxo carboxylate + NH₃ + H₂O₂
Other name(s): ophio-amino-acid oxidase
Systematic name: L-amino-acid:oxygen oxidoreductase (deaminating)
Comments: A flavoprotein (FAD).
References: [2501, 4173]

[EC 1.4.3.2 created 1961]

EC 1.4.3.3

Accepted name: D-amino-acid oxidase
Reaction: a D-amino acid + H₂O + O₂ = a 2-oxo carboxylate + NH₃ + H₂O₂
Other name(s): ophio-amino-acid oxidase; L-amino acid:O₂ oxidoreductase; new yellow enzyme
Systematic name: D-amino-acid:oxygen oxidoreductase (deaminating)
Comments: A flavoprotein (FAD). Wide specificity for D-amino acids. Also acts on glycine.
References: [837, 839, 838, 2434, 2501]

[EC 1.4.3.3 created 1961]

EC 1.4.3.4

Accepted name: monoamine oxidase
Reaction: RCH₂NHR' + H₂O + O₂ = RCHO + R'NH₂ + H₂O₂
Other name(s): adrenalin oxidase; adrenaline oxidase; amine oxidase (ambiguous); amine oxidase (flavin-containing); amine:oxygen oxidoreductase (deaminating) (flavin-containing); epinephrine oxidase; MAO; MAO A; MAO B; MAO-A; MAO-B; monoamine oxidase A; monoamine oxidase B; monoamine:O₂ oxidoreductase (deaminating); polyamine oxidase (ambiguous); serotonin deaminase; spermidine oxidase (ambiguous); spermine oxidase (ambiguous); tyraminase; tyramine oxidase
Systematic name: amine:oxygen oxidoreductase (deaminating)

Comments: A mitochondrial outer-membrane flavoprotein (FAD) that catalyses the oxidative deamination of neurotransmitters and biogenic amines [921]. Acts on primary amines, and also on some secondary and tertiary amines. It differs from EC 1.4.3.21, primary-amine oxidase as it can oxidize secondary and tertiary amines but not methylamine. This enzyme is inhibited by acetylenic compounds such as chlorgyline, 1-deprenyl and pargyline but, unlike EC 1.4.3.21 and EC 1.4.3.22 (diamine oxidase), it is not inhibited by semicarbazide.

References: [319, 860, 921, 3489, 3895, 641, 4393, 4392]

[EC 1.4.3.4 created 1961, modified 1983 (EC 1.4.3.9 created 1972, incorporated 1984), modified 2008]

EC 1.4.3.5

Accepted name: pyridoxal 5'-phosphate synthase

Reaction: (1) pyridoxamine 5'-phosphate + H₂O + O₂ = pyridoxal 5'-phosphate + NH₃ + H₂O₂
(2) pyridoxine 5'-phosphate + O₂ = pyridoxal 5'-phosphate + H₂O₂

Other name(s): pyridoxamine 5'-phosphate oxidase; pyridoxamine phosphate oxidase; pyridoxine (pyridoxamine)phosphate oxidase; pyridoxine (pyridoxamine) 5'-phosphate oxidase; pyridoxaminephosphate oxidase (EC 1.4.3.5: deaminating); PMP oxidase; pyridoxol-5'-phosphate:oxygen oxidoreductase (deaminating) (incorrect); pyridoxamine-phosphate oxidase; PdxH

Systematic name: pyridoxamine-5'-phosphate:oxygen oxidoreductase (deaminating)

Comments: A flavoprotein (FMN). In *Escherichia coli*, the coenzyme pyridoxal 5'-phosphate is synthesized *de novo* by a pathway that involves EC 1.2.1.72 (erythrose-4-phosphate dehydrogenase), EC 1.1.1.290 (4-phosphoerythronate dehydrogenase), EC 2.6.1.52 (phosphoserine transaminase), EC 1.1.1.262 (4-hydroxythreonine-4-phosphate dehydrogenase), EC 2.6.99.2 (pyridoxine 5'-phosphate synthase) and EC 1.4.3.5 (with pyridoxine 5'-phosphate as substrate). N^{4'}-Substituted pyridoxamine derivatives are also oxidized in reaction (1) to form pyridoxal 5-phosphate and the corresponding primary amine.

References: [609, 4075, 2821, 2109, 2675, 3278, 4450]

[EC 1.4.3.5 created 1961, modified 2006]

[1.4.3.6 Deleted entry. amine oxidase (copper-containing). This was classified on the basis of cofactor content rather than reaction catalysed and is now known to contain two distinct enzyme activities. It has been replaced by two enzymes, EC 1.4.3.21 (primary-amine oxidase) and EC 1.4.3.22 (diamine oxidase)]

[EC 1.4.3.6 created 1961, modified 1983, modified 1989, deleted 2008]

EC 1.4.3.7

Accepted name: D-glutamate oxidase

Reaction: D-glutamate + H₂O + O₂ = 2-oxoglutarate + NH₃ + H₂O₂

Other name(s): D-glutamic oxidase; D-glutamic acid oxidase

Systematic name: D-glutamate:oxygen oxidoreductase (deaminating)

References: [3205, 3975]

[EC 1.4.3.7 created 1972]

EC 1.4.3.8

Accepted name: ethanolamine oxidase

Reaction: ethanolamine + H₂O + O₂ = glycolaldehyde + NH₃ + H₂O₂

Systematic name: ethanolamine:oxygen oxidoreductase (deaminating)

Comments: A cobamide-protein.

References: [2735]

[EC 1.4.3.8 created 1972]

[1.4.3.9 Deleted entry. tyramine oxidase. Now included with EC 1.4.3.4 amine oxidase (flavin-containing)]

[EC 1.4.3.9 created 1972, deleted 1984]

EC 1.4.3.10

Accepted name: putrescine oxidase
Reaction: putrescine + O₂ + H₂O = 4-aminobutanal + NH₃ + H₂O₂
Systematic name: putrescine:oxygen oxidoreductase (deaminating)
Comments: A flavoprotein (FAD). 4-Aminobutanal condenses non-enzymically to 1-pyrroline.
References: [802, 4301]

[EC 1.4.3.10 created 1976]

EC 1.4.3.11

Accepted name: L-glutamate oxidase
Reaction: L-glutamate + O₂ + H₂O = 2-oxoglutarate + NH₃ + H₂O₂
Other name(s): glutamate (acceptor) dehydrogenase; glutamate oxidase; glutamic acid oxidase; glutamic dehydrogenase (acceptor); L-glutamic acid oxidase
Systematic name: L-glutamate:oxygen oxidoreductase (deaminating)
Comments: A flavoprotein (FAD). The enzyme from *Azotobacter* previously listed under this number, which did not produce H₂O₂, was a crude cell-free extract that probably contained catalase.
References: [2097]

[EC 1.4.3.11 created 1976, modified 1989]

EC 1.4.3.12

Accepted name: cyclohexylamine oxidase
Reaction: cyclohexylamine + O₂ + H₂O = cyclohexanone + NH₃ + H₂O₂
Systematic name: cyclohexylamine:oxygen oxidoreductase (deaminating)
Comments: A flavoprotein (FAD). Some other cyclic amines can act instead of cyclohexylamine, but not simple aliphatic and aromatic amides.
References: [3902]

[EC 1.4.3.12 created 1978]

EC 1.4.3.13

Accepted name: protein-lysine 6-oxidase
Reaction: [protein]-L-lysine + O₂ + H₂O = [protein]-(S)-2-amino-6-oxohexanoate + NH₃ + H₂O₂
Other name(s): lysyl oxidase
Systematic name: protein-L-lysine:oxygen 6-oxidoreductase (deaminating)
Comments: Also acts on protein 5-hydroxylysine. This enzyme catalyses the final known enzymic step required for collagen and elastin cross-linking in the biosynthesis of normal mature extracellular matrices [2925]. These reactions play an important role for the development, elasticity and extensibility of connective tissue. The enzyme is also active on free amines, such as cadaverine or benzylamine [2925, 1795]. Some isoforms can also use [protein]-N(6)-acetyl-L-lysine as substrate deacetamidating the substrate [3212].
References: [1398, 3142, 3625, 2925, 1795, 3212, 1925, 4284, 2335]

[EC 1.4.3.13 created 1980, modified 1983]

EC 1.4.3.14

Accepted name: L-lysine oxidase
Reaction: L-lysine + O₂ + H₂O = 6-amino-2-oxohexanoate + NH₃ + H₂O₂
Other name(s): L-lysine α-oxidase; L-lysyl-α-oxidase
Systematic name: L-lysine:oxygen 2-oxidoreductase (deaminating)

Comments: Also acts, more slowly, on L-ornithine, L-phenylalanine, L-arginine and L-histidine.

References: [2095, 2314]

[EC 1.4.3.14 created 1981]

EC 1.4.3.15

Accepted name: D-glutamate(D-aspartate) oxidase

Reaction: (1) $\text{D-glutamate} + \text{H}_2\text{O} + \text{O}_2 = 2\text{-oxoglutarate} + \text{NH}_3 + \text{H}_2\text{O}_2$

(2) $\text{D-aspartate} + \text{H}_2\text{O} + \text{O}_2 = \text{oxaloacetate} + \text{NH}_3 + \text{H}_2\text{O}_2$

Other name(s): D-glutamic-aspartic oxidase; D-monoaminodicarboxylic acid oxidase

Systematic name: D-glutamate(D-aspartate):oxygen oxidoreductase (deaminating)

Comments: A flavoprotein (FAD). D-Glutamate and D-aspartate are oxidized at the same rate. Other D-monoaminodicarboxylates, and other D- and L-amino acids, are not oxidized. *cf.* EC 1.4.3.7, D-glutamate oxidase and EC 1.4.3.1, D-aspartate oxidase.

References: [2581]

[EC 1.4.3.15 created 1983, modified 2012]

EC 1.4.3.16

Accepted name: L-aspartate oxidase

Reaction: $\text{L-aspartate} + \text{O}_2 = \text{iminosuccinate} + \text{H}_2\text{O}_2$

Other name(s): NadB; Laspo; AO

Systematic name: L-aspartate:oxygen oxidoreductase

Comments: A flavoprotein (FAD). L-Aspartate oxidase catalyses the first step in the *de novo* biosynthesis of NAD^+ in some bacteria. O_2 can be replaced by fumarate as electron acceptor, yielding succinate [363]. The ability of the enzyme to use both O_2 and fumarate in cofactor reoxidation enables it to function under both aerobic and anaerobic conditions [363]. Iminosuccinate can either be hydrolysed to form oxaloacetate and NH_3 or can be used by EC 2.5.1.72, quinolinate synthase, in the production of quinolinate. The enzyme is a member of the succinate dehydrogenase/fumarate-reductase family of enzymes [363].

References: [2742, 2635, 3841, 2466, 363, 1843]

[EC 1.4.3.16 created 1984, modified 2008]

[1.4.3.17 *Transferred entry. tryptophan α,β -oxidase. Now EC 1.3.3.10, tryptophan α,β -oxidase. Enzyme was incorrectly classified as acting on a CH-NH bond rather than a CH-CH bond*]

[EC 1.4.3.17 created 2000, deleted 2003]

[1.4.3.18 *Deleted entry. cytokinin oxidase. Not approved as the enzyme was shown to be a dehydrogenase and not an oxidase (see EC 1.5.99.12, cytokinin dehydrogenase)*]

[EC 1.4.3.18 proposed 2000]

EC 1.4.3.19

Accepted name: glycine oxidase

Reaction: $\text{glycine} + \text{H}_2\text{O} + \text{O}_2 = \text{glyoxylate} + \text{NH}_3 + \text{H}_2\text{O}_2$ (overall reaction)

(1a) $\text{glycine} + \text{O}_2 = 2\text{-iminoacetate} + \text{H}_2\text{O}_2$

(1b) $2\text{-iminoacetate} + \text{H}_2\text{O} = \text{glyoxylate} + \text{NH}_3$

Systematic name: glycine:oxygen oxidoreductase (deaminating)

Comments: A flavoenzyme containing non-covalently bound FAD. The enzyme from *Bacillus subtilis* is active with glycine, sarcosine, *N*-ethylglycine, D-alanine, D- α -aminobutyrate, D-proline, D-pipecolate and *N*-methyl-D-alanine. It differs from EC 1.4.3.3, D-amino-acid oxidase, due to its activity on sarcosine and D-pipecolate. The intermediate 2-iminoacetate is used directly by EC 2.8.1.10, thiazole synthase.

References: [1749, 2800]

[EC 1.4.3.19 created 2002, modified 2012]

EC 1.4.3.20

- Accepted name:** L-lysine 6-oxidase
Reaction: $\text{L-lysine} + \text{O}_2 + \text{H}_2\text{O} = (S)\text{-2-amino-6-oxohexanoate} + \text{H}_2\text{O}_2 + \text{NH}_3$
Other name(s): L-lysine- ϵ -oxidase; Lod; LodA; marinocine
Systematic name: L-lysine:oxygen 6-oxidoreductase (deaminating)
Comments: Differs from EC 1.4.3.13, protein-lysine 6-oxidase, by using free L-lysine rather than the protein-bound form. *N*²-Acetyl-L-lysine is also a substrate, but *N*⁶-acetyl-L-lysine, which has an acetyl group at position 6, is not a substrate. Also acts on L-ornithine, D-lysine and 4-hydroxy-L-lysine, but more slowly. The amines cadaverine and putrescine are not substrates [1231].
References: [2311, 1231]

[EC 1.4.3.20 created 2006, modified 2011]

EC 1.4.3.21

- Accepted name:** primary-amine oxidase
Reaction: $\text{RCH}_2\text{NH}_2 + \text{H}_2\text{O} + \text{O}_2 = \text{RCHO} + \text{NH}_3 + \text{H}_2\text{O}_2$
Other name(s): amine oxidase (ambiguous); amine oxidase (copper-containing); amine oxidase (pyridoxal containing) (incorrect); benzylamine oxidase (incorrect); CAO (ambiguous); copper amine oxidase (ambiguous); Cu-amine oxidase (ambiguous); Cu-containing amine oxidase (ambiguous); diamine oxidase (incorrect); diamino oxhydrase (incorrect); histamine deaminase (ambiguous); histamine oxidase (ambiguous); monoamine oxidase (ambiguous); plasma monoamine oxidase (ambiguous); polyamine oxidase (ambiguous); semicarbazide-sensitive amine oxidase (ambiguous); SSAO (ambiguous)
Systematic name: primary-amine:oxygen oxidoreductase (deaminating)
Comments: A group of enzymes that oxidize primary monoamines but have little or no activity towards diamines, such as histamine, or towards secondary and tertiary amines. They are copper quinoproteins (2,4,5-trihydroxyphenylalanine quinone) and, unlike EC 1.4.3.4, monoamine oxidase, are sensitive to inhibition by carbonyl-group reagents, such as semicarbazide. In some mammalian tissues the enzyme also functions as a vascular-adhesion protein (VAP-1).
References: [1443, 3894, 2325, 4212, 2182, 1584, 90, 3338, 2906, 40]

[EC 1.4.3.21 created 2007 (EC 1.4.3.6 created 1961, part-incorporated 2008)]

EC 1.4.3.22

- Accepted name:** diamine oxidase
Reaction: $\text{histamine} + \text{H}_2\text{O} + \text{O}_2 = (\text{imidazol-4-yl})\text{acetaldehyde} + \text{NH}_3 + \text{H}_2\text{O}_2$
Other name(s): amine oxidase (ambiguous); amine oxidase (copper-containing) (ambiguous); CAO (ambiguous); Cu-containing amine oxidase (ambiguous); copper amine oxidase (ambiguous); diamine oxidase (ambiguous); diamino oxhydrase (ambiguous); histaminase; histamine deaminase (incorrect); semicarbazide-sensitive amine oxidase (incorrect); SSAO (incorrect)
Systematic name: histamine:oxygen oxidoreductase (deaminating)
Comments: A group of enzymes that oxidize diamines, such as histamine, and also some primary monoamines but have little or no activity towards secondary and tertiary amines. They are copper quinoproteins (2,4,5-trihydroxyphenylalanine quinone) and, like EC 1.4.3.21 (primary-amine oxidase) but unlike EC 1.4.3.4 (monoamine oxidase), they are sensitive to inhibition by carbonyl-group reagents, such as semicarbazide.
References: [4433, 686, 553, 1584, 942]

[EC 1.4.3.22 created 2007 (EC 1.4.3.6 created 1961, part-incorporated 2008)]

EC 1.4.3.23

- Accepted name:** 7-chloro-L-tryptophan oxidase

Reaction: 7-chloro-L-tryptophan + O₂ = 2-imino-3-(7-chloroindol-3-yl)propanoate + H₂O₂
Other name(s): RebO
Systematic name: 7-chloro-L-tryptophan:oxygen oxidoreductase
Comments: Contains a noncovalently bound FAD [2801, 1585]. This enzyme catalyses a step in the biosynthesis of rebeccamycin, an indolocarbazole alkaloid produced by the bacterium *Lechevalieria aerocolonigenes*. During catalysis, the bound FAD is reoxidized at the expense of molecular oxygen, producing one molecule of hydrogen peroxide. The enzyme shows significant preference for 7-chloro-L-tryptophan over L-tryptophan [2801].
References: [2801, 1585]

[EC 1.4.3.23 created 2010]

EC 1.4.3.24

Accepted name: pseudooxynicotine oxidase
Reaction: 4-(methylamino)-1-(pyridin-3-yl)butan-1-one + H₂O + O₂ = 4-oxo-4-(pyridin-3-yl)butanal + methylamine + H₂O₂
Systematic name: 4-(methylamino)-1-(pyridin-3-yl)butan-1-one:oxygen oxidoreductase (methylamine releasing)
Comments: Contains one non-covalently bound FAD molecule per dimer. This enzyme, characterized from the soil bacterium *Pseudomonas* sp. HZN6, is involved the nicotine degradation.
References: [3080]

[EC 1.4.3.24 created 2012]

EC 1.4.3.25

Accepted name: L-arginine oxidase
Reaction: L-arginine + H₂O + O₂ = 5-guanidino-2-oxopentanoate + NH₃ + H₂O₂
Systematic name: L-arginine:oxygen oxidoreductase (deaminating)
Comments: Contains FAD. The enzyme from cyanobacteria can also act on other basic amino acids with lower activity. The enzyme from the bacterium *Pseudomonas* sp. TPU 7192 is highly specific.
References: [2542, 3017, 1166, 2444]

[EC 1.4.3.25 created 2017]

EC 1.4.4 With a disulfide as acceptor

[1.4.4.1 Transferred entry. D-proline reductase (dithiol). Now EC 1.21.4.1, D-proline reductase (dithiol)]

[EC 1.4.4.1 created 1972, modified 1982 (EC 1.4.1.6 created 1961, incorporated 1982), deleted 2003]

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 + CO₂
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 [2764]. Previously known as glycine synthase.
References: [1513, 2983, 2764]

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

EC 1.4.5 With a quinone or other compound as acceptor

EC 1.4.5.1

- Accepted name:** D-amino acid dehydrogenase (quinone)
Reaction: a D-amino acid + H₂O + a quinone = a 2-oxo carboxylate + NH₃ + a quinol
Other name(s): DadA
Systematic name: D-amino acid:quinone oxidoreductase (deaminating)
Comments: An iron-sulfur flavoprotein (FAD). The enzyme from the bacterium *Helicobacter pylori* is highly specific for D-proline, while the enzyme from the bacterium *Escherichia coli B* is most active with D-alanine, D-phenylalanine and D-methionine. This enzyme may be the same as EC 1.4.99.6.
References: [2879, 3813]

[EC 1.4.5.1 created 2010]

EC 1.4.7 With an iron-sulfur protein as acceptor

EC 1.4.7.1

- Accepted name:** glutamate synthase (ferredoxin)
Reaction: 2 L-glutamate + 2 oxidized ferredoxin = L-glutamine + 2-oxoglutarate + 2 reduced ferredoxin + 2 H⁺ (overall reaction)
(1a) L-glutamate + NH₃ = L-glutamine + H₂O
(1b) L-glutamate + 2 oxidized ferredoxin + H₂O = NH₃ + 2-oxoglutarate + 2 reduced ferredoxin + 2 H⁺
Other name(s): ferredoxin-dependent glutamate synthase; ferredoxin-glutamate synthase; glutamate synthase (ferredoxin-dependent)
Systematic name: L-glutamate:ferredoxin oxidoreductase (transaminating)
Comments: Binds a [3Fe-4S] cluster as well as FAD and FMN. The protein is composed of two domains, one hydrolysing L-glutamine to NH₃ and L-glutamate (*cf.* EC 3.5.1.2, glutaminase), the other combining the produced NH₃ with 2-oxoglutarate to produce a second molecule of L-glutamate. The NH₃ is channeled through a 24 Å channel in the active protein. No hydrolysis of glutamine takes place without ferredoxin and 2-oxoglutarate being bound to the protein [3995, 3996].
References: [1147, 2159, 3134, 2747, 3995, 3996]

[EC 1.4.7.1 created 1976, modified 2012]

EC 1.4.9 With a copper protein as acceptor

EC 1.4.9.1

- Accepted name:** methylamine dehydrogenase (amicyanin)
Reaction: methylamine + H₂O + 2 amicyanin = formaldehyde + NH₃ + 2 reduced amicyanin
Other name(s): amine dehydrogenase; primary-amine dehydrogenase; amine: (acceptor) oxidoreductase (deaminating); primary-amine:(acceptor) oxidoreductase (deaminating)
Systematic name: methylamine:amicyanin oxidoreductase (deaminating)
Comments: Contains tryptophan tryptophylquinone (TTQ) cofactor. The enzyme oxidizes aliphatic monoamines and diamines, histamine and ethanolamine, but not secondary and tertiary amines, quaternary ammonium salts or aromatic amines.
References: [241, 902, 904, 523, 2508]

[EC 1.4.9.1 created 1978 as EC 1.4.99.3, modified 1986, transferred 2011 to EC 1.4.98.1, transferred 2011 to EC 1.4.9.1]

EC 1.4.9.2

- Accepted name:** aralkylamine dehydrogenase (azurin)
Reaction: $\text{ArCH}_2\text{NH}_2 + \text{H}_2\text{O} + 2 \text{ azurin} = \text{ArCHO} + \text{NH}_3 + 2 \text{ reduced azurin}$
Other name(s): aromatic amine dehydrogenase; arylamine dehydrogenase; tyramine dehydrogenase; aralkylamine:(acceptor) oxidoreductase (deaminating)
Systematic name: aralkylamine:azurin oxidoreductase (deaminating)
Comments: Phenazine methosulfate can act as acceptor. Acts on aromatic amines and, more slowly, on some long-chain aliphatic amines, but not on methylamine or ethylamine
References: [1695, 1619, 1620, 754, 3723]

[EC 1.4.9.2 created 1986 as EC 1.4.99.4, transferred 2011 to EC 1.4.9.2]

EC 1.4.98 With a copper protein as acceptor

[1.4.98.1 *Transferred entry. amine dehydrogenase. Now EC 1.4.9.1, methylamine dehydrogenase (amicyanin)]*

[EC 1.4.98.1 created 1978 as EC 1.4.99.3, modified 1986, transferred 2011 to EC 1.4.98.1, deleted 2011]

EC 1.4.99 With unknown physiological acceptors

[1.4.99.1 *Transferred entry. D-amino-acid dehydrogenase. Now listed as EC 1.4.99.6, D-arginine dehydrogenase]*

[EC 1.4.99.1 created 1972, deleted 2015]

EC 1.4.99.2

- Accepted name:** taurine dehydrogenase
Reaction: $\text{taurine} + \text{H}_2\text{O} + \text{acceptor} = 2\text{-sulfoacetaldehyde} + \text{NH}_3 + \text{reduced acceptor}$
Other name(s): taurine:(acceptor) oxidoreductase (deaminating)
Systematic name: taurine:acceptor oxidoreductase (deaminating)
References: [2021]

[EC 1.4.99.2 created 1976]

[1.4.99.3 *Transferred entry. amine dehydrogenase. Now EC 1.4.9.1, methylamine dehydrogenase (amicyanin)]*

[EC 1.4.99.3 created 1978, modified 1986, deleted 2011]

[1.4.99.4 *Transferred entry. aralkylamine dehydrogenase. Now EC 1.4.9.2, aralkylamine dehydrogenase (azurin)]*

[EC 1.4.99.4 created 1986, deleted 2011]

EC 1.4.99.5

- Accepted name:** glycine dehydrogenase (cyanide-forming)
Reaction: $\text{glycine} + 2 \text{ acceptor} = \text{hydrogen cyanide} + \text{CO}_2 + 2 \text{ reduced acceptor}$
Other name(s): hydrogen cyanide synthase; HCN synthase
Systematic name: glycine:acceptor oxidoreductase (hydrogen-cyanide-forming)
Comments: The enzyme from *Pseudomonas* sp. contains FAD. The enzyme is membrane-bound, and the 2-electron acceptor is a component of the respiratory chain. The enzyme can act with various artificial electron acceptors, including phenazine methosulfate.
References: [4230, 520, 2153, 326]

[EC 1.4.99.5 created 2002]

EC 1.4.99.6

Accepted name: D-arginine dehydrogenase
Reaction: D-arginine + acceptor + H₂O = 5-guanidino-2-oxopentanoate + NH₃ + reduced acceptor (overall reaction)
 (1a) D-arginine + acceptor = iminoarginine + reduced acceptor
 (1b) iminoarginine + H₂O = 5-guanidino-2-oxopentanoate + NH₃ (spontaneous)
Other name(s): D-amino-acid:(acceptor) oxidoreductase (deaminating); D-amino-acid dehydrogenase; D-amino-acid:acceptor oxidoreductase (deaminating)
Systematic name: D-arginine:acceptor oxidoreductase (deaminating)
Comments: Contains a non-covalent FAD cofactor. The enzyme, which has been isolated from the bacterium *Pseudomonas aeruginosa* PAO1, forms with EC 1.4.1.25, L-arginine dehydrogenase, a two-enzyme complex involved in the racemization of D- and L-arginine. The enzyme has a broad substrate range and can act on most D-amino acids with the exception of D-glutamate and D-aspartate. However, activity is maximal with D-arginine and D-lysine. Not active on glycine.
References: [3940, 2221, 1086, 4408, 1087, 4409]

[EC 1.4.99.6 created 1972 as EC 1.4.99.1, transferred 2015 to EC 1.4.99.6, modified 2017]

EC 1.5 Acting on the CH-NH group of donors

This subclass contains enzymes that dehydrogenate secondary amines, introducing a C=N double bond as the primary reaction. In some cases, this is later hydrolysed. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.5.1), oxygen (EC 1.5.3), a disulfide (EC 1.5.4), a quinone or similar compound (EC 1.5.5), an iron-sulfur protein (EC 1.5.7), a flavin (EC 1.5.8), or some other acceptor (EC 1.5.99).

EC 1.5.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.5.1.1

Accepted name: 1-piperideine-2-carboxylate/1-pyrroline-2-carboxylate reductase [NAD(P)H]
Reaction: (1) L-pipecolate + NAD(P)⁺ = 1-piperideine-2-carboxylate + NAD(P)H + H⁺
 (2) L-proline + NAD(P)⁺ = 1-pyrroline-2-carboxylate + NAD(P)H + H⁺
Other name(s): Δ¹-pyrroline-2-carboxylate reductase; DELTA1-pyrroline-2-carboxylate reductase; DELTA1-piperideine-2-carboxylate/1-pyrroline-2-carboxylate reductase (ambiguous); AbLhpI; pyrroline-2-carboxylate reductase; L-proline:NAD(P)⁺ 2-oxidoreductase
Systematic name: L-pipecolate/L-proline:NAD(P)⁺ 2-oxidoreductase
Comments: The enzymes, characterized from the bacterium *Azospirillum brasilense*, is involved in *trans*-3-hydroxy-L-proline metabolism. In contrast to EC 1.5.1.21, 1-piperideine-2-carboxylate/1-pyrroline-2-carboxylate reductase (NADPH), which is specific for NADPH, this enzyme shows similar activity with NADPH and NADH.
References: [2500, 4148]

[EC 1.5.1.1 created 1961, modified 2015]

EC 1.5.1.2

Accepted name: pyrroline-5-carboxylate reductase
Reaction: L-proline + NAD(P)⁺ = 1-pyrroline-5-carboxylate + NAD(P)H + H⁺
Other name(s): proline oxidase; L-proline oxidase; 1-pyrroline-5-carboxylate reductase; NADPH-L-Δ¹-pyrroline carboxylic acid reductase; L-proline-NAD(P)⁺ 5-oxidoreductase
Systematic name: L-proline:NAD(P)⁺ 5-oxidoreductase
Comments: Also reduces 1-pyrroline-3-hydroxy-5-carboxylate to L-hydroxyproline.
References: [20, 2500, 3562, 4414]

[EC 1.5.1.2 created 1961]

EC 1.5.1.3

- Accepted name:** dihydrofolate reductase
Reaction: 5,6,7,8-tetrahydrofolate + NADP⁺ = 7,8-dihydrofolate + NADPH + H⁺
Other name(s): tetrahydrofolate dehydrogenase; DHFR; pteridine reductase:dihydrofolate reductase; dihydrofolate reductase:thymidylate synthase; thymidylate synthetase-dihydrofolate reductase; folic acid reductase; folic reductase; dihydrofolic acid reductase; dihydrofolic reductase; 7,8-dihydrofolate reductase; NADPH-dihydrofolate reductase
Systematic name: 5,6,7,8-tetrahydrofolate:NADP⁺ oxidoreductase
Comments: The enzyme from animals and some micro-organisms also slowly reduces folate to 5,6,7,8-tetrahydrofolate.
References: [315, 338, 1849, 4395]

[EC 1.5.1.3 created 1961, modified 1976 (EC 1.5.1.4 created 1961, incorporated 1976)]

[1.5.1.4 Deleted entry. dihydrofolate dehydrogenase. Now included with EC 1.5.1.3 dihydrofolate reductase]

[EC 1.5.1.4 created 1961, deleted 1976]

EC 1.5.1.5

- Accepted name:** methylenetetrahydrofolate dehydrogenase (NADP⁺)
Reaction: 5,10-methylenetetrahydrofolate + NADP⁺ = 5,10-methenyltetrahydrofolate + NADPH + H⁺
Other name(s): N⁵,N¹⁰-methylenetetrahydrofolate dehydrogenase; 5,10-methylenetetrahydrofolate:NADP oxidoreductase; 5,10-methylenetetrahydrofolate dehydrogenase; methylenetetrahydrofolate dehydrogenase; methylenetetrahydrofolate dehydrogenase (NADP)
Systematic name: 5,10-methylenetetrahydrofolate:NADP⁺ oxidoreductase
Comments: In eukaryotes, occurs as a trifunctional enzyme also having methenyltetrahydrofolate cyclohydrolase (EC 3.5.4.9) and formate—tetrahydrofolate ligase (EC 6.3.4.3) activity. In some prokaryotes occurs as a bifunctional enzyme also having methenyltetrahydrofolate cyclohydrolase activity (EC 3.5.4.9).
References: [1419, 2899, 3120, 4358]

[EC 1.5.1.5 created 1961]

EC 1.5.1.6

- Accepted name:** formyltetrahydrofolate dehydrogenase
Reaction: 10-formyltetrahydrofolate + NADP⁺ + H₂O = tetrahydrofolate + CO₂ + NADPH + H⁺
Other name(s): 10-formyl tetrahydrofolate:NADP oxidoreductase; 10-formyl-H₂PtGlu:NADP oxidoreductase; 10-formyl-H₄folate dehydrogenase; N¹⁰-formyltetrahydrofolate dehydrogenase; 10-formyltetrahydrofolate dehydrogenase
Systematic name: 10-formyltetrahydrofolate:NADP⁺ oxidoreductase
References: [2101]

[EC 1.5.1.6 created 1972]

EC 1.5.1.7

- Accepted name:** saccharopine dehydrogenase (NAD⁺, L-lysine-forming)
Reaction: N⁶-(L-1,3-dicarboxypropyl)-L-lysine + NAD⁺ + H₂O = L-lysine + 2-oxoglutarate + NADH + H⁺
Other name(s): lysine-2-oxoglutarate reductase; dehydrogenase, saccharopine (nicotinamide adenine dinucleotide, lysine forming); ε-N-(L-glutaryl-2)-L-lysine:NAD oxidoreductase (L-lysine forming); N⁶-(glutar-2-yl)-L-lysine:NAD oxidoreductase (L-lysine-forming); 6-N-(L-1,3-dicarboxypropyl)-L-lysine:NAD⁺ oxidoreductase (L-lysine-forming)
Systematic name: N⁶-(L-1,3-dicarboxypropyl)-L-lysine:NAD⁺ oxidoreductase (L-lysine-forming)
References: [1093, 3326]

[EC 1.5.1.7 created 1972]

EC 1.5.1.8

- Accepted name:** saccharopine dehydrogenase (NADP⁺, L-lysine-forming)
Reaction: N^6 -(L-1,3-dicarboxypropyl)-L-lysine + NADP⁺ + H₂O = L-lysine + 2-oxoglutarate + NADPH + H⁺
Other name(s): lysine-2-oxoglutarate reductase; lysine-ketoglutarate reductase; L-lysine- α -ketoglutarate reductase; lysine: α -ketoglutarate:TPNH oxidoreductase (ϵ -N-[gultaryl-2]-L-lysine forming); saccharopine (nicotinamide adenine dinucleotide phosphate, lysine-forming) dehydrogenase; 6-*N*-(L-1,3-dicarboxypropyl)-L-lysine:NADP⁺ oxidoreductase (L-lysine-forming)
Systematic name: N^6 -(L-1,3-dicarboxypropyl)-L-lysine:NADP⁺ oxidoreductase (L-lysine-forming)
References: [1616, 2401]

[EC 1.5.1.8 created 1972]

EC 1.5.1.9

- Accepted name:** saccharopine dehydrogenase (NAD⁺, L-glutamate-forming)
Reaction: N^6 -(L-1,3-dicarboxypropyl)-L-lysine + NAD⁺ + H₂O = L-glutamate + (*S*)-2-amino-6-oxohexanoate + NADH + H⁺
Other name(s): dehydrogenase, saccharopine (nicotinamide adenine dinucleotide, glutamate-forming); saccharopin dehydrogenase; NAD⁺ oxidoreductase (L-2-aminoadipic- δ -semialdehyde and glutamate forming); aminoadipic semialdehyde synthase; 6-*N*-(L-1,3-dicarboxypropyl)-L-lysine:NAD⁺ oxidoreductase (L-glutamate-forming)
Systematic name: N^6 -(L-1,3-dicarboxypropyl)-L-lysine:NAD⁺ oxidoreductase (L-glutamate-forming)
Comments: The activities of this enzyme along with EC 1.5.1.8, saccharopine dehydrogenase (NADP⁺, L-lysine-forming), occur on a single protein.
References: [1616, 2401]

[EC 1.5.1.9 created 1972, modified 2011]

EC 1.5.1.10

- Accepted name:** saccharopine dehydrogenase (NADP⁺, L-glutamate-forming)
Reaction: N^6 -(L-1,3-dicarboxypropyl)-L-lysine + NADP⁺ + H₂O = L-glutamate + (*S*)-2-amino-6-oxohexanoate + NADPH + H⁺
Other name(s): saccharopine (nicotinamide adenine dinucleotide phosphate, glutamate-forming) dehydrogenase; aminoadipic semialdehyde-glutamic reductase; aminoadipate semialdehyde-glutamate reductase; aminoadipic semialdehyde-glutamate reductase; ϵ -*N*-(L-glutaryl-2)-L-lysine:NAD⁺(P) oxidoreductase (L-2-aminoadipate-semialdehyde forming); saccharopine reductase; 6-*N*-(L-1,3-dicarboxypropyl)-L-lysine:NADP⁺ oxidoreductase (L-glutamate-forming)
Systematic name: N^6 -(L-1,3-dicarboxypropyl)-L-lysine:NADP⁺ oxidoreductase (L-glutamate-forming)
References: [1769]

[EC 1.5.1.10 created 1972, modified 2011]

EC 1.5.1.11

- Accepted name:** D-octopine dehydrogenase
Reaction: N^2 -(D-1-carboxyethyl)-L-arginine + NAD⁺ + H₂O = L-arginine + pyruvate + NADH + H⁺
Other name(s): D-octopine synthase; octopine dehydrogenase; octopine:NAD⁺ oxidoreductase; ODH; 2-*N*-(D-1-carboxyethyl)-L-arginine:NAD⁺ oxidoreductase (L-arginine-forming)
Systematic name: N^2 -(D-1-carboxyethyl)-L-arginine:NAD⁺ oxidoreductase (L-arginine-forming)
Comments: In the reverse direction, acts also on L-ornithine, L-lysine and L-histidine.
References: [1879, 4012]

[EC 1.5.1.11 created 1972]

[1.5.1.12 Transferred entry. 1-pyrroline-5-carboxylate dehydrogenase. Now EC 1.2.1.88, L-glutamate γ -semialdehyde dehydrogenase.]

[EC 1.5.1.12 created 1972, modified 2008, deleted 2013]

[1.5.1.13 *Transferred entry. nicotinate dehydrogenase. Now EC 1.17.1.5, nicotinate dehydrogenase. The enzyme was incorrectly classified as acting on a CH-NH group*]

[EC 1.5.1.13 created 1972, deleted 2004]

[1.5.1.14 *Deleted entry. 1,2-didehydropipecolate reductase. Now included with EC 1.5.1.21 Δ^1 -piperidine-2-carboxylate reductase*]

[EC 1.5.1.14 created 1976, deleted 1989]

EC 1.5.1.15

Accepted name: methylenetetrahydrofolate dehydrogenase (NAD⁺)
Reaction: 5,10-methylenetetrahydrofolate + NAD⁺ = 5,10-methenyltetrahydrofolate + NADH + H⁺
Other name(s): methylenetetrahydrofolate dehydrogenase (NAD⁺)
Systematic name: 5,10-methylenetetrahydrofolate:NAD⁺ oxidoreductase
References: [2608]

[EC 1.5.1.15 created 1978]

EC 1.5.1.16

Accepted name: D-lysopine dehydrogenase
Reaction: N²-(D-1-carboxyethyl)-L-lysine + NADP⁺ + H₂O = L-lysine + pyruvate + NADPH + H⁺
Other name(s): D-lysopine synthase; lysopine dehydrogenase; D(+)-lysopine dehydrogenase; 2-N-(D-1-carboxyethyl)-L-lysine:NADP⁺ oxidoreductase (L-lysine-forming)
Systematic name: N²-(D-1-carboxyethyl)-L-lysine:NADP⁺ oxidoreductase (L-lysine-forming)
Comments: In the reverse reaction, a number of L-amino acids can act instead of L-lysine, and 2-oxobutanoate and, to a lesser extent, glyoxylate can act instead of pyruvate.
References: [2911]

[EC 1.5.1.16 created 1978]

EC 1.5.1.17

Accepted name: alanopine dehydrogenase
Reaction: 2,2'-iminodipropoanoate + NAD⁺ + H₂O = L-alanine + pyruvate + NADH + H⁺
Other name(s): ALPDH ; alanopine[*meso*-N-(1-carboxyethyl)-alanine]dehydrogenase; *meso*-N-(1-carboxyethyl)-alanine:NAD⁺ oxidoreductase; alanopine: NAD oxidoreductase; ADH; alanopine:NAD oxidoreductase
Systematic name: 2,2'-iminodipropoanoate:NAD⁺ oxidoreductase (L-alanine-forming)
Comments: In the reverse reaction, L-alanine can be replaced by L-cysteine, L-serine or L-threonine; glycine acts very slowly (*cf.* EC 1.5.1.22 strombine dehydrogenase).
References: [736, 1012, 1013]

[EC 1.5.1.17 created 1983, modified 1986]

EC 1.5.1.18

Accepted name: ephedrine dehydrogenase
Reaction: (-)-ephedrine + NAD⁺ = (R)-2-methylimino-1-phenylpropan-1-ol + NADH + H⁺
Systematic name: (-)-ephedrine:NAD⁺ 2-oxidoreductase
Comments: The product immediately hydrolyses to methylamine and 1-hydroxy-1-phenylpropan-2-one. Acts on a number of related compounds including (-)-sympatol, (+)-pseudoephedrine and (+)-norephedrine.
References: [1958]

[EC 1.5.1.18 created 1984]

EC 1.5.1.19

- Accepted name:** D-nopaline dehydrogenase
Reaction: N^2 -(D-1,3-dicarboxypropyl)-L-arginine + NADP⁺ + H₂O = L-arginine + 2-oxoglutarate + NADPH + H⁺
Other name(s): D-nopaline synthase; nopaline dehydrogenase; nopaline synthase; NOS; 2-*N*-(D-1,3-dicarboxypropyl)-L-arginine:NADP⁺ oxidoreductase (L-arginine-forming)
Systematic name: N^2 -(D-1,3-dicarboxypropyl)-L-arginine:NADP⁺ oxidoreductase (L-arginine-forming)
Comments: In the reverse direction, forms D-nopaline from L-arginine and D-ornaline from L-ornithine.
References: [1880]

[EC 1.5.1.19 created 1984]

EC 1.5.1.20

- Accepted name:** methylenetetrahydrofolate reductase [NAD(P)H]
Reaction: 5-methyltetrahydrofolate + NAD(P)⁺ = 5,10-methylenetetrahydrofolate + NAD(P)H + H⁺
Other name(s): methylenetetrahydrofolate (reduced nicotinamide adenine dinucleotide phosphate) reductase; 5,10-methylenetetrahydrofolate reductase (NADPH); 5,10-methylenetetrahydrofolic acid reductase; 5,10-CH₂-H₄folate reductase; methylenetetrahydrofolate reductase (NADPH₂); 5-methyltetrahydrofolate:NAD⁺ oxidoreductase; 5-methyltetrahydrofolate:NAD⁺ oxidoreductase; methylenetetrahydrofolate (reduced riboflavin adenine dinucleotide) reductase; 5,10-methylenetetrahydrofolate reductase; methylenetetrahydrofolate reductase; *N*⁵,10-methylenetetrahydrofolate reductase; 5,10-methylenetetrahydropteroylglutamate reductase; *N*₅,*N*₁₀-methylenetetrahydrofolate reductase; methylenetetrahydrofolic acid reductase; 5-methyltetrahydrofolate:(acceptor) oxidoreductase (incorrect); 5,10-methylenetetrahydrofolate reductase (FADH₂); MetF; methylenetetrahydrofolate reductase (NADPH); 5-methyltetrahydrofolate:NADP⁺ oxidoreductase
Systematic name: 5-methyltetrahydrofolate:NAD(P)⁺ oxidoreductase
Comments: A flavoprotein (FAD). Menadione can also serve as an electron acceptor.
References: [750, 2102, 3479, 1308]

[EC 1.5.1.20 created 1978 as EC 1.1.1.171, transferred 1984 to EC 1.5.1.20 (EC 1.7.99.5 incorporated 2005), modified 2005]

EC 1.5.1.21

- Accepted name:** 1-piperideine-2-carboxylate/1-pyrroline-2-carboxylate reductase (NADPH)
Reaction: (1) L-pipecolate + NADP⁺ = 1-piperideine-2-carboxylate + NADPH + H⁺
(2) L-proline + NADP⁺ = 1-pyrroline-2-carboxylate + NADPH + H⁺
Other name(s): Pyr2C reductase; 1,2-didehydropipecolate reductase; P₂C reductase; 1,2-didehydropipecolic reductase; DELTA1-piperideine-2-carboxylate/1-pyrroline-2-carboxylate reductase (ambiguous); L-pipecolate:NADP⁺ 2-oxidoreductase; DELTA1-piperideine-2-carboxylate reductase; Δ¹-piperideine-2-carboxylate reductase
Systematic name: L-pipecolate/L-proline:NADP⁺ 2-oxidoreductase
Comments: The enzyme is involved in the catabolism of D-lysine and D-proline in bacteria that belong to the *Pseudomonas* genus. In contrast to EC 1.5.1.1, 1-piperideine-2-carboxylate/1-pyrroline-2-carboxylate reductase [NAD(P)H], which shows similar activity with NADPH and NADH, this enzyme is specific for NADPH.
References: [2968, 2667, 4148]

[EC 1.5.1.21 created 1984 (EC 1.5.1.14 created 1976, incorporated 1989), modified 2015]

EC 1.5.1.22

- Accepted name:** strombine dehydrogenase

Reaction: N -(carboxymethyl)-D-alanine + NAD⁺ + H₂O = glycine + pyruvate + NADH + H⁺
Other name(s): strombine[*N*-(carboxymethyl)-D-alanine]dehydrogenase; *N*-(carboxymethyl)-D-alanine: NAD⁺ oxidoreductase
Systematic name: *N*-(carboxymethyl)-D-alanine:NAD⁺ oxidoreductase (glycine-forming)
Comments: Also catalyses the reaction of EC 1.5.1.17 alanopine dehydrogenase, but more slowly. Does not act on L-strombine.
References: [736]

[EC 1.5.1.22 created 1986]

EC 1.5.1.23

Accepted name: tauropine dehydrogenase
Reaction: tauropine + NAD⁺ + H₂O = taurine + pyruvate + NADH + H⁺
Other name(s): 2-*N*-(D-1-carboxyethyl)taurine:NAD⁺ oxidoreductase (taurine-forming)
Systematic name: *N*²-(D-1-carboxyethyl)taurine:NAD⁺ oxidoreductase (taurine-forming)
Comments: In the reverse reaction, alanine can act instead of taurine, but more slowly, and 2-oxobutanoate and 2-oxopentanoate can act instead of pyruvate.
References: [1138]

[EC 1.5.1.23 created 1989]

EC 1.5.1.24

Accepted name: *N*⁵-(carboxyethyl)ornithine synthase
Reaction: *N*⁵-(L-1-carboxyethyl)-L-ornithine + NADP⁺ + H₂O = L-ornithine + pyruvate + NADPH + H⁺
Other name(s): 5-*N*-(L-1-carboxyethyl)-L-ornithine:NADP⁺ oxidoreductase (L-ornithine-forming)
Systematic name: *N*⁵-(L-1-carboxyethyl)-L-ornithine:NADP⁺ oxidoreductase (L-ornithine-forming)
Comments: In the reverse direction, L-lysine can act instead of L-ornithine, but more slowly. Acts on the amino group. *cf.* EC 1.5.1.16, D-lysopine dehydrogenase.
References: [3875]

[EC 1.5.1.24 created 1990]

EC 1.5.1.25

Accepted name: thiomorpholine-carboxylate dehydrogenase
Reaction: thiomorpholine 3-carboxylate + NAD(P)⁺ = 3,4-dehydro-thiomorpholine-3-carboxylate + NAD(P)H + H⁺
Other name(s): ketimine reductase; ketimine-reducing enzyme
Systematic name: thiomorpholine-3-carboxylate:NAD(P)⁺ 5,6-oxidoreductase
Comments: The product is the cyclic imine of the 2-oxoacid corresponding to *S*-(2-aminoethyl)cysteine. In the reverse direction, a number of other cyclic unsaturated compounds can act as substrates, but more slowly.
References: [2733]

[EC 1.5.1.25 created 1990]

EC 1.5.1.26

Accepted name: β-alanopine dehydrogenase
Reaction: β-alanopine + NAD⁺ + H₂O = β-alanine + pyruvate + NADH + H⁺
Systematic name: *N*-(D-1-carboxyethyl)-β-alanine:NAD⁺ oxidoreductase (β-alanine-forming)
References: [3318]

[EC 1.5.1.26 created 1990]

EC 1.5.1.27

- Accepted name:** 1,2-dehydroreticulinium reductase (NADPH)
Reaction: (*R*)-reticuline + NADP⁺ = 1,2-dehydroreticulinium + NADPH + H⁺
Other name(s): 1,2-dehydroreticulinium ion reductase
Systematic name: (*R*)-reticuline:NADP⁺ oxidoreductase
Comments: Reduces the 1,2-dehydroreticulinium ion to (*R*)-reticuline, which is a direct precursor of morphinan alkaloids in the poppy plant. The enzyme does not catalyse the reverse reaction to any significant extent under physiological conditions.
References: [760]

[EC 1.5.1.27 created 1999, modified 2004]

EC 1.5.1.28

- Accepted name:** opine dehydrogenase
Reaction: (2*S*)-2-[1-(*R*)-carboxyethyl]aminopentanoate + NAD⁺ + H₂O = L-2-aminopentanoic acid + pyruvate + NADH + H⁺
Other name(s): (2*S*)-2-[1-(*R*)-carboxyethyl]aminopentanoate dehydrogenase (NAD⁺, L-aminopentanoate-forming)
Systematic name: (2*S*)-2-[1-(*R*)-carboxyethyl]aminopentanoate:NAD⁺ oxidoreductase (L-aminopentanoate-forming)
Comments: In the forward direction, the enzyme from *Arthrobacter* sp. acts also on secondary amine dicarboxylates such as *N*-(1-carboxyethyl)methionine and *N*-(1-carboxyethyl)phenylalanine. Dehydrogenation forms an imine, which dissociates to the amino acid and pyruvate. In the reverse direction, the enzyme acts also on neutral amino acids as an amino donor. They include L-amino acids such as 2-aminopentanoic acid, 2-aminobutyric acid, 2-aminohexanoic acid, 3-chloroalanine, *O*-acetylserine, methionine, isoleucine, valine, phenylalanine, leucine and alanine. The amino acceptors include 2-oxoacids such as pyruvate, oxaloacetate, glyoxylate and 2-oxobutyrate.
References: [128, 730, 1842]

[EC 1.5.1.28 created 1999]

[1.5.1.29 Deleted entry. FMN reductase [NAD(P)H]. Now covered by EC 1.5.1.38 [FMN reductase (NADPH)], EC 1.5.1.39 [FMN reductase [NAD(P)H]] and EC 1.5.1.41 (riboflavin reductase [NAD(P)H])]

[EC 1.5.1.29 created 1981 as EC 1.6.8.1, transferred 2002 to EC 1.5.1.29, modified 2002, deleted 2011]

EC 1.5.1.30

- Accepted name:** flavin reductase (NADPH)
Reaction: reduced riboflavin + NADP⁺ = riboflavin + NADPH + H⁺
Other name(s): NADPH:flavin oxidoreductase; riboflavin mononucleotide (reduced nicotinamide adenine dinucleotide phosphate) reductase; flavin mononucleotide reductase; flavine mononucleotide reductase; FMN reductase (NADPH); NADPH-dependent FMN reductase; NADPH-flavin reductase; NADPH-FMN reductase; NADPH-specific FMN reductase; riboflavin mononucleotide reductase; riboflavine mononucleotide reductase; NADPH₂ dehydrogenase (flavin); NADPH₂:riboflavin oxidoreductase
Systematic name: reduced-riboflavin:NADP⁺ oxidoreductase
Comments: The enzyme reduces riboflavin, and, less efficiently, FMN and FAD. NADH is oxidized less efficiently than NADPH.
References: [4410, 709]

[EC 1.5.1.30 created 1982 as EC 1.6.8.2, transferred 2002 to EC 1.5.1.30, modified 2011]

EC 1.5.1.31

- Accepted name:** berberine reductase
Reaction: (*R*)-canadine + 2 NADP⁺ = berberine + 2 NADPH + H⁺
Other name(s): (*R*)-canadine synthase
Systematic name: (*R*)-tetrahydroberberine:NADP⁺ oxidoreductase

Comments: Involved in alkaloid biosynthesis in *Corydalis cava* to give (*R*)-canadine with the opposite configuration to the precursor of berberine (see EC 1.3.3.8 tetrahydroberberine oxidase). Also acts on 7,8-dihydroberberine.

References: [219]

[EC 1.5.1.31 created 2002]

EC 1.5.1.32

Accepted name: vomilenine reductase

Reaction: 1,2-dihydrovomilenine + NADP⁺ = vomilenine + NADPH + H⁺

Systematic name: 1,2-dihydrovomilenine:NADP⁺ oxidoreductase

Comments: Forms part of the ajmaline biosynthesis pathway.

References: [4061]

[EC 1.5.1.32 created 2002]

EC 1.5.1.33

Accepted name: pteridine reductase

Reaction: 5,6,7,8-tetrahydrobiopterin + 2 NADP⁺ = biopterin + 2 NADPH + 2 H⁺

Other name(s): PTR1; pteridine reductase 1

Systematic name: 5,6,7,8-tetrahydrobiopterin:NADP⁺ oxidoreductase

Comments: The enzyme from *Leishmania* (both amastigote and promastigote forms) catalyses the reduction by NADPH of folate and a wide variety of unconjugated pterins, including biopterin, to their tetrahydro forms. It also catalyses the reduction of 7,8-dihydropterins and 7,8-dihydrofolate to their tetrahydro forms. In contrast to EC 1.5.1.3 (dihydrofolate reductase) and EC 1.5.1.34 (6,7-dihydropteridine reductase), pteridine reductase will not catalyse the reduction of the quinonoid form of dihydrobiopterin. The enzyme is specific for NADPH; no activity has been detected with NADH. It also differs from EC 1.5.1.3 (dihydrofolate reductase) in being specific for the *Si*-face of NADPH.

References: [2734, 1254, 1023]

[EC 1.5.1.33 created 1999 as EC 1.1.1.253, transferred 2003 to EC 1.5.1.33]

EC 1.5.1.34

Accepted name: 6,7-dihydropteridine reductase

Reaction: a 5,6,7,8-tetrahydropteridine + NAD(P)⁺ = a 6,7-dihydropteridine + NAD(P)H + H⁺

Other name(s): 6,7-dihydropteridine:NAD(P)H oxidoreductase; DHPR; NAD(P)H:6,7-dihydropteridine oxidoreductase; NADH-dihydropteridine reductase; NADPH-dihydropteridine reductase; NADPH-specific dihydropteridine reductase; dihydropteridine (reduced nicotinamide adenine dinucleotide) reductase; dihydropteridine reductase; dihydropteridine reductase (NADH); 5,6,7,8-tetrahydropteridine:NAD(P)H⁺ oxidoreductase

Systematic name: 5,6,7,8-tetrahydropteridine:NAD(P)⁺ oxidoreductase

Comments: The substrate is the quinonoid form of dihydropteridine. Not identical with EC 1.5.1.3 dihydrofolate reductase.

References: [1391, 1407, 1852, 2259, 2711]

[EC 1.5.1.34 created 1972 as EC 1.6.99.7, modified 1981 (EC 1.6.99.10 created 1978, incorporated 1981), transferred 2003 to EC 1.5.1.34]

[1.5.1.35 Deleted entry. 1-pyrroline dehydrogenase. The enzyme is identical to EC 1.2.1.19, aminobutyraldehyde dehydrogenase, as the substrates 1-pyrroline and 4-aminobutanal are interconvertible]

[EC 1.5.1.35 created 2006, deleted 2007]

EC 1.5.1.36

Accepted name: flavin reductase (NADH)

Reaction: reduced flavin + NAD⁺ = flavin + NADH + H⁺
Other name(s): NADH-dependent flavin reductase; flavin:NADH oxidoreductase
Systematic name: flavin:NAD⁺ oxidoreductase
Comments: The enzyme from *Escherichia coli* W catalyses the reduction of free flavins by NADH. The enzyme has similar affinity to FAD, FMN and riboflavin. Activity with NADPH is more than 2 orders of magnitude lower than activity with NADH.
References: [1141]

[EC 1.5.1.36 created 2011]

EC 1.5.1.37

Accepted name: FAD reductase (NADH)
Reaction: FADH₂ + NAD⁺ = FAD + NADH + H⁺
Other name(s): NADH-FAD reductase; NADH-dependent FAD reductase; NADH:FAD oxidoreductase; NADH:flavin adenine dinucleotide oxidoreductase
Systematic name: FADH₂:NAD⁺ oxidoreductase
Comments: The enzyme from *Burkholderia phenoliruptrix* can reduce either FAD or flavin mononucleotide (FMN) but prefers FAD. Unlike EC 1.5.1.36, flavin reductase (NADH), the enzyme can not reduce riboflavin. The enzyme does not use NADPH as acceptor.
References: [1209]

[EC 1.5.1.37 created 2011]

EC 1.5.1.38

Accepted name: FMN reductase (NADPH)
Reaction: FMNH₂ + NADP⁺ = FMN + NADPH + H⁺
Other name(s): FRP; flavin reductase P; SsuE
Systematic name: FMNH₂:NADP⁺ oxidoreductase
Comments: The enzymes from bioluminescent bacteria contain FMN [2191], while the enzyme from *Escherichia coli* does not [930]. The enzyme often forms a two-component system with monooxygenases such as luciferase. Unlike EC 1.5.1.39, this enzyme does not use NADH as acceptor [1185, 1702]. While FMN is the preferred substrate, the enzyme can also use FAD and riboflavin with lower activity [3,6,8].
References: [1185, 1702, 1703, 2191, 3819, 2281, 2192, 930]

[EC 1.5.1.38 created 2011]

EC 1.5.1.39

Accepted name: FMN reductase [NAD(P)H]
Reaction: FMNH₂ + NAD(P)⁺ = FMN + NAD(P)H + H⁺
Other name(s): FRG
Systematic name: FMNH₂:NAD(P)⁺ oxidoreductase
Comments: Contains FMN. The enzyme can utilize NADH and NADPH with similar reaction rates. Different from EC 1.5.1.42, FMN reductase (NADH) and EC 1.5.1.38, FMN reductase (NADPH). The luminescent bacterium *Vibrio harveyi* possesses all three enzymes [4141]. Also reduces riboflavin and FAD, but more slowly.
References: [4141]

[EC 1.5.1.39 created 2011]

EC 1.5.1.40

Accepted name: 8-hydroxy-5-deazaflavin:NADPH oxidoreductase
Reaction: reduced coenzyme F₄₂₀ + NADP⁺ = oxidized coenzyme F₄₂₀ + NADPH + H⁺

Other name(s): 8-OH-5dFl:NADPH oxidoreductase
Systematic name: reduced coenzyme F₄₂₀:NADP⁺ oxidoreductase
Comments: The enzyme has an absolute requirement for both the 5-deazaflavin structure and the presence of an 8-hydroxy group in the substrate [935].
References: [935]

[EC 1.5.1.40 created 2011]

EC 1.5.1.41

Accepted name: riboflavin reductase [NAD(P)H]
Reaction: reduced riboflavin + NAD(P)⁺ = riboflavin + NAD(P)H + H⁺
Other name(s): NAD(P)H-FMN reductase (ambiguous); NAD(P)H-dependent FMN reductase (ambiguous); NAD(P)H:FMN oxidoreductase (ambiguous); NAD(P)H:flavin oxidoreductase (ambiguous); NAD(P)H₂ dehydrogenase (FMN) (ambiguous); NAD(P)H₂:FMN oxidoreductase (ambiguous); riboflavin mononucleotide reductase (ambiguous); flavine mononucleotide reductase (ambiguous); riboflavin mononucleotide (reduced nicotinamide adenine dinucleotide (phosphate)) reductase; flavin mononucleotide reductase (ambiguous); riboflavine mononucleotide reductase (ambiguous); Fre
Systematic name: riboflavin:NAD(P)⁺ oxidoreductase
Comments: Catalyses the reduction of soluble flavins by reduced pyridine nucleotides. Highest activity with riboflavin. When NADH is used as acceptor, the enzyme can also utilize FMN and FAD as substrates, with lower activity than riboflavin. When NADPH is used as acceptor, the enzyme has a very low activity with FMN and no activity with FAD [1029].
References: [1029, 3609, 1648]

[EC 1.5.1.41 created 2011]

EC 1.5.1.42

Accepted name: FMN reductase (NADH)
Reaction: FMNH₂ + NAD⁺ = FMN + NADH + H⁺
Other name(s): NADH-FMN reductase; NADH-dependent FMN reductase; NADH:FMN oxidoreductase; NADH:flavin oxidoreductase
Systematic name: FMNH₂:NAD⁺ oxidoreductase
Comments: The enzyme often forms a two-component system with monooxygenases. Unlike EC 1.5.1.38, FMN reductase (NADPH), and EC 1.5.1.39, FMN reductase [NAD(P)H], this enzyme has a strong preference for NADH over NADPH, although some activity with the latter is observed [879, 1185]. While FMN is the preferred substrate, FAD can also be used with much lower activity [879, 3966].
References: [879, 1185, 3966, 1699]

[EC 1.5.1.42 created 2011]

EC 1.5.1.43

Accepted name: carboxynorspermidine synthase
Reaction: (1) carboxynorspermidine + H₂O + NADP⁺ = L-aspartate 4-semialdehyde + propane-1,3-diamine + NADPH + H⁺
(2) carboxyspermidine + H₂O + NADP⁺ = L-aspartate 4-semialdehyde + putrescine + NADPH + H⁺
Other name(s): carboxynorspermidine dehydrogenase; carboxyspermidine dehydrogenase; CASDH; CANSDH; VC1624 (gene name)
Systematic name: carboxynorspermidine:NADP⁺ oxidoreductase
Comments: The reaction takes place in the opposite direction. Part of a bacterial polyamine biosynthesis pathway. L-aspartate 4-semialdehyde and propane-1,3-diamine/putrescine form a Schiff base that is reduced to form carboxynorspermidine/carboxyspermidine, respectively [2718]. The enzyme from the bacterium *Vibrio cholerae* is essential for biofilm formation [2169]. The enzyme from *Campylobacter jejuni* only produces carboxyspermidine *in vivo* even though it also can produce carboxynorspermidine *in vitro* [1367].

References: [2718, 2169, 1367]

[EC 1.5.1.43 created 2012]

EC 1.5.1.44

Accepted name: festuclavine dehydrogenase
Reaction: festuclavine + NAD⁺ = 6,8-dimethyl-6,7-didehydroergoline + NADH + H⁺
Other name(s): FgaFS; festuclavine synthase
Systematic name: festuclavine:NAD⁺ oxidoreductase
Comments: The enzyme participates in the biosynthesis of fumigaclavine C, an ergot alkaloid produced by some fungi of the *Trichocomaceae* family. The reaction proceeds *in vivo* in the opposite direction to the one shown here.
References: [4097]

[EC 1.5.1.44 created 2012]

EC 1.5.1.45

Accepted name: FAD reductase [NAD(P)H]
Reaction: FADH₂ + NAD(P)⁺ = FAD + NAD(P)H + H⁺
Other name(s): GTNG_3158 (gene name)
Systematic name: FADH₂:NAD(P)⁺ oxidoreductase
Comments: This enzyme, isolated from the bacterium *Geobacillus thermodenitrificans*, participates in the pathway of tryptophan degradation. The enzyme is part of a system that also includes a bifunctional riboflavin kinase/FMN adenylyltransferase and EC 1.14.14.8, anthranilate 3-monooxygenase (FAD). It can reduce either FAD or flavin mononucleotide (FMN) but prefers FAD. The enzyme has a slight preference for NADPH as acceptor. *cf.* EC 1.5.1.37, FAD reductase (NADH).
References: [2285]

[EC 1.5.1.45 created 2012]

EC 1.5.1.46

Accepted name: agroclavine dehydrogenase
Reaction: agroclavine + NADP⁺ = 6,8-dimethyl-6,7,8,9-tetrahydroergoline + NADPH + H⁺
Other name(s): *easG* (gene name)
Systematic name: agroclavine:NADP⁺ oxidoreductase
Comments: The enzyme participates in the biosynthesis of ergotamine, an ergot alkaloid produced by some fungi of the Clavicipitaceae family. The reaction is catalysed in the opposite direction to that shown. The substrate for the enzyme is an iminium intermediate that is formed spontaneously from chanoclavine-I aldehyde in the presence of glutathione.
References: [2468]

[EC 1.5.1.46 created 2013]

EC 1.5.1.47

Accepted name: dihydromethanopterin reductase [NAD(P)⁺]
Reaction: 5,6,7,8-tetrahydromethanopterin + NAD(P)⁺ = 7,8-dihydromethanopterin + NAD(P)H + H⁺
Other name(s): DmrA; H₂MPT reductase; 5,6,7,8-tetrahydromethanopterin 5,6-oxidoreductase; dihydromethanopterin reductase
Systematic name: 5,6,7,8-tetrahydromethanopterin:NAD(P)⁺ 5,6-oxidoreductase
Comments: The enzyme, characterized from the bacterium *Methylobacterium extorquens*, is involved in biosynthesis of dephospho-tetrahydromethanopterin. The specific activity with NADH is 15% of that with NADPH at the same concentration [466]. It does not reduce 7,8-dihydrofolate (*cf.* EC 1.5.1.3, dihydrofolate reductase).
References: [466]

[EC 1.5.1.47 created 2013, modified 2014]

EC 1.5.1.48

Accepted name: 2-methyl-1-pyrroline reductase
Reaction: (R)-2-methylpyrrolidine + NADP⁺ = 2-methyl-1-pyrroline + NADPH + H⁺
Other name(s): (R)-imine reductase (ambiguous)
Systematic name: (R)-2-methylpyrrolidine:NADP⁺ 2-oxidoreductase
Comments: The enzyme from the bacterium *Streptomyces* sp. GF3587 is highly specific for its substrate and forms only the (R) isomer.
References: [2567]

[EC 1.5.1.48 created 2014]

EC 1.5.1.49

Accepted name: 1-pyrroline-2-carboxylate reductase [NAD(P)H]
Reaction: L-proline + NAD(P)⁺ = 1-pyrroline-2-carboxylate + NAD(P)H + H⁺
Systematic name: L-proline:NAD(P)⁺ 2-oxidoreductase
Comments: The enzyme from the bacterium *Colwellia psychrerythraea* is involved in *trans*-3-hydroxy-L-proline metabolism. In contrast to EC 1.5.1.1, 1-piperidine-2-carboxylate/1-pyrroline-2-carboxylate reductase [NAD(P)H], which shows similar activity with 1-piperidine-2-carboxylate and 1-pyrroline-2-carboxylate, this enzyme is specific for the latter. While the enzyme is active with both NADH and NADPH, activity is higher with NADPH.
References: [4148]

[EC 1.5.1.49 created 2015]

EC 1.5.1.50

Accepted name: dihydromonapterin reductase
Reaction: 5,6,7,8-tetrahydromonapterin + NADP⁺ = 7,8-dihydromonapterin + NADPH + H⁺
Other name(s): FolM; H₂-MPt reductase
Systematic name: 5,6,7,8-tetrahydromonapterin:NADP⁺ oxidoreductase
Comments: The enzyme, found in many Gram negative bacteria, also slowly reduces 7,8-dihydrofolate to 5,6,7,8-tetrahydrofolate (*cf.* EC 1.5.1.3, dihydrofolate reductase). The enzyme has no activity with NADH.
References: [3061]

[EC 1.5.1.50 created 2015]

EC 1.5.1.51

Accepted name: N-[(2S)-2-amino-2-carboxyethyl]-L-glutamate dehydrogenase
Reaction: N-[(2S)-2-amino-2-carboxyethyl]-L-glutamate + NAD⁺ + H₂O = 2-oxoglutarate + L-2,3-diaminopropanoate + NADH + H⁺
Other name(s): SbnB
Systematic name: N-[(2S)-2-amino-2-carboxyethyl]-L-glutamate:NAD⁺ dehydrogenase (L-2,3-diaminopropanoate-forming)
Comments: The enzyme, characterized from the bacterium *Staphylococcus aureus*, is involved in the biosynthesis of the siderophore staphyloferrin B.
References: [230, 1984]

[EC 1.5.1.51 created 2017]

EC 1.5.1.52

Accepted name: staphylopine dehydrogenase

Reaction: staphylopine + NADP⁺ + H₂O = (2*S*)-2-amino-4-[(1*R*)-1-carboxy-2-(1*H*-imidazol-4-yl)ethyl]aminobutanoate + pyruvate + NADPH + H⁺

Other name(s): *cntM* (gene name); staphylopine synthase

Systematic name: staphylopine:NADP⁺ oxidoreductase [(2*S*)-2-amino-4-[(1*R*)-1-carboxy-2-(1*H*-imidazol-4-yl)ethyl]aminobutanoate]-forming

Comments: The enzyme, characterized from the bacterium *Staphylococcus aureus*, catalyses the last reaction in the biosynthesis of the metallophore staphylopine, which is involved in the acquisition of nickel, copper, and cobalt.

References: [1195, 2484]

[EC 1.5.1.52 created 2018]

EC 1.5.3 With oxygen as acceptor

EC 1.5.3.1

Accepted name: sarcosine oxidase

Reaction: sarcosine + H₂O + O₂ = glycine + formaldehyde + H₂O₂

Systematic name: sarcosine:oxygen oxidoreductase (demethylating)

Comments: A flavoprotein (FAD). The flavin is both covalently and non-covalently bound in a molar ratio of 1:1.

References: [1441, 2620, 3753]

[EC 1.5.3.1 created 1961]

EC 1.5.3.2

Accepted name: *N*-methyl-L-amino-acid oxidase

Reaction: an *N*-methyl-L-amino acid + H₂O + O₂ = an L-amino acid + formaldehyde + H₂O₂

Other name(s): *N*-methylamino acid oxidase; demethylase

Systematic name: *N*-methyl-L-amino-acid:oxygen oxidoreductase (demethylating)

Comments: A flavoprotein.

References: [2626, 2627, 2628]

[EC 1.5.3.2 created 1961]

[1.5.3.3 Deleted entry. spermine oxidase]

[EC 1.5.3.3 created 1961, deleted 1972]

EC 1.5.3.4

Accepted name: *N*⁶-methyl-lysine oxidase

Reaction: *N*⁶-methyl-L-lysine + H₂O + O₂ = L-lysine + formaldehyde + H₂O₂

Other name(s): ε-alkyl-L-lysine:oxygen oxidoreductase; *N*⁶-methyllysine oxidase; ε-*N*-methyllysine demethylase; ε-alkyllysine; 6-*N*-methyl-L-lysine:oxygen oxidoreductase (demethylating)

Systematic name: *N*⁶-methyl-L-lysine:oxygen oxidoreductase (demethylating)

References: [1917]

[EC 1.5.3.4 created 1972]

EC 1.5.3.5

Accepted name: (*S*)-6-hydroxynicotine oxidase

Reaction: (*S*)-6-hydroxynicotine + H₂O + O₂ = 1-(6-hydroxypyridin-3-yl)-4-(methylamino)butan-1-one + H₂O₂ (overall reaction)
 (1a) (*S*)-6-hydroxynicotine + O₂ = 5-(*N*-methyl-4,5-dihydro-1*H*-pyrrol-2-yl)pyridin-2-ol + H₂O₂

(1b) 5-(*N*-methyl-4,5-dihydro-1*H*-pyrrol-2-yl)pyridin-2-ol + H₂O = 1-(6-hydroxypyridin-3-yl)-4-(methylamino)butan-1-one (spontaneous)

- Other name(s):** L-6-hydroxynicotine oxidase; 6-hydroxy-L-nicotine oxidase; 6-hydroxy-L-nicotine:oxygen oxidoreductase; *nctB* (gene name)
- Systematic name:** (*S*)-6-hydroxynicotine:oxygen oxidoreductase
- Comments:** A flavoprotein (FAD). The enzyme, which participates in nicotine degradation, is specific for the (*S*) isomer of 6-hydroxynicotine. The bacterium *Arthrobacter nicotinovorans*, in which this enzyme was originally discovered, has a different enzyme that catalyses a similar reaction with the less common (*R*)-isomer (*cf.* EC 1.5.3.6, (*R*)-6-hydroxynicotine oxidase).
- References:** [774, 721, 3356, 3081]

[EC 1.5.3.5 created 1972, modified 2015]

EC 1.5.3.6

- Accepted name:** (*R*)-6-hydroxynicotine oxidase
- Reaction:** (*R*)-6-hydroxynicotine + H₂O + O₂ = 1-(6-hydroxypyridin-3-yl)-4-(methylamino)butan-1-one + H₂O₂ (overall reaction)
- (1a) (*R*)-6-hydroxynicotine + O₂ = 5-(*N*-methyl-4,5-dihydro-1*H*-pyrrol-2-yl)pyridin-2-ol + H₂O₂
- (1b) 5-(*N*-methyl-4,5-dihydro-1*H*-pyrrol-2-yl)pyridin-2-ol + H₂O = 1-(6-hydroxypyridin-3-yl)-4-(methylamino)butan-1-one (spontaneous)
- Other name(s):** D-6-hydroxynicotine oxidase; 6-hydroxy-D-nicotine oxidase
- Systematic name:** (*R*)-6-hydroxynicotine:oxygen oxidoreductase
- Comments:** A flavoprotein (FAD). The enzyme, which participates in nicotine degradation, is specific for (*R*) isomer of 6-hydroxynicotine, derived from the uncommon (*R*)-nicotine. The bacterium *Arthrobacter nicotinovorans*, in which this enzyme was originally discovered, has a different enzyme that catalyses a similar reaction with the (*S*)-isomer (*cf.* EC 1.5.3.5, (*S*)-6-hydroxynicotine oxidase).
- References:** [774, 426, 386, 3356, 1997]

[EC 1.5.3.6 created 1972, modified 2015]

EC 1.5.3.7

- Accepted name:** L-pipecolate oxidase
- Reaction:** L-pipecolate + O₂ = (*S*)-2,3,4,5-tetrahydropyridine-2-carboxylate + H₂O₂
- Other name(s):** pipecolate oxidase; L-pipecolic acid oxidase
- Systematic name:** L-pipecolate:oxygen 1,6-oxidoreductase
- Comments:** The product reacts with water to form (*S*)-2-amino-6-oxohexanoate.
- References:** [161, 1936]

[EC 1.5.3.7 created 1986, modified 2011]

[1.5.3.8 Deleted entry. (*S*)-tetrahydroprotoberberine oxidase. Now included with EC 1.3.3.8, tetrahydroberberine oxidase]

[EC 1.5.3.8 created 1989, deleted 1992]

[1.5.3.9 Transferred entry. reticuline oxidase. Now EC 1.21.3.3, reticuline oxidase]

[EC 1.5.3.9 created 1989, modified 1999, deleted 2002]

EC 1.5.3.10

- Accepted name:** dimethylglycine oxidase
- Reaction:** *N,N*-dimethylglycine + H₂O + O₂ = sarcosine + formaldehyde + H₂O₂
- Systematic name:** *N,N*-dimethylglycine:oxygen oxidoreductase (demethylating)
- Comments:** A flavoprotein (FAD). Does not oxidize sarcosine.
- References:** [2619]

[EC 1.5.3.10 created 1992]

[1.5.3.11 Deleted entry. polyamine oxidase. Now included with EC 1.5.3.13 (*N*¹-acetylpolyamine oxidase), EC 1.5.3.14 (polyamine oxidase (propane-1,3-diamine-forming)), EC 1.5.3.15 (*N*⁸-acetylspermidine oxidase (propane-1,3-diamine-forming)), EC 1.5.3.16 (spermine oxidase) and EC 1.5.3.17 (non-specific polyamine oxidase)]

[EC 1.5.3.11 created 1992, deleted 2009]

EC 1.5.3.12

Accepted name: dihydrobenzophenanthridine oxidase
Reaction: (1) dihydrosanguinarine + O₂ = sanguinarine + H₂O₂
(2) dihydrochelirubine + O₂ = chelirubine + H₂O₂
(3) dihydromacarpine + O₂ = macarpine + H₂O₂
Systematic name: dihydrobenzophenanthridine:oxygen oxidoreductase
Comments: A Cu^{II} enzyme found in higher plants that produces oxidized forms of the benzophenanthridine alkaloids
References: [3402, 109]

[EC 1.5.3.12 created 1999]

EC 1.5.3.13

Accepted name: *N*¹-acetylpolyamine oxidase
Reaction: (1) *N*¹-acetylspermidine + O₂ + H₂O = putrescine + 3-acetamidopropanal + H₂O₂
(2) *N*¹-acetylspermine + O₂ + H₂O = spermidine + 3-acetamidopropanal + H₂O₂
Other name(s): hPAO-1; PAO (ambiguous); mPAO; hPAO; polyamine oxidase (ambiguous)
Systematic name: *N*¹-acetylpolyamine:oxygen oxidoreductase (3-acetamidopropanal-forming)
Comments: The enzyme also catalyses the reaction: *N*¹,*N*¹²-diacetylspermine + O₂ + H₂O = *N*¹-acetylspermidine + 3-acetamidopropanal + H₂O₂ [4072]. No or very weak activity with spermine, or spermidine in absence of aldehydes. In presence of aldehydes the enzyme catalyses the reactions: 1. spermine + O₂ + H₂O = spermidine + 3-aminopropanal + H₂O₂, and with weak efficiency 2. spermidine + O₂ + H₂O = putrescine + 3-aminopropanal + H₂O₂ [1725]. A flavoprotein (FAD). This enzyme, encoded by the PAOX gene, is found in mammalian peroxisomes and oxidizes *N*¹-acetylated polyamines at the exo (three-carbon) side of the secondary amine, forming 3-acetamidopropanal. Since the products of the reactions are deacetylated polyamines, this process is known as polyamine back-conversion. Differs in specificity from EC 1.5.3.14 [polyamine oxidase (propane-1,3-diamine-forming)], EC 1.5.3.15 [*N*⁸-acetylspermidine oxidase (propane-1,3-diamine-forming)], EC 1.5.3.16 (spermine oxidase) and EC 1.5.3.17 (non-specific polyamine oxidase).
References: [4072, 1725, 4125, 4262]

[EC 1.5.3.13 created 2009]

EC 1.5.3.14

Accepted name: polyamine oxidase (propane-1,3-diamine-forming)
Reaction: spermidine + O₂ + H₂O = propane-1,3-diamine + 4-aminobutanal + H₂O₂
Other name(s): MPAO; maize PAO
Systematic name: spermidine:oxygen oxidoreductase (propane-1,3-diamine-forming)
Comments: As the products of the reaction cannot be converted directly to other polyamines, this class of polyamine oxidases is considered to be involved in the terminal catabolism of polyamines [3831]. This enzyme less efficiently catalyses the oxidation of *N*¹-acetylspermine and spermine. A flavoprotein (FAD). Differs in specificity from EC 1.5.3.13 (*N*¹-acetylpolyamine oxidase), EC 1.5.3.15 (*N*⁸-acetylspermidine oxidase (propane-1,3-diamine-forming)), EC 1.5.3.16 (spermine oxidase) and EC 1.5.3.17 (non-specific polyamine oxidase).
References: [3831, 993]

[EC 1.5.3.14 created 2009]

EC 1.5.3.15

- Accepted name:** N^8 -acetylspermidine oxidase (propane-1,3-diamine-forming)
Reaction: N^8 -acetylspermidine + O_2 + H_2O = propane-1,3-diamine + 4-acetamidobutanal + H_2O_2
Systematic name: N^8 -acetylspermidine:oxygen oxidoreductase (propane-1,3-diamine-forming)
Comments: Also active with N^1 -acetylsperrmine, weak activity with N^1,N^{12} -diacetylspermine. No activity with diaminopropane, putrescine, cadaverine, diaminohehexane, norspermidine, spermine and spermidine. Absence of monoamine oxidase (EC 1.4.3.4) activity. Differs in specificity from EC 1.5.3.13 (N^1 -acetylpolyamine oxidase), EC 1.5.3.14 (polyamine oxidase (propane-1,3-diamine-forming)), EC 1.5.3.16 (spermine oxidase) and EC 1.5.3.17 (non-specific polyamine oxidase).
References: [3524]

[EC 1.5.3.15 created 2009]

EC 1.5.3.16

- Accepted name:** spermine oxidase
Reaction: spermine + O_2 + H_2O = spermidine + 3-aminopropanal + H_2O_2
Other name(s): PAOh1/SMO; PAOh1 (ambiguous); AtPAO1; AtPAO4; SMO; mSMO; SMO(PAOh1); SMO/PAOh1; SMO5; mSMOmu
Systematic name: spermidine:oxygen oxidoreductase (spermidine-forming)
Comments: The enzyme from *Arabidopsis thaliana* (AtPAO1) oxidizes norspermine to norspermidine with high efficiency [3830]. The mammalian enzyme, encoded by the SMOX gene, is a cytosolic enzyme that catalyses the oxidation of spermine at the exo (three-carbon) side of the tertiary amine. No activity with spermidine. Weak activity with N^1 -acetylsperrmine. A flavoprotein (FAD). Differs in specificity from EC 1.5.3.13 (N^1 -acetylpolyamine oxidase), EC 1.5.3.14 (polyamine oxidase (propane-1,3-diamine-forming)), EC 1.5.3.15 (N^8 -acetylspermidine oxidase (propane-1,3-diamine-forming)) and EC 1.5.3.17 (non-specific polyamine oxidase).
References: [2672, 530, 3830, 4126]

[EC 1.5.3.16 created 2009]

EC 1.5.3.17

- Accepted name:** non-specific polyamine oxidase
Reaction: (1) spermine + O_2 + H_2O = spermidine + 3-aminopropanal + H_2O_2
(2) spermidine + O_2 + H_2O = putrescine + 3-aminopropanal + H_2O_2
(3) N^1 -acetylsperrmine + O_2 + H_2O = spermidine + 3-acetamidopropanal + H_2O_2
(4) N^1 -acetylspermidine + O_2 + H_2O = putrescine + 3-acetamidopropanal + H_2O_2
Other name(s): polyamine oxidase (ambiguous); Fms1; AtPAO3
Systematic name: polyamine:oxygen oxidoreductase (3-aminopropanal or 3-acetamidopropanal-forming)
Comments: A flavoprotein (FAD). The non-specific polyamine oxidases may differ from each other considerably. The enzyme from *Saccharomyces cerevisiae* shows a rather broad specificity and also oxidizes N^8 -acetylspermidine [2125]. The enzyme from *Ascaris suum* shows high activity with spermine and spermidine, but also oxidizes norspermine [2655]. The enzyme from *Arabidopsis thaliana* shows high activity with spermidine, but also oxidizes other polyamines [2636]. The specific polyamine oxidases are classified as EC 1.5.3.13 (N^1 -acetylpolyamine oxidase), EC 1.5.3.14 (polyamine oxidase (propane-1,3-diamine-forming)), EC 1.5.3.15 (N^8 -acetylspermidine oxidase (propane-1,3-diamine-forming)) and EC 1.5.3.16 (spermine oxidase).
References: [2636, 2655, 2125]

[EC 1.5.3.17 created 2009]

EC 1.5.3.18

Accepted name: L-saccharopine oxidase
Reaction: N^6 -(L-1,3-dicarboxypropyl)-L-lysine + H₂O + O₂ = (S)-2-amino-6-oxohexanoate + L-glutamate + H₂O₂
Other name(s): FAP2
Systematic name: L-saccharopine:oxygen oxidoreductase (L-glutamate forming)
Comments: The enzyme is involved in pipercolic acid biosynthesis. A flavoprotein (FAD).
References: [4379, 4204]

[EC 1.5.3.18 created 2011]

EC 1.5.3.19

Accepted name: 4-methylaminobutanoate oxidase (formaldehyde-forming)
Reaction: 4-methylaminobutanoate + O₂ + H₂O = 4-aminobutanoate + formaldehyde + H₂O₂
Other name(s): *mabO* (gene name)
Systematic name: 4-methylaminobutanoate:oxygen oxidoreductase (formaldehyde-forming)
Comments: A flavoprotein (FAD). In the enzyme from the soil bacterium *Arthrobacter nicotinovorans* the cofactor is covalently bound. Participates in the nicotine degradation pathway of this organism.
References: [596]

[EC 1.5.3.19 created 2012]

EC 1.5.3.20

Accepted name: *N*-alkylglycine oxidase
Reaction: *N*-alkylglycine + H₂O + O₂ = alkylamine + glyoxalate + H₂O₂
Other name(s): *N*-carboxymethylalkylamine:oxygen oxidoreductase (decarboxymethylating)
Systematic name: *N*-alkylglycine:oxygen oxidoreductase (alkylamine forming)
Comments: Isolated from the mold *Cladosporium* sp. G-10. Acts on *N*⁶-(carboxymethyl)lysine, 6-[(carboxymethyl)amino]hexanoic acid, sarcosine and *N*-ethylglycine. It has negligible action on glycine (*cf.* EC 1.4.3.19 glycine oxidase).
References: [1235]

[EC 1.5.3.20 created 2012]

EC 1.5.3.21

Accepted name: 4-methylaminobutanoate oxidase (methylamine-forming)
Reaction: 4-methylaminobutanoate + O₂ + H₂O = succinate semialdehyde + methylamine + H₂O₂
Other name(s): *mao* (gene name, ambiguous)
Systematic name: 4-methylaminobutanoate methylamidohydrolase
Comments: The enzyme participates in the nicotine degradation pathway of the soil bacterium *Arthrobacter nicotinovorans*. Has a very weak monoamine oxidase (EC 1.4.3.4) activity with 4-aminobutanoate [596].
References: [596, 595]

[EC 1.5.3.21 created 2012]

EC 1.5.3.22

Accepted name: coenzyme F₄₂₀H₂ oxidase
Reaction: 2 reduced coenzyme F₄₂₀ + O₂ = 2 oxidized coenzyme F₄₂₀ + 2 H₂O
Other name(s): FprA
Systematic name: reduced coenzyme F₄₂₀:oxygen oxidoreductase
Comments: The enzyme contains FMN and a binuclear iron center. The enzyme from the archaeon *Methanothermobacter marburgensis* is *Si*-face specific with respect to C-5 of coenzyme F₄₂₀ [3424].
References: [3422, 3424, 3423]

[EC 1.5.3.22 created 2013]

EC 1.5.3.23

- Accepted name:** glyphosate oxidoreductase
Reaction: 2 glyphosate + O₂ = 2 aminomethylphosphonate + 2 glyoxylate
Other name(s): *gox* (gene name)
Systematic name: glyphosate oxidoreductase (aminomethylphosphonate-forming)
Comments: The enzyme, characterized from the bacterium *Ochrobactrum* sp. G-1, contains an FAD cofactor. The catalytic cycle starts with a reduction of the FAD cofactor by one molecule of glyphosate, yielding reduced FAD and a Schiff base of aminomethylphosphonate with glyoxylate that is hydrolysed to the single components. The reduced FAD is reoxidized by oxygen, generating water and an oxygenated flavin intermediate, which catalyses the oxygenation of a second molecule of glyphosate, forming the second pair of aminomethylphosphonate and glyoxylate.
References: [976, 3758]

[EC 1.5.3.23 created 2016]

EC 1.5.4 With a disulfide as acceptor

EC 1.5.4.1

- Accepted name:** pyrimidodiazepine synthase
Reaction: 2-amino-6-acetyl-3,7,8,9-tetrahydro-3*H*-pyrimido[4,5-*b*][1,4]diazepin-4-one + glutathione disulfide + H₂O = 6-pyruvoyltetrahydropterin + 2 glutathione
Other name(s): PDA synthase; pyrimidodiazepine:oxidized-glutathione oxidoreductase (ring-opening, cyclizing); pyrimidodiazepine:glutathione-disulfide oxidoreductase (ring-opening, cyclizing)
Systematic name: 2-amino-6-acetyl-3,7,8,9-tetrahydro-3*H*-pyrimido[4,5-*b*][1,4]diazepin-4-one:glutathione-disulfide oxidoreductase (ring-opening, cyclizing)
Comments: In the reverse direction, the reduction of 6-pyruvoyl-tetrahydropterin is accompanied by the opening of the 6-membered pyrazine ring and the formation of the 7-membered diazepine ring. The pyrimidodiazepine formed is an acetyldihydro derivative. Involved in the formation of the eye pigment drosopterin in *Drosophila melanogaster*.
References: [4207, 1910]

[EC 1.5.4.1 created 1990, modified 2014]

EC 1.5.5 With a quinone or similar compound as acceptor

EC 1.5.5.1

- Accepted name:** electron-transferring-flavoprotein dehydrogenase
Reaction: reduced electron-transferring flavoprotein + ubiquinone = electron-transferring flavoprotein + ubiquinol
Other name(s): ETF-QO; ETF:ubiquinone oxidoreductase; electron transfer flavoprotein dehydrogenase; electron transfer flavoprotein Q oxidoreductase; electron transfer flavoprotein-ubiquinone oxidoreductase; electron transfer flavoprotein reductase
Systematic name: electron-transferring-flavoprotein:ubiquinone oxidoreductase
Comments: An iron-sulfur flavoprotein, forming part of the mitochondrial electron-transfer system.
References: [239, 3266]

[EC 1.5.5.1 created 1986]

EC 1.5.5.2

Accepted name: proline dehydrogenase
Reaction: L-proline + a quinone = (S)-1-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 [2641]. 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: [3339, 416, 2641]

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

EC 1.5.5.3

Accepted name: hydroxyproline dehydrogenase
Reaction: *trans*-4-hydroxy-L-proline + a quinone = (3*R*,5*S*)-3-hydroxy-1-pyrroline-5-carboxylate + a quinol
Other name(s): HYPDH; OH-POX; hydroxyproline oxidase; PRODH2 (gene name)
Systematic name: *trans*-4-hydroxy-L-proline:quinone oxidoreductase
Comments: A flavoprotein (FAD). The enzyme from human also has low activity with L-proline (*cf.* EC 1.5.5.2, proline dehydrogenase).
References: [658, 3730]

[EC 1.5.5.3 created 2017]

EC 1.5.7 With an iron-sulfur protein as acceptor

EC 1.5.7.1

Accepted name: methylenetetrahydrofolate reductase (ferredoxin)
Reaction: 5-methyltetrahydrofolate + 2 oxidized ferredoxin = 5,10-methylenetetrahydrofolate + 2 reduced ferredoxin + 2 H⁺
Other name(s): 5,10-methylenetetrahydrofolate reductase
Systematic name: 5-methyltetrahydrofolate:ferredoxin oxidoreductase
Comments: An iron-sulfur flavoprotein that also contains zinc. The enzyme from *Clostridium formicoaceticum* catalyses the reduction of methylene blue, menadione, benzyl viologen, rubredoxin or FAD with 5-methyltetrahydrofolate and the oxidation of reduced ferredoxin or FADH₂ with 5,10-methylenetetrahydrofolate. However, unlike EC 1.5.1.20, methylenetetrahydrofolate reductase [NAD(P)H], there is no activity with NAD(P)H.
References: [627]

[EC 1.5.7.1 created 2005]

EC 1.5.7.2

Accepted name: coenzyme F₄₂₀ oxidoreductase (ferredoxin)
Reaction: reduced coenzyme F₄₂₀ + 2 oxidized ferredoxin = oxidized coenzyme F₄₂₀ + 2 reduced ferredoxin + 2 H⁺
Other name(s): Fd:F420 oxidoreductase; FpoF protein; ferredoxin:F420 oxidoreductase
Systematic name: coenzyme F₄₂₀:ferredoxin oxidoreductase
Comments: The enzyme from the archaeon *Methanosarcina mazei* contains iron-sulfur centres and FAD.
References: [4174]

[EC 1.5.7.2 created 2013]

EC 1.5.8 With a flavin or flavoprotein as acceptor

EC 1.5.8.1

Accepted name: dimethylamine dehydrogenase
Reaction: dimethylamine + H₂O + electron-transfer flavoprotein = methylamine + formaldehyde + reduced electron-transfer flavoprotein
Systematic name: dimethylamine:electron-transfer flavoprotein oxidoreductase
Comments: Contains FAD and a [4Fe-4S] cluster.
References: [4336]

[EC 1.5.8.1 created 1999 as EC 1.5.99.10, transferred 2002 to EC 1.5.8.1]

EC 1.5.8.2

Accepted name: trimethylamine dehydrogenase
Reaction: trimethylamine + H₂O + electron-transfer flavoprotein = dimethylamine + formaldehyde + reduced electron-transfer flavoprotein
Systematic name: trimethylamine:electron-transfer flavoprotein oxidoreductase (demethylating)
Comments: A number of alkyl-substituted derivatives of trimethylamine can also act as electron donors; phenazine methosulfate and 2,6-dichloroindophenol can act as electron acceptors. Contains FAD and a [4Fe-4S] cluster.
References: [639, 3629, 1596, 1773, 3420]

[EC 1.5.8.2 created 1976 as EC 1.5.99.7, transferred 2002 to EC 1.5.8.2]

EC 1.5.8.3

Accepted name: sarcosine dehydrogenase
Reaction: sarcosine + H₂O + electron-transfer flavoprotein = glycine + formaldehyde + reduced electron-transfer flavoprotein
Other name(s): sarcosine *N*-demethylase; monomethylglycine dehydrogenase; sarcosine:(acceptor) oxidoreductase (demethylating)
Systematic name: sarcosine:electron-transfer flavoprotein oxidoreductase (demethylating)
Comments: A flavoprotein (FMN). Tetrahydrofolate is also a substrate, being converted to *N*⁵,*N*¹⁰-methylenetetrahydrofolate.
References: [1580, 1078, 3628]

[EC 1.5.8.3 created 1972 as EC 1.5.99.1, transferred 2012 to EC 1.5.8.3]

EC 1.5.8.4

Accepted name: dimethylglycine dehydrogenase
Reaction: *N,N*-dimethylglycine + 5,6,7,8-tetrahydrofolate + electron-transfer flavoprotein = sarcosine + 5,10-methylenetetrahydrofolate + reduced electron-transfer flavoprotein
Other name(s): *N,N*-dimethylglycine oxidase; *N,N*-dimethylglycine:(acceptor) oxidoreductase (demethylating); Me2GlyDH; *N,N*-dimethylglycine:electron-transfer flavoprotein oxidoreductase (demethylating)
Systematic name: *N,N*-dimethylglycine,5,6,7,8-tetrahydrofolate:electron-transfer flavoprotein oxidoreductase (demethylating,5,10-methylenetetrahydrofolate-forming)
Comments: A flavoprotein, containing a histidyl(*N*^π)-(8α)FAD linkage at position 91 in the human protein. An imine intermediate is channeled from the FAD binding site to the 5,6,7,8-tetrahydrofolate binding site through a 40 Å tunnel [5,8,9]. In the absence of 5,6,7,8-tetrahydrofolate the enzyme forms formaldehyde [3041, 140].
References: [1078, 1580, 4236, 4235, 3041, 406, 407, 2313, 140]

[EC 1.5.8.4 created 1972 as EC 1.5.99.2, transferred 2012 to EC 1.5.8.4, modified 2017]

EC 1.5.98 With other, known, physiological acceptors

EC 1.5.98.1

- Accepted name:** methylenetetrahydromethanopterin dehydrogenase
Reaction: 5,10-methylenetetrahydromethanopterin + oxidized coenzyme F₄₂₀ = 5,10-methenyltetrahydromethanopterin + reduced coenzyme F₄₂₀
Other name(s): N⁵,N¹⁰-methylenetetrahydromethanopterin dehydrogenase; 5,10-methylenetetrahydromethanopterin dehydrogenase
Systematic name: 5,10-methylenetetrahydromethanopterin:coenzyme-F₄₂₀ oxidoreductase
Comments: Coenzyme F₄₂₀ is a 7,8-didemethyl-8-hydroxy-5-deazariboflavin derivative; methanopterin is a pterin analogue. The enzyme is involved in the formation of methane from CO₂ in the methanogen *Methanothermobacter thermautotrophicus*.
References: [1403, 3838]

[EC 1.5.98.1 created 1989 as EC 1.5.99.9, modified 2004, transferred to EC 1.5.98.1 2014]

EC 1.5.98.2

- Accepted name:** 5,10-methylenetetrahydromethanopterin reductase
Reaction: 5-methyltetrahydromethanopterin + oxidized coenzyme F₄₂₀ = 5,10-methylenetetrahydromethanopterin + reduced coenzyme F₄₂₀
Other name(s): 5,10-methylenetetrahydromethanopterin cyclohydrolase; N⁵,N¹⁰-methylenetetrahydromethanopterin reductase; methylene-H₄MPT reductase; coenzyme F₄₂₀-dependent N⁵,N¹⁰-methenyltetrahydromethanopterin reductase; N⁵,N¹⁰-methylenetetrahydromethanopterin:coenzyme-F₄₂₀ oxidoreductase
Systematic name: 5-methyltetrahydromethanopterin:coenzyme-F₄₂₀ oxidoreductase
Comments: Catalyses an intermediate step in methanogenesis from CO₂ and H₂ in methanogenic archaea.
References: [2331, 3838, 2332, 3840, 3839]

[EC 1.5.98.2 created 2000 as EC 1.5.99.11, modified 2004, transferred to EC 1.5.98.2 2014]

EC 1.5.98.3

- Accepted name:** coenzyme F₄₂₀:methanophenazine dehydrogenase
Reaction: reduced coenzyme F₄₂₀ + methanophenazine = oxidized coenzyme F₄₂₀ + dihydromethanophenazine
Other name(s): F₄₂₀H₂ dehydrogenase; fpoBCDIF (gene names)
Systematic name: reduced coenzyme F₄₂₀:methanophenazine oxidoreductase
Comments: The enzyme, found in some methanogenic archaea, is responsible for the reoxidation of coenzyme F₄₂₀, which is reduced during methanogenesis, and for the reduction of methanophenazine to dihydromethanophenazine, which is required by EC 1.8.98.1, dihydromethanophenazine:CoB-CoM heterodisulfide reductase. The enzyme is membrane-bound, and is coupled to proton translocation across the cytoplasmic membrane, generating a proton motive force that is used for ATP generation.
References: [409, 221, 799, 1700]

[EC 1.5.98.3 created 2017]

EC 1.5.99 With unknown physiological acceptors

[1.5.99.1 Transferred entry. sarcosine dehydrogenase. Now EC 1.5.8.3, sarcosine dehydrogenase]

[EC 1.5.99.1 created 1972, deleted 2012]

[1.5.99.2 Transferred entry. dimethylglycine dehydrogenase. Now EC 1.5.8.4, dimethylglycine dehydrogenase]

[EC 1.5.99.2 created 1972, deleted 2012]

EC 1.5.99.3

Accepted name: L-pipecolate dehydrogenase
Reaction: L-pipecolate + acceptor = (*S*)-2,3,4,5-tetrahydropyridine-2-carboxylate + reduced acceptor
Other name(s): L-pipecolate:(acceptor) 1,6-oxidoreductase
Systematic name: L-pipecolate:acceptor 1,6-oxidoreductase
Comments: The product reacts with water to form (*S*)-2-amino-6-oxohexanoate.
References: [161]

[EC 1.5.99.3 created 1972, modified 1986, modified 2011]

EC 1.5.99.4

Accepted name: nicotine dehydrogenase
Reaction: (*S*)-nicotine + acceptor + H₂O = (*S*)-6-hydroxynicotine + reduced acceptor
Other name(s): nicotine oxidase; D-nicotine oxidase; nicotine:(acceptor) 6-oxidoreductase (hydroxylating); L-nicotine oxidase
Systematic name: nicotine:acceptor 6-oxidoreductase (hydroxylating)
Comments: A metalloprotein (FMN). The enzyme can act on both the naturally found (*S*)-enantiomer and the synthetic (*R*)-enantiomer of nicotine, with retention of configuration in both cases [1529].
References: [245, 774, 1527, 1529]

[EC 1.5.99.4 created 1972]

EC 1.5.99.5

Accepted name: methylglutamate dehydrogenase
Reaction: *N*-methyl-L-glutamate + acceptor + H₂O = L-glutamate + formaldehyde + reduced acceptor
Other name(s): *N*-methylglutamate dehydrogenase; *N*-methyl-L-glutamate:(acceptor) oxidoreductase (demethylating)
Systematic name: *N*-methyl-L-glutamate:acceptor oxidoreductase (demethylating)
Comments: A number of *N*-methyl-substituted amino acids can act as donor; 2,6-dichloroindophenol is the best acceptor.
References: [1482]

[EC 1.5.99.5 created 1976]

EC 1.5.99.6

Accepted name: spermidine dehydrogenase
Reaction: spermidine + acceptor + H₂O = propane-1,3-diamine + 4-aminobutanal + reduced acceptor
Other name(s): spermidine:(acceptor) oxidoreductase
Systematic name: spermidine:acceptor oxidoreductase
Comments: A flavohemoprotein (FAD). Ferricyanide, 2,6-dichloroindophenol and cytochrome *c* can act as acceptor. 4-Aminobutanal condenses non-enzymically to 1-pyrroline.
References: [3769, 3770]

[EC 1.5.99.6 created 1976]

[1.5.99.7 *Transferred entry. trimethylamine dehydrogenase. Now EC 1.5.8.2, trimethylamine dehydrogenase*]

[EC 1.5.99.7 created 1976, deleted 2002]

[1.5.99.8 *Transferred entry. proline dehydrogenase. Now EC 1.5.5.2, proline dehydrogenase.]*

[EC 1.5.99.8 created 1980, deleted 2013]

[1.5.99.9 *Transferred entry. methylenetetrahydromethanopterin dehydrogenase. As the acceptor is known the enzyme has been transferred to EC 1.5.98.1, methylenetetrahydromethanopterin dehydrogenase*]

[EC 1.5.99.9 created 1989, modified 2004, deleted 2014]

[1.5.99.10 Transferred entry. dimethylamine dehydrogenase. Now EC 1.5.8.1, dimethylamine dehydrogenase]

[EC 1.5.99.10 created 1999, deleted 2002]

[1.5.99.11 Transferred entry. methylenetetrahydromethanopterin dehydrogenase. As the acceptor is known the enzyme has been transferred to EC 1.5.98.2, 5,10-methylenetetrahydromethanopterin reductase]

[EC 1.5.99.11 created 2000, modified 2004, deleted 2014]

EC 1.5.99.12

Accepted name: cytokinin dehydrogenase
Reaction: N^6 -dimethylallyladenine + acceptor + H_2O = adenine + 3-methylbut-2-enal + reduced acceptor
Other name(s): N^6 -dimethylallyladenine:(acceptor) oxidoreductase; 6- N -dimethylallyladenine:acceptor oxidoreductase; OsCKX2; CKX; cytokinin oxidase/dehydrogenase
Systematic name: N^6 -dimethylallyladenine:acceptor oxidoreductase
Comments: A flavoprotein(FAD). Catalyses the oxidation of cytokinins, a family of N^6 -substituted adenine derivatives that are plant hormones, where the substituent is a dimethylallyl or other prenyl group. Although this activity was previously thought to be catalysed by a hydrogen-peroxide-forming oxidase, this enzyme does not require oxygen for activity and does not form hydrogen peroxide. 2,6-Dichloroindophenol, methylene blue, nitroblue tetrazolium, phenazine methosulfate and Cu(II) in the presence of imidazole can act as acceptors. This enzyme plays a part in regulating rice-grain production, with lower levels of the enzyme resulting in enhanced grain production [129].
References: [1146, 129]

[EC 1.5.99.12 created 2001]

EC 1.5.99.13

Accepted name: D-proline dehydrogenase
Reaction: D-proline + acceptor = 1-pyrroline-2-carboxylate + reduced acceptor
Other name(s): D-Pro DH; D-Pro dehydrogenase; dye-linked D-proline dehydrogenase
Systematic name: D-proline:acceptor oxidoreductase
Comments: A flavoprotein (FAD). The enzyme prefers D-proline and acts on other D-amino acids with lower efficiency.
References: [3812, 3323]

[EC 1.5.99.13 created 2010, modified 2011]

EC 1.5.99.14

Accepted name: 6-hydroxypseudoxynicotine dehydrogenase
Reaction: 1-(6-hydroxypyridin-3-yl)-4-(methylamino)butan-1-one + acceptor + H_2O = 1-(2,6-dihydroxypyridin-3-yl)-4-(methylamino)butan-1-one + reduced acceptor
Systematic name: 1-(6-hydroxypyridin-3-yl)-4-(methylamino)butan-1-one:acceptor 6-oxidoreductase (hydroxylating)
Comments: Contains a cytidyl molybdenum cofactor [3274]. The enzyme, which participates in the nicotine degradation pathway, has been characterized from the soil bacterium *Arthrobacter nicotinovorans* [1062, 1281].
References: [1062, 1281, 3274]

[EC 1.5.99.14 created 2012]

EC 1.5.99.15

Accepted name: dihydromethanopterin reductase (acceptor)
Reaction: 5,6,7,8-tetrahydromethanopterin + oxidized acceptor = 7,8-dihydromethanopterin + reduced acceptor
Other name(s): DmrX
Systematic name: 5,6,7,8-tetrahydromethanopterin:acceptor 5,6-oxidoreductase

Comments: This archaeal enzyme catalyses the last step in the biosynthesis of tetrahydromethanopterin, a coenzyme used in methanogenesis. The enzyme, characterized from the archaea *Methanosarcina mazei* and *Methanocaldococcus jannaschii*, is an iron-sulfur flavoprotein. *cf.* EC 1.5.1.47, dihydromethanopterin reductase [NAD(P)⁺].

References: [4120]

[EC 1.5.99.15 created 2014]

EC 1.6 Acting on NADH or NADPH

In general, enzymes using NADH or NADPH to reduce a substrate are classified according to the reverse reaction, in which NAD⁺ or NADP⁺ is formally regarded as acceptor. This subclass contains only those enzymes in which some other redox carrier is the acceptor. This can be NAD⁺ or NADP⁺ (EC 1.6.1), a heme protein (EC 1.6.2), oxygen (EC 1.6.3), a quinone or similar compound (EC 1.6.5), a nitrogenous group (EC 1.6.6), or some other acceptor (EC 1.6.99).

EC 1.6.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.6.1.1

Accepted name: NAD(P)⁺ transhydrogenase (*Si*-specific)
Reaction: NADPH + NAD⁺ = NADP⁺ + NADH
Other name(s): pyridine nucleotide transhydrogenase; transhydrogenase; NAD(P)⁺ transhydrogenase; nicotinamide adenine dinucleotide (phosphate) transhydrogenase; NAD⁺ transhydrogenase; NADH transhydrogenase; nicotinamide nucleotide transhydrogenase; NADPH-NAD⁺ transhydrogenase; pyridine nucleotide transferase; NADPH-NAD⁺ oxidoreductase; NADH-NADP⁺-transhydrogenase; NADPH:NAD⁺ transhydrogenase; H⁺-Thase; non-energy-linked transhydrogenase; NADPH:NAD⁺ oxidoreductase (B-specific); NAD(P)⁺ transhydrogenase (B-specific)
Systematic name: NADPH:NAD⁺ oxidoreductase (*Si*-specific)
Comments: The enzyme from *Azotobacter vinelandii* is a flavoprotein (FAD). It is *Si*-specific with respect to both NAD⁺ and NADP⁺. Also acts on deamino coenzymes [*cf.* EC 1.6.1.2 NAD(P)⁺ transhydrogenase (*Re/Si*-specific)].
References: [1610, 4388]

[EC 1.6.1.1 created 1961, modified 1986, modified 2013]

EC 1.6.1.2

Accepted name: NAD(P)⁺ transhydrogenase (*Re/Si*-specific)
Reaction: NADPH + NAD⁺ = NADP⁺ + NADH
Other name(s): pyridine nucleotide transhydrogenase; transhydrogenase; NAD(P)⁺ transhydrogenase; nicotinamide adenine dinucleotide (phosphate) transhydrogenase; NAD⁺ transhydrogenase; NADH transhydrogenase; nicotinamide nucleotide transhydrogenase; NADPH-NAD⁺ transhydrogenase; pyridine nucleotide transferase; NADPH-NAD⁺ oxidoreductase; NADH-NADP⁺-transhydrogenase; NADPH:NAD⁺ transhydrogenase; H⁺-Thase; energy-linked transhydrogenase; NAD(P) transhydrogenase (AB-specific); NAD(P)⁺ transhydrogenase (AB-specific); NADPH:NAD⁺ oxidoreductase (AB-specific)
Systematic name: NADPH:NAD⁺ oxidoreductase (*Re/Si*-specific)
Comments: The enzyme from heart mitochondria is *Re*-specific with respect to NAD⁺ and *Si*-specific with respect to NADP⁺ [*cf.* EC 1.6.1.1 NAD(P)⁺ transhydrogenase (*Si*-specific)].
References: [1021, 4388]

[EC 1.6.1.2 created 1986, modified 2013]

EC 1.6.1.3

Accepted name: NAD(P)⁺ transhydrogenase
Reaction: NADPH + NAD⁺ = NADP⁺ + NADH
Other name(s): pyridine nucleotide transhydrogenase; transhydrogenase (ambiguous); nicotinamide adenine dinucleotide (phosphate) transhydrogenase (ambiguous); NAD⁺ transhydrogenase (ambiguous); NADH transhydrogenase (misleading); nicotinamide nucleotide transhydrogenase (ambiguous); NADPH-NAD⁺ transhydrogenase (ambiguous); pyridine nucleotide transferase (ambiguous); NADPH-NAD⁺ oxidoreductase (ambiguous); NADH-NADP⁺-transhydrogenase (ambiguous); NADPH:NAD⁺ transhydrogenase; H⁺-Thase (ambiguous); non-energy-linked transhydrogenase (ambiguous)
Systematic name: NADPH:NAD⁺ oxidoreductase
Comments: The enzyme catalyses the NADPH-driven reduction of NAD⁺. This entry stands for enzymes whose stereo-specificity with respect to NADPH is not known. [*cf.* EC 1.6.1.1, NAD(P)⁺ transhydrogenase (*Si*-specific) and EC 1.6.1.2 NAD(P)⁺ transhydrogenase (*Re/Si*-specific)].
References: [841]

[EC 1.6.1.3 created 2013]

EC 1.6.1.4

Accepted name: NAD(P)⁺ transhydrogenase (ferredoxin)
Reaction: NADH + H⁺ + 2 NADP⁺ + 2 reduced ferredoxin [iron-sulfur] cluster = NAD⁺ + 2 NADPH + 2 oxidized ferredoxin [iron-sulfur] cluster
Other name(s): NADH-dependent reduced ferredoxin:NADP⁺ oxidoreductase; Nfn; *nfnAB* (gene names)
Systematic name: NADH:NADP⁺, ferredoxin oxidoreductase
Comments: The iron-sulfur flavoprotein complex, originally isolated from the bacterium *Clostridium kluyveri*, couples the exergonic reduction of NADP⁺ with reduced ferredoxin and the endergonic reduction of NADP⁺ with NADH.
References: [4119, 789, 2310]

[EC 1.6.1.4 created 2015]

[1.6.1.5 *Transferred entry. proton-translocating NAD(P)⁺ transhydrogenase. Now EC 7.1.1.1, proton-translocating NAD(P)⁺ transhydrogenase]*

[EC 1.6.1.5 created 2015, deleted 2018]

EC 1.6.2 With a heme protein as acceptor

[1.6.2.1 *Transferred entry. NADH₂ cytochrome c reductase. Now EC 1.6.99.3, NADH dehydrogenase]*

[EC 1.6.2.1 created 1961, deleted 1965]

EC 1.6.2.2

Accepted name: cytochrome-*b*₅ reductase
Reaction: NADH + 2 ferricytochrome *b*₅ = NAD⁺ + H⁺ + 2 ferrocycytochrome *b*₅
Other name(s): cytochrome *b*₅ reductase; dihydronicotinamide adenine dinucleotide-cytochrome *b*₅ reductase; reduced nicotinamide adeninedinucleotide-cytochrome *b*₅ reductase; NADH-ferricytochrome *b*₅ oxidoreductase; NADH-cytochrome *b*₅ reductase; NADH 5α-reductase ; NADH-cytochrome-*b*₅ reductase
Systematic name: NADH:ferricytochrome-*b*₅ oxidoreductase
Comments: A flavoprotein (FAD).
References: [2369, 3683, 3685]

[EC 1.6.2.2 created 1961]

[1.6.2.3 *Deleted entry. cytochrome reductase (NADPH)]*

[EC 1.6.2.3 created 1972, deleted 1965]

EC 1.6.2.4

- Accepted name:** NADPH—hemoprotein reductase
Reaction: $\text{NADPH} + \text{H}^+ + n \text{ oxidized hemoprotein} = \text{NADP}^+ + n \text{ reduced hemoprotein}$
Other name(s): CPR; FAD-cytochrome *c* reductase; NADP-cytochrome *c* reductase; NADP-cytochrome reductase; NADPH-dependent cytochrome *c* reductase; NADPH:*P*-450 reductase; NADPH:ferrihemoprotein oxidoreductase; NADPH—cytochrome *P*-450 oxidoreductase; NADPH-cytochrome *c* oxidoreductase; NADPH-cytochrome *c* reductase; NADPH—cytochrome *p*-450 reductase; NADPH-ferricytochrome *c* oxidoreductase; NADPH-ferrihemoprotein reductase; TPNH₂ cytochrome *c* reductase; TPNH-cytochrome *c* reductase; aldehyde reductase (NADPH-dependent); cytochrome *P*-450 reductase; cytochrome *c* reductase (reduced nicotinamide adenine dinucleotide phosphate, NADPH, NADPH-dependent); dihydroxynicotinamide adenine dinucleotide phosphate-cytochrome *c* reductase; ferrihemoprotein *P*-450 reductase; reduced nicotinamide adenine dinucleotide phosphate-cytochrome *c* reductase; reductase, cytochrome *c* (reduced nicotinamide adenine dinucleotide phosphate)
- Systematic name:** NADPH:hemoprotein oxidoreductase
Comments: A flavoprotein containing both FMN and FAD. This enzyme catalyses the transfer of electrons from NADPH, an obligatory two-electron donor, to microsomal *P*-450 monooxygenases (e.g. EC 1.14.14.1, unspecific monooxygenase) by stabilizing the one-electron reduced form of the flavin cofactors FAD and FMN. It also reduces cytochrome *b*₅ and cytochrome *c*. The number *n* in the equation is 1 if the hemoprotein undergoes a 2-electron reduction, and is 2 if it undergoes a 1-electron reduction.
References: [1330, 1566, 2305, 2438, 4216, 2437, 3453, 4111, 2663, 1324]

[EC 1.6.2.4 created 1972, modified 2003]

EC 1.6.2.5

- Accepted name:** NADPH—cytochrome-*c*₂ reductase
Reaction: $\text{NADPH} + 2 \text{ ferricytochrome } c_2 = \text{NADP}^+ + \text{H}^+ + 2 \text{ ferrocycytochrome } c_2$
Other name(s): cytochrome *c*₂ reductase (reduced nicotinamide adenine dinucleotide phosphate); cytochrome *c*₂ reductase (reduced nicotinamide adenine dinucleotide phosphate, NADPH)
Systematic name: NADPH:ferricytochrome-*c*₂ oxidoreductase
Comments: A flavoprotein (FAD).
References: [3273]

[EC 1.6.2.5 created 1972]

EC 1.6.2.6

- Accepted name:** leghemoglobin reductase
Reaction: $\text{NAD(P)H} + \text{H}^+ + 2 \text{ ferrileghemoglobin} = \text{NAD(P)}^+ + 2 \text{ ferroleghemoglobin}$
Other name(s): ferric leghemoglobin reductase
Systematic name: NAD(P)H:ferrileghemoglobin oxidoreductase
References: [3272]

[EC 1.6.2.6 created 1989]

EC 1.6.3 With oxygen as acceptor

EC 1.6.3.1

- Accepted name:** NAD(P)H oxidase (H₂O₂-forming)
Reaction: $\text{NAD(P)H} + \text{H}^+ + \text{O}_2 = \text{NAD(P)}^+ + \text{H}_2\text{O}_2$
Other name(s): THOX2; ThOX; dual oxidase; p138tox; thyroid NADPH oxidase; thyroid oxidase; thyroid oxidase 2; NADPH oxidase; NAD(P)H:oxygen oxidoreductase; NAD(P)H oxidase
Systematic name: NAD(P)H:oxygen 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.

References: [2615, 779, 780, 891, 2203, 892]

[EC 1.6.3.1 created 2003, modified 2013]

EC 1.6.3.2

Accepted name: NAD(P)H oxidase (H₂O-forming)
Reaction: $2 \text{NAD(P)H} + 2 \text{H}^+ + \text{O}_2 = 2 \text{NAD(P)}^+ + 2 \text{H}_2\text{O}$
Systematic name: NAD(P)H:oxygen oxidoreductase (H₂O-forming)
Comments: A flavoprotein (FAD). NADPH is a better substrate than NADH [415, 1740]. 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: [415, 2229, 1740, 1739]

[EC 1.6.3.2 created 2013]

EC 1.6.3.3

Accepted name: NADH oxidase (H₂O₂-forming)
Reaction: $\text{NADH} + \text{H}^+ + \text{O}_2 = \text{NAD}^+ + \text{H}_2\text{O}_2$
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)) [1498]. The enzymes from the anaerobic archaea *Methanocaldococcus jannaschii* [515] and *Pyrococcus furiosus* [1881] also produce low amounts of H₂O. Unlike EC 1.6.3.1 (NAD(P)H oxidase) it has no activity towards NADPH.
References: [1498, 4130, 1881, 4338, 1514, 515]

[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)) [3376].
References: [3376, 1498, 2446, 1862, 4449]

[EC 1.6.3.4 created 2013]

EC 1.6.3.5

Accepted name: renalase
Reaction: (1) $1,2\text{-dihydro-}\beta\text{-NAD(P)} + \text{H}^+ + \text{O}_2 = \beta\text{-NAD(P)}^+ + \text{H}_2\text{O}_2$
(2) $1,6\text{-dihydro-}\beta\text{-NAD(P)} + \text{H}^+ + \text{O}_2 = \beta\text{-NAD(P)}^+ + \text{H}_2\text{O}_2$
Other name(s): α NAD(P)H oxidase/anomerase (incorrect); NAD(P)H:oxygen oxidoreductase (H₂O₂-forming, epimerising) (incorrect)

Systematic name: dihydro-NAD(P):oxygen oxidoreductase (H₂O₂-forming)

Comments: Requires FAD. Renalase, previously thought to be a hormone, is a flavoprotein secreted into the blood by the kidney that oxidizes the 1,2-dihydro- and 1,6-dihydro- isomeric forms of β-NAD(P)H back to β-NAD(P)⁺. These isomeric forms, generated by nonspecific reduction of β-NAD(P)⁺ or by tautomerization of β-NAD(P)H, are potent inhibitors of primary metabolism dehydrogenases and pose a threat to normal respiration.

References: [4283, 235]

[EC 1.6.3.5 created 2014, modified 2015]

EC 1.6.4 With a disulfide as acceptor (deleted sub-subclass)

[1.6.4.1 *Transferred entry. cystine reductase (NADH). Now EC 1.8.1.6, cystine reductase*]

[EC 1.6.4.1 created 1961, deleted 2002]

[1.6.4.2 *Transferred entry. glutathione reductase (NADPH). Now EC 1.8.1.7, glutathione-disulfide reductase*]

[EC 1.6.4.2 created 1961, modified 1989, deleted 2002]

[1.6.4.3 *Transferred entry. dihydrolipoamide reductase (NAD⁺). Now EC 1.8.1.4, dihydrolipoyl dehydrogenase*]

[EC 1.6.4.3 created 1961, modified 1976, deleted 1983]

[1.6.4.4 *Transferred entry. protein-disulfide reductase [NAD(P)H]. Now EC 1.8.1.8, protein-disulfide reductase*]

[EC 1.6.4.4 created 1965, deleted 2002]

[1.6.4.5 *Transferred entry. thioredoxin reductase (NADPH). Now EC 1.8.1.9, thioredoxin-disulfide reductase*]

[EC 1.6.4.5 created 1972, deleted 2002]

[1.6.4.6 *Transferred entry. CoA-glutathione reductase (NADPH). Now EC 1.8.1.10, CoA-glutathione reductase*]

[EC 1.6.4.6 created 1972, deleted 2002]

[1.6.4.7 *Transferred entry. asparaguate reductase (NADH). Now EC 1.8.1.11, asparaguate reductase*]

[EC 1.6.4.7 created 1978, deleted 2002]

[1.6.4.8 *Transferred entry. trypanothione reductase. Now EC 1.8.1.12, trypanothione-disulfide reductase*]

[EC 1.6.4.8 created 1989, deleted 2002]

[1.6.4.9 *Transferred entry. bis-γ-glutamylcystine reductase (NADPH). Now EC 1.8.1.13, bis-γ-glutamylcystine reductase*]

[EC 1.6.4.9 created 1992, deleted 2002]

[1.6.4.10 *Transferred entry. CoA-disulfide reductase (NADH). Now EC 1.8.1.14, CoA-disulfide reductase*]

[EC 1.6.4.10 created 1992, deleted 2002]

EC 1.6.5 With a quinone or similar compound as acceptor

[1.6.5.1 *Deleted entry. quinone reductase*]

[EC 1.6.5.1 created 1961, deleted 1965]

EC 1.6.5.2

- Accepted name:** NAD(P)H dehydrogenase (quinone)
Reaction: $\text{NAD(P)H} + \text{H}^+ + \text{a quinone} = \text{NAD(P)}^+ + \text{a hydroquinone}$
Other name(s): menadione reductase; phyloquinone reductase; quinone reductase; dehydrogenase, reduced nicotinamide adenine dinucleotide (phosphate, quinone); DT-diaphorase; flavoprotein NAD(P)H-quinone reductase; menadione oxidoreductase; NAD(P)H dehydrogenase; NAD(P)H menadione reductase; NAD(P)H-quinone dehydrogenase; NAD(P)H-quinone oxidoreductase; NAD(P)H: (quinone-acceptor)oxidoreductase; NAD(P)H: menadione oxidoreductase; NADH-menadione reductase; naphthoquinone reductase; *p*-benzoquinone reductase; reduced NAD(P)H dehydrogenase; viologen accepting pyridine nucleotide oxidoreductase; vitamin K reductase; diaphorase; reduced nicotinamide-adenine dinucleotide (phosphate) dehydrogenase; vitamin-K reductase; NAD(P)H₂ dehydrogenase (quinone); NQO1; QR1; NAD(P)H:(quinone-acceptor) oxidoreductase
- Systematic name:** NAD(P)H:quinone oxidoreductase
Comments: A flavoprotein. The enzyme catalyses a two-electron reduction and has a preference for short-chain acceptor quinones, such as ubiquinone, benzoquinone, juglone and duroquinone [3590]. The animal, but not the plant, form of the enzyme is inhibited by dicoumarol.
References: [812, 1211, 2399, 2554, 4255, 3590, 387, 1710, 2231]

[EC 1.6.5.2 created 1961, transferred 1965 to EC 1.6.99.2, transferred 2005 to EC 1.6.5.2]

[1.6.5.3 *Transferred entry. NADH:ubiquinone reductase (H⁺-translocating). Now EC 7.1.1.2, NADH:ubiquinone reductase (H⁺-translocating)*]

[EC 1.6.5.3 created 1961, deleted 1965, reinstated 1983, modified 2011, modified 2013, deleted 2018]

EC 1.6.5.4

- Accepted name:** monodehydroascorbate reductase (NADH)
Reaction: $\text{NADH} + \text{H}^+ + 2 \text{ monodehydroascorbate} = \text{NAD}^+ + 2 \text{ ascorbate}$
Other name(s): NADH:semidehydroascorbic acid oxidoreductase; MDHA; semidehydroascorbate reductase; AFR; AFR-reductase; ascorbic free radical reductase; ascorbate free radical reductase; SOR; MDAsA reductase (NADPH); SDA reductase; NADH:ascorbate radical oxidoreductase; NADH-semidehydroascorbate oxidoreductase; ascorbate free-radical reductase; NADH:AFR oxidoreductase; monodehydroascorbate reductase (NADH₂)
- Systematic name:** NADH:monodehydroascorbate oxidoreductase
References: [3401]

[EC 1.6.5.4 created 1961]

EC 1.6.5.5

- Accepted name:** NADPH:quinone reductase
Reaction: $\text{NADPH} + \text{H}^+ + 2 \text{ quinone} = \text{NADP}^+ + 2 \text{ semiquinone}$
Other name(s): NADPH₂:quinone reductase
Systematic name: NADPH:quinone oxidoreductase
Comments: A zinc enzyme, specific for NADPH. Catalyses the one-electron reduction of certain quinones, with the orthoquinones 1,2-naphthoquinone and 9,10-phenanthrenequinone being the best substrates [3125]. Dicoumarol [*cf.* EC 1.6.5.2 NAD(P)H dehydrogenase (quinone)] and nitrofurantoin are competitive inhibitors with respect to the quinone substrate. The semiquinone free-radical product may be non-enzymically reduced to the hydroquinone or oxidized back to quinone in the presence of O₂ [3125]. In some mammals, the enzyme is abundant in the lens of the eye, where it is identified with the protein ζ-crystallin.
References: [3125, 884, 225, 3807]

[EC 1.6.5.5 created 1999]

EC 1.6.5.6

Accepted name: *p*-benzoquinone reductase (NADPH)
Reaction: NADPH + H⁺ + *p*-benzoquinone = NADP⁺ + hydroquinone
Systematic name: NADPH:*p*-benzoquinone oxidoreductase
Comments: Involved in the 4-nitrophenol degradation pathway in bacteria.
References: [3589]

[EC 1.6.5.6 created 2000]

EC 1.6.5.7

Accepted name: 2-hydroxy-1,4-benzoquinone reductase
Reaction: 2-hydroxy-1,4-benzoquinone + NADH + H⁺ = hydroxyquinol + NAD⁺
Other name(s): hydroxybenzoquinone reductase; 1,2,4-trihydroxybenzene:NAD oxidoreductase
Systematic name: NADH:2-hydroxy-1,4-benzoquinone oxidoreductase
Comments: A flavoprotein (FMN) that differs in substrate specificity from other quinone reductases. The enzyme in *Burkholderia cepacia* is inducible by 2,4,5-trichlorophenoxyacetate.
References: [4417]

[EC 1.6.5.7 created 2000, modified 2004]

[1.6.5.8 *Transferred entry. NADH:ubiquinone reductase (Na⁺-transporting). Now EC 7.2.1.1, NADH:ubiquinone reductase (Na⁺-transporting)*]

[EC 1.6.5.8 created 2011, deleted 2018]

EC 1.6.5.9

Accepted name: NADH:ubiquinone reductase (non-electrogenic)
Reaction: NADH + H⁺ + ubiquinone = NAD⁺ + ubiquinol
Other name(s): ubiquinone reductase (ambiguous); coenzyme Q reductase (ambiguous); dihydronicotinamide adenine dinucleotide-coenzyme Q reductase (ambiguous); DPNH-coenzyme Q reductase (ambiguous); DPNH-ubiquinone reductase (ambiguous); NADH-coenzyme Q oxidoreductase (ambiguous); NADH-coenzyme Q reductase (ambiguous); NADH-CoQ oxidoreductase (ambiguous); NADH-CoQ reductase (ambiguous); NADH-ubiquinone reductase (ambiguous); NADH-ubiquinone oxidoreductase (ambiguous); reduced nicotinamide adenine dinucleotide-coenzyme Q reductase (ambiguous); NADH-Q6 oxidoreductase (ambiguous); NADH₂ dehydrogenase (ubiquinone) (ambiguous)
Systematic name: NADH:ubiquinone oxidoreductase
Comments: A flavoprotein (FAD). Occurs in mitochondria of yeast and plants, and in aerobic bacteria. Has low activity with NADPH.
References: [2596, 770, 1884, 3128]

[EC 1.6.5.9 created 2011]

EC 1.6.5.10

Accepted name: NADPH dehydrogenase (quinone)
Reaction: NADPH + H⁺ + a quinone = NADP⁺ + a quinol
Other name(s): reduced nicotinamide adenine dinucleotide phosphate (quinone) dehydrogenase; NADPH oxidase; NADPH₂ dehydrogenase (quinone)
Systematic name: NADPH:(quinone-acceptor) oxidoreductase
Comments: A flavoprotein [1, 2]. The enzyme from *Escherichia coli* is specific for NADPH and is most active with quinone derivatives and ferricyanide as electron acceptors [1440]. Menaquinone can act as acceptor. The enzyme from hog liver is inhibited by dicoumarol and folic acid derivatives but not by 2,4-dinitrophenol [2016].
References: [2016, 1439, 1440]

[EC 1.6.5.10 created 1972 as EC 1.6.99.6, transferred 2011 to EC 1.6.5.10]

EC 1.6.5.11

- Accepted name:** NADH dehydrogenase (quinone)
Reaction: $\text{NADH} + \text{H}^+ + \text{a quinone} = \text{NAD}^+ + \text{a quinol}$
Other name(s): reduced nicotinamide adenine dinucleotide (quinone) dehydrogenase; NADH-quinone oxidoreductase; DPNH-menadione reductase; D-diaphorase; NADH_2 dehydrogenase (quinone)
Systematic name: NADH:(quinone-acceptor) oxidoreductase
Comments: Menaquinone can act as acceptor. Inhibited by AMP and 2,4-dinitrophenol but not by dicoumarol or folic acid derivatives.
References: [2016]

[EC 1.6.5.11 created 1972 as EC 1.6.99.5, transferred 2015 to EC 1.6.5.11]

EC 1.6.5.12

- Accepted name:** demethylphyloquinone reductase
Reaction: $\text{demethylphyloquinone} + \text{NADPH} + \text{H}^+ = \text{demethylphyloquinol} + \text{NADP}^+$
Other name(s): *ndbB* (gene name); NDC1 (gene name); demethylphyloquinone:NADPH oxidoreductase
Systematic name: NADPH:demethylphyloquinone oxidoreductase
Comments: The enzyme, found in plants and cyanobacteria, is involved in the biosynthesis of phyloquinone (vitamin K_1), an electron carrier associated with photosystem I. The enzyme is a type II NADPH dehydrogenase and requires a flavine adenine dinucleotide cofactor.
References: [992]

[EC 1.6.5.12 created 2015]

EC 1.6.6 With a nitrogenous group as acceptor

- [1.6.6.1 *Transferred entry. nitrate reductase (NADH). Now EC 1.7.1.1, nitrate reductase (NADH)*]
[EC 1.6.6.1 created 1961, deleted 2002]
- [1.6.6.2 *Transferred entry. nitrate reductase [NAD(P)H]. Now EC 1.7.1.2, nitrate reductase [NAD(P)H]*]
[EC 1.6.6.2 created 1961, deleted 2002]
- [1.6.6.3 *Transferred entry. nitrate reductase (NADPH). Now EC 1.7.1.3, nitrate reductase (NADPH)*]
[EC 1.6.6.3 created 1961, deleted 2002]
- [1.6.6.4 *Transferred entry. nitrite reductase [NAD(P)H]. Now EC 1.7.1.4, nitrite reductase [NAD(P)H]*]
[EC 1.6.6.4 created 1961, deleted 2002]
- [1.6.6.5 *Transferred entry. now EC 1.7.2.1, nitrite reductase (NO-forming)*]
[EC 1.6.6.5 created 1961, deleted 1964]
- [1.6.6.6 *Transferred entry. hyponitrite reductase. Now EC 1.7.1.5, hyponitrite reductase*]
[EC 1.6.6.6 created 1961, deleted 2002]
- [1.6.6.7 *Transferred entry. azobenzene reductase. Now EC 1.7.1.6, azobenzene reductase*]
[EC 1.6.6.7 created 1961, deleted 2002]
- [1.6.6.8 *Transferred entry. GMP reductase. Now EC 1.7.1.7, GMP reductase*]
[EC 1.6.6.8 created 1965, deleted 2002]
- [1.6.6.9 *Deleted entry. The activity is now known to be catalysed by EC 1.7.2.3, trimethylamine-N-oxide reductase.*]
[EC 1.6.6.9 created 1972, deleted 2018]

[1.6.6.10 Transferred entry. *nitroquinoline-N-oxide reductase*. Now EC 1.7.1.9, *nitroquinoline-N-oxide reductase*]

[EC 1.6.6.10 created 1972, deleted 2002]

[1.6.6.11 Transferred entry. *hydroxylamine reductase (NADH)*. Now EC 1.7.1.10, *hydroxylamine reductase (NADH)*]

[EC 1.6.6.11 created 1972, deleted 2002]

[1.6.6.12 Transferred entry. *4-(dimethylamino)phenylazoxybenzene reductase*. Now EC 1.7.1.11, *4-(dimethylamino)phenylazoxybenzene reductase*]

[EC 1.6.6.12 created 1989, deleted 2002]

[1.6.6.13 Transferred entry. *N-hydroxy-2-acetamidofluorene reductase*. Now EC 1.7.1.12, *N-hydroxy-2-acetamidofluorene reductase*]

[EC 1.6.6.13 created 1989, deleted 2002]

EC 1.6.7 With an iron-sulfur protein as acceptor (deleted sub-subclass)

[1.6.7.1 Transferred entry. *ferredoxin—NADP⁺ reductase*. Now EC 1.18.1.2, *ferredoxin—NADP⁺ reductase*]

[EC 1.6.7.1 created 1972, deleted 1978]

[1.6.7.2 Transferred entry. *rubredoxin—NAD⁺ reductase*. Now EC 1.18.1.1, *rubredoxin—NAD⁺ reductase*]

[EC 1.6.7.2 created 1972, deleted 1978]

[1.6.7.3 Transferred entry. now EC 1.18.1.3, *ferredoxin—NAD⁺ reductase*]

[EC 1.6.7.3 created 1978, deleted 1978]

EC 1.6.8 With a flavin as acceptor (deleted sub-subclass)

[1.6.8.1 Transferred entry. *NAD(P)H dehydrogenase (FMN)*. Now EC 1.5.1.29, *FMN reductase*]

[EC 1.6.8.1 created 1981, deleted 2002]

[1.6.8.2 Transferred entry. *NADPH dehydrogenase (flavin)*. Now EC 1.5.1.30, *flavin reductase*]

[EC 1.6.8.2 created 1982, deleted 2002]

EC 1.6.99 With unknown physiological acceptors

EC 1.6.99.1

Accepted name: NADPH dehydrogenase

Reaction: NADPH + H⁺ + acceptor = NADP⁺ + reduced acceptor

Other name(s): NADPH₂ diaphorase; NADPH diaphorase; OYE; diaphorase; dihydronicotinamide adenine dinucleotide phosphate dehydrogenase; NADPH-dehydrogenase; NADPH-diaphorase; NADPH₂-dehydrogenase; old yellow enzyme; reduced nicotinamide adenine dinucleotide phosphate dehydrogenase; TPNH dehydrogenase; TPNH-diaphorase; triphosphopyridine diaphorase; triphosphopyridine nucleotide diaphorase; NADPH₂ dehydrogenase; NADPH:(acceptor) oxidoreductase

Systematic name: NADPH:acceptor oxidoreductase

Comments: A flavoprotein (FMN in yeast, FAD in plants).

References: [46, 147, 1708, 3858, 3861]

[EC 1.6.99.1 created 1961, modified 1976]

[1.6.99.2 *Transferred entry. NAD(P)H dehydrogenase (quinone). Now EC 1.6.5.2, NAD(P)H dehydrogenase (quinone). The enzyme was erroneously transferred from this sub-subclass in 1965*]

[EC 1.6.99.2 created 1961 as EC 1.6.5.2, transferred 1965 to EC 1.6.99.2, deleted 2005]

EC 1.6.99.3

Accepted name: NADH dehydrogenase

Reaction: NADH + H⁺ + acceptor = NAD⁺ + reduced acceptor

Other name(s): cytochrome *c* reductase; type 1 dehydrogenase; β-NADH dehydrogenase dinucleotide; diaphorase; dihydrocodehydrogenase I dehydrogenase; dihydronicotinamide adenine dinucleotide dehydrogenase; diphosphopyridine diaphorase; DPNH diaphorase; NADH diaphorase; NADH hydrogenase; NADH oxidoreductase; NADH-menadione oxidoreductase; reduced diphosphopyridine nucleotide diaphorase; NADH:cytochrome *c* oxidoreductase; NADH₂ dehydrogenase; NADH:(acceptor) oxidoreductase

Systematic name: NADH:acceptor oxidoreductase

Comments: A flavoprotein containing iron-sulfur centres. After preparations have been subjected to certain treatments, cytochrome *c* may act as an acceptor. Under normal conditions, two protons are extruded from the cytoplasm or the intramitochondrial or stromal compartment. Present in a mitochondrial complex as EC 7.1.1.2, NADH:ubiquinone reductase (H⁺-translocating).

References: [11, 1420, 1528, 1811]

[EC 1.6.99.3 created 1961 as EC 1.6.2.1, transferred 1965 to EC 1.6.99.3, modified 2018]

[1.6.99.4 *Transferred entry. nitrite reductase. Now EC 1.18.1.2, ferredoxin—NADP⁺ reductase*]

[EC 1.6.99.4 created 1965, deleted 1972]

[1.6.99.5 *Transferred entry. NADH dehydrogenase (quinone). Transferred to EC 1.6.5.11, NADH dehydrogenase (quinone)*]

[EC 1.6.99.5 created 1972, deleted 2014]

[1.6.99.6 *Transferred entry. NADPH dehydrogenase (quinone). Now EC 1.6.5.10, NADPH dehydrogenase (quinone)*]

[EC 1.6.99.6 created 1972, deleted 2011]

[1.6.99.7 *Transferred entry. dihydropteridine reductase. Now EC 1.5.1.34, 6,7-dihydropteridine reductase*]

[EC 1.6.99.7 created 1972, modified 1981 (EC 1.6.99.10 created 1978, incorporated 1981), deleted 2003]

[1.6.99.8 *Transferred entry. aquacobalamin reductase. Now EC 1.16.1.3, aquacobalamin reductase*]

[EC 1.6.99.8 created 1972, deleted 2002]

[1.6.99.9 *Transferred entry. cob(II)alamin reductase. Now EC 1.16.1.4, cob(II)alamin reductase*]

[EC 1.6.99.9 created 1972, deleted 2002]

[1.6.99.10 *Deleted entry. dihydropteridine reductase (NADH). Now included with EC 1.5.1.34, 6,7-dihydropteridine reductase*]

[EC 1.6.99.10 created 1978, deleted 1981]

[1.6.99.11 *Transferred entry. aquacobalamin reductase (NADPH). Now EC 1.16.1.5, aquacobalamin reductase (NADPH)*]

[EC 1.6.99.11 created 1989, deleted 2002]

[1.6.99.12 *Transferred entry. cyanocobalamin reductase (NADPH, cyanide-eliminating). Now EC 1.16.1.6, cyanocobalamin reductase (cyanide-eliminating)*]

[EC 1.6.99.12 created 1989, deleted 2002]

[1.6.99.13 *Transferred entry. ferric-chelate reductase. Now EC 1.16.1.7, ferric-chelate reductase*]

[EC 1.6.99.13 created 1992, deleted 2002]

EC 1.7 Acting on other nitrogenous compounds as donors

This subclass contains a small group of enzymes that oxidize diverse nitrogenous substrates. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.7.1), a cytochrome (EC 1.7.2), oxygen (EC 1.7.3), an iron-sulfur protein (EC 1.7.7), or some other acceptor (EC 1.7.99).

EC 1.7.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.7.1.1

Accepted name: nitrate reductase (NADH)
Reaction: nitrite + NAD⁺ + H₂O = nitrate + NADH + H⁺
Other name(s): assimilatory nitrate reductase; NADH-nitrate reductase; NADH-dependent nitrate reductase; assimilatory NADH: nitrate reductase; nitrate reductase (NADH₂); NADH₂:nitrate oxidoreductase
Systematic name: nitrite:NAD⁺ oxidoreductase
Comments: An iron-sulfur molybdenum flavoprotein.
References: [1008, 2740, 2781, 3595, 269]

[EC 1.7.1.1 created 1961 as EC 1.6.6.1, transferred 2002 to EC 1.7.1.1]

EC 1.7.1.2

Accepted name: nitrate reductase [NAD(P)H]
Reaction: nitrite + NAD(P)⁺ + H₂O = nitrate + NAD(P)H + H⁺
Other name(s): assimilatory nitrate reductase; assimilatory NAD(P)H-nitrate reductase; NAD(P)H bispecific nitrate reductase; nitrate reductase (reduced nicotinamide adenine dinucleotide (phosphate)); nitrate reductase NAD(P)H; NAD(P)H-nitrate reductase; nitrate reductase [NAD(P)H₂]; NAD(P)H₂:nitrate oxidoreductase
Systematic name: nitrite:NAD(P)⁺ oxidoreductase
Comments: An iron-sulfur molybdenum flavoprotein.
References: [2740, 2931, 490, 269]

[EC 1.7.1.2 created 1961 as EC 1.6.6.2, transferred 2002 to EC 1.7.1.2]

EC 1.7.1.3

Accepted name: nitrate reductase (NADPH)
Reaction: nitrite + NADP⁺ + H₂O = nitrate + NADPH + H⁺
Other name(s): assimilatory nitrate reductase; assimilatory reduced nicotinamide adenine dinucleotide phosphate-nitrate reductase; NADPH-nitrate reductase; assimilatory NADPH-nitrate reductase; triphosphopyridine nucleotide-nitrate reductase; NADPH: nitrate reductase; nitrate reductase (NADPH₂); NADPH₂:nitrate oxidoreductase
Systematic name: nitrite:NADP⁺ oxidoreductase
Comments: An iron-sulfur molybdenum flavoprotein.
References: [2740, 2741, 2780, 3815, 269]

[EC 1.7.1.3 created 1961 as EC 1.6.6.3, transferred 2002 to EC 1.7.1.3]

EC 1.7.1.4

Accepted name: nitrite reductase [NAD(P)H]
Reaction: NH₃ + 3 NAD(P)⁺ + 2 H₂O = nitrite + 3 NAD(P)H + 5 H⁺
Other name(s): nitrite reductase (reduced nicotinamide adenine dinucleotide (phosphate)); assimilatory nitrite reductase (ambiguous); nitrite reductase [NAD(P)H₂]; NAD(P)H₂:nitrite oxidoreductase; nit-6 (gene name)
Systematic name: ammonia:NAD(P)⁺ oxidoreductase

Comments: An iron-sulfur flavoprotein (FAD) containing siroheme. The enzymes from the fungi *Neurospora crassa* [2779], *Emericella nidulans* [2960] and *Candida nitratophila* [3196] and the bacterium *Aliivibrio fischeri* [3053] can use either NADPH or NADH as electron donor. *cf.* EC 1.7.1.15, nitrite reductase (NADH).

References: [2779, 2960, 3053, 3196, 2113, 4024, 1273, 3067, 974, 638]

[EC 1.7.1.4 created 1961 as EC 1.6.6.4, transferred 2002 to EC 1.7.1.4, modified 2013]

EC 1.7.1.5

Accepted name: hyponitrite reductase
Reaction: 2 hydroxylamine + 2 NAD⁺ = hyponitrous acid + 2 NADH + 2 H⁺
Other name(s): NADH₂:hyponitrite oxidoreductase
Systematic name: hydroxylamine:NAD⁺ oxidoreductase
Comments: A metalloprotein.
References: [2494]

[EC 1.7.1.5 created 1961 as EC 1.6.6.6, transferred 2002 to EC 1.7.1.5]

EC 1.7.1.6

Accepted name: azobenzene reductase
Reaction: *N,N*-dimethyl-1,4-phenylenediamine + aniline + 2 NADP⁺ = 4-(dimethylamino)azobenzene + 2 NADPH + 2 H⁺
Other name(s): new coccine (NC)-reductase; NC-reductase; azo-dye reductase; orange II azoreductase; NAD(P)H:1-(4'-sulfophenylazo)-2-naphthol oxidoreductase; orange I azoreductase; azo reductase; azoreductase; nicotinamide adenine dinucleotide (phosphate) azoreductase; NADPH₂-dependent azoreductase; dimethylaminobenzene reductase; *p*-dimethylaminoazobenzene azoreductase; dibromopropylaminophenylazobenzoic azoreductase; *N,N*-dimethyl-4-phenylazoaniline azoreductase; *p*-aminoazobenzene reductase; methyl red azoreductase; NADPH₂:4-(dimethylamino)azobenzene oxidoreductase
Systematic name: *N,N*-dimethyl-1,4-phenylenediamine, aniline:NADP⁺ oxidoreductase
Comments: The reaction occurs in the reverse direction to that shown above. Other azo dyes, such as Methyl Red, Rocceline, Solar Orange and Sumifix Black B can also be reduced [3757].
References: [2644, 3757]

[EC 1.7.1.6 created 1961 as EC 1.6.6.7, transferred 2002 to EC 1.7.1.6]

EC 1.7.1.7

Accepted name: GMP reductase
Reaction: IMP + NH₃ + NADP⁺ = GMP + NADPH + H⁺
Other name(s): guanosine 5'-monophosphate reductase; NADPH:GMP oxidoreductase (deaminating); guanosine monophosphate reductase; guanylate reductase; NADPH₂:guanosine-5'-phosphate oxidoreductase (deaminating); guanosine 5'-phosphate reductase
Systematic name: inosine-5'-phosphate:NADP⁺ oxidoreductase (aminating)
References: [2347, 2361]

[EC 1.7.1.7 created 1965 as EC 1.6.6.8, transferred 2002 to EC 1.7.1.7]

[1.7.1.8 Deleted entry. withdrawn in the light of further information on the acceptor]

[EC 1.7.1.8 created 2002, deleted 2002]

EC 1.7.1.9

Accepted name: nitroquinoline-*N*-oxide reductase

Reaction: 4-(hydroxyamino)quinoline *N*-oxide + 2 NAD(P)⁺ + H₂O = 4-nitroquinoline *N*-oxide + 2 NAD(P)H + 2 H⁺
Other name(s): 4-nitroquinoline 1-oxide reductase; 4NQO reductase; NAD(P)H₂:4-nitroquinoline-*N*-oxide oxidoreductase
Systematic name: 4-(hydroxyamino)quinoline *N*-oxide:NADP⁺ oxidoreductase
References: [3914, 3620]

[EC 1.7.1.9 created 1972 as EC 1.6.6.10, transferred 2002 to EC 1.7.1.9]

EC 1.7.1.10

Accepted name: hydroxylamine reductase (NADH)
Reaction: NH₃ + NAD⁺ + H₂O = hydroxylamine + NADH + H⁺
Other name(s): hydroxylamine reductase; ammonium dehydrogenase; NADH-hydroxylamine reductase; *N*-hydroxyamine reductase; hydroxylamine reductase (NADH₂); NADH₂:hydroxylamine oxidoreductase
Systematic name: ammonium:NAD⁺ oxidoreductase
Comments: Also acts on some hydroxamates.
References: [274, 275, 4117]

[EC 1.7.1.10 created 1972 as EC 1.6.6.11, transferred 2002 to EC 1.7.1.10]

EC 1.7.1.11

Accepted name: 4-(dimethylamino)phenylazoxybenzene reductase
Reaction: 4-(dimethylamino)phenylazobenzene + NADP⁺ + H₂O = 4-(dimethylamino)phenylazoxybenzene + NADPH + H⁺
Other name(s): *N,N*-dimethyl-*p*-aminoazobenzene oxide reductase; dimethylaminoazobenzene *N*-oxide reductase; NADPH-dependent DMAB *N*-oxide reductase; NADPH:4-(dimethylamino)phenylazoxybenzene oxidoreductase
Systematic name: 4-(dimethylamino)phenylazobenzene:NADP⁺ oxidoreductase
References: [1762]

[EC 1.7.1.11 created 1989 as EC 1.6.6.12, transferred 2002 to EC 1.7.1.11]

EC 1.7.1.12

Accepted name: *N*-hydroxy-2-acetamidofluorene reductase
Reaction: 2-acetamidofluorene + NAD(P)⁺ + H₂O = *N*-hydroxy-2-acetamidofluorene + NAD(P)H + H⁺
Other name(s): *N*-hydroxy-2-acetylaminofluorene reductase; NAD(P)H₂:*N*-hydroxy-2-acetamidofluorene *N*-oxidoreductase
Systematic name: 2-acetamidofluorene:NAD(P)⁺ oxidoreductase
Comments: Also acts, more slowly, on *N*-hydroxy-4-acetamidobiphenyl.
References: [1326, 1944]

[EC 1.7.1.12 created 1989 as EC 1.6.6.13, transferred 2002 to EC 1.7.1.12]

EC 1.7.1.13

Accepted name: preQ₁ synthase
Reaction: 7-aminomethyl-7-carbaguanine + 2 NADP⁺ = 7-cyano-7-carbaguanine + 2 NADPH + 2 H⁺
Other name(s): YkvM; QueF; preQ₀ reductase; preQ₀ oxidoreductase; 7-cyano-7-deazaguanine reductase; queuine synthase (incorrect as queuine is not the product); queuine:NADP⁺ oxidoreductase (incorrect as queuine is not the product)
Systematic name: 7-aminomethyl-7-carbaguanine:NADP⁺ oxidoreductase

Comments: The reaction occurs in the reverse direction. This enzyme catalyses one of the early steps in the synthesis of queuosine (Q-tRNA), and is followed by the action of EC 2.4.2.29, tRNA-guanosine³⁴ transglycosylase. Queuosine is found in the wobble position of tRNA_{GUN} in Eukarya and Bacteria [4366] and is thought to be involved in translational modulation. The enzyme is not a GTP cyclohydrolase, as was thought previously based on sequence-homology studies.

References: [2127, 4366, 2067, 2859, 2811, 3759]

[EC 1.7.1.13 created 2006]

EC 1.7.1.14

Accepted name: nitric oxide reductase [NAD(P)⁺, nitrous oxide-forming]
Reaction: $\text{N}_2\text{O} + \text{NAD(P)}^+ + \text{H}_2\text{O} = 2 \text{NO} + \text{NAD(P)H} + \text{H}^+$
Other name(s): fungal nitric oxide reductase; cytochrome P450_{nor}; NOR (ambiguous)
Systematic name: nitrous oxide:NAD(P) oxidoreductase
Comments: A heme-thiolate protein (P-450). The enzyme from *Fusarium oxysporum* utilizes only NADH, but the isozyme from *Trichosporon cutaneum* utilizes both NADH and NADPH. The electron transfer from NAD(P)H to heme occurs directly, not requiring flavin or other redox cofactors.
References: [3520, 3517, 4441, 2900]

[EC 1.7.1.14 created 2011]

EC 1.7.1.15

Accepted name: nitrite reductase (NADH)
Reaction: $\text{NH}_3 + 3 \text{NAD}^+ + 2 \text{H}_2\text{O} = \text{nitrite} + 3 \text{NADH} + 5 \text{H}^+$
Other name(s): nitrite reductase (reduced nicotinamide adenine dinucleotide); NADH-nitrite oxidoreductase; assimilatory nitrite reductase (ambiguous); *nirB* (gene name); *nirD* (gene name)
Systematic name: ammonia:NAD⁺ oxidoreductase
Comments: An iron-sulfur flavoprotein (FAD) containing siroheme. This prokaryotic enzyme is specific for NADH. In addition to catalysing the 6-electron reduction of nitrite to ammonia, the enzyme from *Escherichia coli* can also catalyse the 2-electron reduction of hydroxylamine to ammonia. *cf.* EC 1.7.1.4, nitrite reductase [NAD(P)H].
References: [4025, 1705, 487, 1393]

[EC 1.7.1.15 created 2013]

EC 1.7.1.16

Accepted name: nitrobenzene nitroreductase
Reaction: $N\text{-phenylhydroxylamine} + 2 \text{NADP}^+ + \text{H}_2\text{O} = \text{nitrobenzene} + 2 \text{NADPH} + 2 \text{H}^+$ (overall reaction)
(1a) $N\text{-phenylhydroxylamine} + \text{NADP}^+ = \text{nitrosobenzene} + \text{NADPH} + \text{H}^+$
(1b) $\text{nitrosobenzene} + \text{NADP}^+ + \text{H}_2\text{O} = \text{nitrobenzene} + \text{NADPH} + \text{H}^+$
Other name(s): *cnbA* (gene name)
Systematic name: *N*-phenylhydroxylamine:NADP⁺ oxidoreductase
Comments: Contains FMN. The enzyme, characterized from *Pseudomonas* species, catalyses two successive reductions of nitrobenzene, via a nitrosobenzene intermediate. It is also active on 1-chloro-4-nitrobenzene.
References: [3577, 4258]

[EC 1.7.1.16 created 2017]

EC 1.7.1.17

Accepted name: FMN-dependent NADH-azoreductase
Reaction: $\text{anthranilate} + N,N\text{-dimethyl-1,4-phenylenediamine} + 2 \text{NAD}^+ = 2\text{-(4-dimethylaminophenyl)diazenylbenzoate} + 2 \text{NADH} + 2 \text{H}^+$

Other name(s): *azoR* (gene name); NADH-azoreductase
Systematic name: *N,N*-dimethyl-1,4-phenylenediamine, anthranilate:NAD⁺ oxidoreductase
Comments: Requires FMN. The enzyme catalyses the reductive cleavage of an azo bond in aromatic azo compounds to form the corresponding amines. Does not accept NADPH. *cf.* EC 1.7.1.6, azobenzene reductase.
References: [2710, 1683, 1684, 2507]

[EC 1.7.1.17 created 2018]

EC 1.7.2 With a cytochrome as acceptor

EC 1.7.2.1

Accepted name: nitrite reductase (NO-forming)
Reaction: nitric oxide + H₂O + ferricytochrome *c* = nitrite + ferrocycytochrome *c* + 2 H⁺
Other name(s): *cd*-cytochrome nitrite reductase; [nitrite reductase (cytochrome)] [misleading, see comments.]; cytochrome *c*-551:O₂, NO₂⁺ oxidoreductase; cytochrome *cd*; cytochrome *cd*₁; hydroxylamine (acceptor) reductase; methyl viologen-nitrite reductase; nitrite reductase (cytochrome; NO-forming)
Systematic name: nitric-oxide:ferricytochrome-*c* oxidoreductase
Comments: The reaction is catalysed by two types of enzymes, found in the periplasm of denitrifying bacteria. One type comprises proteins containing multiple copper centres, the other a heme protein, cytochrome *cd*₁. Acceptors include *c*-type cytochromes such as cytochrome *c*-550 or cytochrome *c*-551 from *Paracoccus denitrificans* or *Pseudomonas aeruginosa*, and small blue copper proteins such as azurin and pseudoazurin. Cytochrome *cd*₁ also has oxidase and hydroxylamine reductase activities. May also catalyse the reaction of hydroxylamine reductase (EC 1.7.99.1) since this is a well-known activity of cytochrome *cd*₁.
References: [2572, 622, 4090, 3537, 2525, 1228, 4221, 1542, 4496, 998, 4044]

[EC 1.7.2.1 created 1961, modified 1976, modified 2001, modified 2002 (EC 1.7.99.3 created 1961 as EC 1.6.6.5, transferred 1964 to EC 1.7.99.3, modified 1976, incorporated 2002, EC 1.9.3.2 created 1965, incorporated 2002)]

EC 1.7.2.2

Accepted name: nitrite reductase (cytochrome; ammonia-forming)
Reaction: NH₃ + 2 H₂O + 6 ferricytochrome *c* = nitrite + 6 ferrocycytochrome *c* + 7 H⁺
Other name(s): cytochrome *c* nitrite reductase; multiheme nitrite reductase
Systematic name: ammonia:ferricytochrome-*c* oxidoreductase
Comments: Found as a multiheme cytochrome in many bacteria. The enzyme from *Escherichia coli* contains five hemes *c* and requires Ca²⁺. It also reduces nitric oxide and hydroxylamine to ammonia, and sulfite to sulfide.
References: [932]

[EC 1.7.2.2 created 2001]

EC 1.7.2.3

Accepted name: trimethylamine-*N*-oxide reductase
Reaction: trimethylamine + 2 (ferricytochrome *c*)-subunit + H₂O = trimethylamine *N*-oxide + 2 (ferrocycytochrome *c*)-subunit + 2 H⁺
Other name(s): TMAO reductase; TOR; *torA* (gene name); *torZ* (gene name); *bisZ* (gene name); trimethylamine-*N*-oxide reductase (cytochrome *c*)
Systematic name: trimethylamine:cytochrome *c* oxidoreductase
Comments: Contains bis(molybdopterin guanine dinucleotide)molybdenum cofactor. The reductant is a membrane-bound multiheme cytochrome *c*. Also reduces dimethyl sulfoxide to dimethyl sulfide.
References: [113, 1969, 715, 1236, 4442, 4362]

[EC 1.7.2.3 created 2002, modified 2018]

EC 1.7.2.4

Accepted name: nitrous-oxide reductase
Reaction: nitrogen + H₂O + 2 ferricytochrome *c* = nitrous oxide + 2 ferrocycytochrome *c* + 2 H⁺
Other name(s): nitrous oxide reductase; N₂O reductase; nitrogen:(acceptor) oxidoreductase (N₂O-forming)
Systematic name: nitrogen:cytochrome *c* oxidoreductase (N₂O-forming)
Comments: The reaction is observed only in the direction of nitrous oxide reduction. Contains the mixed-valent dinuclear CuA species at the electron entry site of the enzyme, and the tetranuclear Cu-Z centre in the active site. In *Paracoccus pantotrophus*, the electron donor is cytochrome *c*₅₅₂.
References: [681, 4497, 788]

[EC 1.7.2.4 created 1989 as EC 1.7.99.6, modified 1999, transferred 2011 to EC 1.7.2.4]

EC 1.7.2.5

Accepted name: nitric oxide reductase (cytochrome *c*)
Reaction: nitrous oxide + 2 ferricytochrome *c* + H₂O = 2 nitric oxide + 2 ferrocycytochrome *c* + 2 H⁺
Systematic name: nitrous oxide:ferricytochrome-*c* oxidoreductase
Comments: The enzyme from *Pseudomonas aeruginosa* contains a dinuclear centre comprising a non-heme iron centre and heme *b*₃, plus heme *c*, heme *b* and calcium; the acceptor is cytochrome *c*₅₅₁
References: [1477, 1476, 1465, 563, 2075, 1511]

[EC 1.7.2.5 created 1992 as EC 1.7.99.7, transferred 2011 to EC 1.7.2.5]

EC 1.7.2.6

Accepted name: hydroxylamine dehydrogenase
Reaction: (1) hydroxylamine + H₂O + 4 ferricytochrome *c* = nitrite + 4 ferrocycytochrome *c* + 5 H⁺
(2) hydroxylamine + 3 ferricytochrome *c* = nitric oxide + 3 ferrocycytochrome *c* + 3 H⁺
Other name(s): HAO (ambiguous); hydroxylamine oxidoreductase (ambiguous); hydroxylamine oxidase (misleading)
Systematic name: hydroxylamine:ferricytochrome-*c* oxidoreductase
Comments: The enzymes from the nitrifying bacterium *Nitrosomonas europaea* [3152, 2269] and the methylotrophic bacterium *Methylococcus capsulatus* [3039] are hemoproteins with seven *c*-type hemes and one specialized *P*-460-type heme per subunit. The enzyme converts hydroxylamine to nitrite via an enzyme-bound nitroxyl intermediate [1556]. While nitrite is the main product, the enzyme from *Nitrosomonas europaea* can produce nitric oxide as well [1557].
References: [3152, 1557, 1556, 2269, 3039]

[EC 1.7.2.6 created 1972 as EC 1.7.3.4, part transferred 2012 to EC 1.7.2.6]

EC 1.7.2.7

Accepted name: hydrazine synthase
Reaction: hydrazine + H₂O + 3 ferricytochrome *c* = nitric oxide + ammonium + 3 ferrocycytochrome *c*
Other name(s): HZS
Systematic name: hydrazine:ferricytochrome-*c* oxidoreductase
Comments: The enzyme, characterized from anaerobic ammonia oxidizers (anammox bacteria), is one of only two enzymes that are known to form an N-N bond (the other being EC 1.7.1.14, nitric oxide reductase [NAD(P)⁺, nitrous oxide-forming]). The enzyme from the bacterium *Candidatus Kuenenia stuttgartiensis* is heterotrimeric and contains multiple *c*-type cytochromes.
References: [1821]

[EC 1.7.2.7 created 2016]

EC 1.7.2.8

Accepted name: hydrazine dehydrogenase
Reaction: hydrazine + 4 ferricytochrome *c* = N₂ + 4 ferrocycytochrome *c*
Other name(s): HDH
Systematic name: hydrazine:ferricytochrome *c* oxidoreductase
Comments: The enzyme, which is involved in the pathway of anaerobic ammonium oxidation in anammox bacteria, has been purified from the bacterium *Candidatus Kuenenia stuttgartiensis*. The electrons derived from hydrazine are eventually transferred to the quinone pool.
References: [3349, 1737, 1821, 1820]

[EC 1.7.2.8 created 2003 as EC 1.7.99.8, modified 2010, transferred 2016 to EC 1.7.2.8]

EC 1.7.3 With oxygen as acceptor

EC 1.7.3.1

Accepted name: nitroalkane oxidase
Reaction: a nitroalkane + H₂O + O₂ = an aldehyde or ketone + nitrite + H₂O₂
Other name(s): nitroethane oxidase; NAO; nitroethane:oxygen oxidoreductase
Systematic name: nitroalkane:oxygen oxidoreductase
Comments: Has an absolute requirement for FAD [1024]. While nitroethane may be the physiological substrate [1902], the enzyme also acts on several other nitroalkanes, including 1-nitropropane, 2-nitropropane, 1-nitrobutane, 1-nitropentane, 1-nitrohexane, nitrocyclohexane and some nitroalkanols [1024]. Differs from EC 1.13.11.16, nitronate monooxygenase, in that the preferred substrates are neutral nitroalkanes rather than anionic nitronates [1024].
References: [2273, 1902, 749, 1024, 3988]

[EC 1.7.3.1 created 1961, modified 2006, modified 2009]

EC 1.7.3.2

Accepted name: acetyloxindoxyl oxidase
Reaction: *N*-acetyloxindoxyl + O₂ = *N*-acetylisatin + (?)
Systematic name: *N*-acetyloxindoxyl:oxygen oxidoreductase
References: [243]

[EC 1.7.3.2 created 1961]

EC 1.7.3.3

Accepted name: factor-independent urate hydroxylase
Reaction: urate + O₂ + H₂O = 5-hydroxyisourate + H₂O₂
Other name(s): uric acid oxidase; uricase; uricase II; urate oxidase
Systematic name: urate:oxygen oxidoreductase
Comments: This enzyme was previously thought to be a copper protein, but it is now known that the enzymes from soy bean (*Glycine max*), the mould *Aspergillus flavus* and *Bacillus subtilis* contains no copper nor any other transition-metal ion. The 5-hydroxyisourate formed decomposes spontaneously to form allantoin and CO₂, although there is an enzyme-catalysed pathway in which EC 3.5.2.17, hydroxyisourate hydrolase, catalyses the first step. The enzyme is different from EC 1.14.13.113 (FAD-dependent urate hydroxylase).
References: [2295, 2367, 3202, 1800, 643, 1645]

[EC 1.7.3.3 created 1961, modified 2002, modified 2005, modified 2010]

[1.7.3.4 Transferred entry. hydroxylamine oxidase. Now covered by EC 1.7.2.6, hydroxylamine dehydrogenase, and EC 1.7.3.6, hydroxylamine oxidase (cytochrome)]

[EC 1.7.3.4 created 1972, deleted 2013]

EC 1.7.3.5

- Accepted name:** 3-*aci*-nitropropanoate oxidase
Reaction: 3-*aci*-nitropropanoate + O₂ + H₂O = 3-oxopropanoate + nitrite + H₂O₂
Other name(s): propionate-3-nitronate oxidase
Systematic name: 3-*aci*-nitropropanoate:oxygen oxidoreductase
Comments: A flavoprotein (FMN). The primary products of the enzymic reaction are probably the nitropropanoate free radical and superoxide. Also acts, more slowly, on 4-*aci*-nitrobutanoate.
References: [3042]

[EC 1.7.3.5 created 1990]

EC 1.7.3.6

- Accepted name:** hydroxylamine oxidase (cytochrome)
Reaction: hydroxylamine + O₂ = nitrite + H₂O + H⁺ (overall reaction)
(1a) hydroxylamine + 2 ferricytochrome *c* = nitroxyl + 2 ferrocycytochrome *c* + 2 H⁺
(1b) nitroxyl + 2 ferrocycytochrome *c* + O₂ + H⁺ = nitrite + 2 ferricytochrome *c* + H₂O (spontaneous)
Other name(s): HAO (ambiguous); hydroxylamine oxidoreductase (ambiguous); hydroxylamine oxidase (misleading)
Systematic name: hydroxylamine:oxygen oxidoreductase
Comments: The enzyme from the heterotrophic nitrifying bacterium *Paracoccus denitrificans* contains three to five non-heme, non-iron-sulfur iron atoms and interacts with cytochrome *c*₅₅₆ and pseudoazurin [4161, 2592]. Under anaerobic conditions *in vitro* only nitrous oxide is formed [2592]. Presumably nitroxyl is released and combines with a second nitroxyl to give nitrous oxide and water. When oxygen is present, nitrite is formed.
References: [2091, 4161, 2592, 4160]

[EC 1.7.3.6 created 1972 as EC 1.7.3.4, part transferred 2013 to EC 1.7.3.6, modified 2015]

EC 1.7.5 With a quinone or similar compound as acceptor

EC 1.7.5.1

- Accepted name:** nitrate reductase (quinone)
Reaction: nitrate + a quinol = nitrite + a quinone + H₂O
Other name(s): nitrate reductase A; nitrate reductase Z; quinol/nitrate oxidoreductase; quinol-nitrate oxidoreductase; quinol:nitrate oxidoreductase; NarA; NarZ; NarGHI; dissimilatory nitrate reductase
Systematic name: nitrite:quinone oxidoreductase
Comments: A membrane-bound enzyme which supports anaerobic respiration on nitrate under anaerobic conditions and in the presence of nitrate. Contains the bicyclic form of the molybdo-bis(molybdopterin guanine dinucleotide) cofactor, iron-sulfur clusters and heme *b*. *Escherichia coli* expresses two forms NarA and NarZ, both being comprised of three subunits.
References: [953, 280, 2123, 279, 345, 1310, 1660]

[EC 1.7.5.1 created 2010]

EC 1.7.5.2

- Accepted name:** nitric oxide reductase (menaquinol)
Reaction: 2 nitric oxide + menaquinol = nitrous oxide + menaquinone + H₂O
Comments: Contains copper.
References: [687, 3722, 3721]

[EC 1.7.5.2 created 2011]

EC 1.7.6 With a nitrogenous group as acceptor

EC 1.7.6.1

- Accepted name:** nitrite dismutase
Reaction: $3 \text{ nitrite} + 2 \text{ H}^+ = 2 \text{ nitric oxide} + \text{ nitrate} + \text{ H}_2\text{O}$
Other name(s): Prolixin S; Nitrophorin 7
Systematic name: nitrite:nitrite oxidoreductase
Comments: Contains ferriheme *b*. The enzyme is one of the nitrophorins from the salivary gland of the blood-feeding insect *Rhodnius prolixus*. Nitric oxide produced induces vasodilation after injection. Nitrophorins 2 and 4 can also catalyze this reaction.
References: [1444, 1445]

[EC 1.7.6.1 created 2011]

EC 1.7.7 With an iron-sulfur protein as acceptor

EC 1.7.7.1

- Accepted name:** ferredoxin—nitrite reductase
Reaction: $\text{NH}_3 + 2 \text{ H}_2\text{O} + 6 \text{ oxidized ferredoxin} = \text{ nitrite} + 6 \text{ reduced ferredoxin} + 7 \text{ H}^+$
Systematic name: ammonia:ferredoxin oxidoreductase
Comments: An iron protein. Contains siroheme and [4Fe-4S] clusters.
References: [1780, 3121, 4499]

[EC 1.7.7.1 created 1972, modified 1999]

EC 1.7.7.2

- Accepted name:** ferredoxin—nitrate reductase
Reaction: $\text{ nitrite} + \text{ H}_2\text{O} + 2 \text{ oxidized ferredoxin} = \text{ nitrate} + 2 \text{ reduced ferredoxin} + 2 \text{ H}^+$
Other name(s): assimilatory nitrate reductase; nitrate (ferredoxin) reductase; assimilatory ferredoxin-nitrate reductase
Systematic name: nitrite:ferredoxin oxidoreductase
Comments: A molybdenum-iron-sulfur protein.
References: [2537]

[EC 1.7.7.2 created 1986]

EC 1.7.99 With unknown physiological acceptors

EC 1.7.99.1

- Accepted name:** hydroxylamine reductase
Reaction: $\text{NH}_3 + \text{H}_2\text{O} + \text{acceptor} = \text{hydroxylamine} + \text{reduced acceptor}$
Other name(s): hydroxylamine (acceptor) reductase; ammonia:(acceptor) oxidoreductase
Systematic name: ammonia:acceptor oxidoreductase
Comments: A flavoprotein. Reduced pyocyanine, methylene blue and flavins act as donors for the reduction of hydroxylamine. May be identical to EC 1.7.2.1, nitrite reductase (NO-forming).
References: [3815, 4089, 3183]

[EC 1.7.99.1 created 1961, modified 1999, modified 2002]

[1.7.99.2 Deleted entry. nitric-oxide reductase. Reaction may have been due to the combined action of EC 1.7.99.6 nitrous-oxide reductase and EC 1.7.99.7 nitric-oxide reductase]

[EC 1.7.99.2 created 1961, modified 1976, deleted 1992]

[1.7.99.3 Transferred entry. nitrite reductase. Now included with EC 1.7.2.1, nitrite reductase (NO-forming)]

[EC 1.7.99.3 created 1961 as EC 1.6.6.5, transferred 1964 to EC 1.7.99.3, modified 1976, deleted 2002]

[1.7.99.4 Transferred entry. nitrate reductase, Now EC 1.7.1.1, nitrate reductase (NADH), EC 1.7.1.2, nitrate reductase [NAD(P)H], EC 1.7.1.3, nitrate reductase (NADPH), EC 1.7.5.1, nitrate reductase (quinone), EC 1.7.7.2, nitrate reductase (ferredoxin) and EC 1.9.6.1, nitrate reductase (cytochrome)]

[EC 1.7.99.4 created 1972, modified 1976, deleted 2017]

[1.7.99.5 Deleted entry. 5,10-methylenetetrahydrofolate reductase (FADH₂). Now included with EC 1.5.1.20, methylenetetrahydrofolate reductase [NAD(P)H]. Based on the reference, it had been thought that this was a separate enzyme from EC 1.5.1.20 but the reference upon which the entry was based has since been disproved]

[EC 1.7.99.5 created 1965 as EC 1.1.1.68, transferred 1978 to EC 1.1.99.15, transferred 1980 to EC 1.7.99.5, deleted 2005]

[1.7.99.6 Transferred entry. EC 1.7.99.6, nitrous-oxide reductase. Now EC 1.7.2.4.]

[EC 1.7.99.6 created 1989, modified 1999, deleted 2011]

[1.7.99.7 Transferred entry. nitric-oxide reductase. Now EC 1.7.2.5 nitric oxide reductase (cytochrome c)]

[EC 1.7.99.7 created 1992, modified 1999, deleted 2011]

[1.7.99.8 Transferred entry. hydrazine oxidoreductase. Now classified as EC 1.7.2.8, hydrazine dehydrogenase.]

[EC 1.7.99.8 created 2003, modified 2010, deleted 2016]

EC 1.8 Acting on a sulfur group of donors

This small subclass contains enzymes that act either on inorganic substrates or organic thiols. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.8.1), a cytochrome (EC 1.8.2), oxygen (EC 1.8.3), a disulfide (EC 1.8.4); a quinone or similar compound (EC 1.8.5), an iron-sulfur protein (EC 1.8.7), other, known, acceptors (EC 1.8.98), or some other acceptor (EC 1.8.99).

EC 1.8.1 With NAD⁺ or NADP⁺ as acceptor

[1.8.1.1 Deleted entry. cysteamine dehydrogenase]

[EC 1.8.1.1 created 1961, deleted 1972]

EC 1.8.1.2

- Accepted name:** assimilatory sulfite reductase (NADPH)
Reaction: hydrogen sulfide + 3 NADP⁺ + 3 H₂O = sulfite + 3 NADPH + 3 H⁺
Other name(s): sulfite reductase (NADPH); sulfite (reduced nicotinamide adenine dinucleotide phosphate) reductase; NADPH-sulfite reductase; NADPH-dependent sulfite reductase; H₂S-NADP oxidoreductase; sulfite reductase (NADPH₂); MET5 (gene name); MET10 (gene name); *cysI* (gene name); *cysJ* (gene name)
Systematic name: hydrogen-sulfide:NADP⁺ oxidoreductase
Comments: Contains siroheme, [4Fe-4S] cluster, FAD and FMN. The enzyme, which catalyses the six-electron reduction of sulfite to sulfide, is involved in sulfate assimilation in bacteria and yeast. Different from EC 1.8.99.5, dissimilatory sulfite reductase, which is involved in prokaryotic sulfur-based energy metabolism. *cf.* EC 1.8.7.1, assimilatory sulfite reductase (ferredoxin).
References: [1508, 4386, 3529, 1981, 3530, 679, 689]

[EC 1.8.1.2 created 1961, modified 2015]

EC 1.8.1.3

Accepted name: hypotaurine dehydrogenase

Reaction: hypotaurine + H₂O + NAD⁺ = taurine + NADH + H⁺
Systematic name: hypotaurine:NAD⁺ oxidoreductase
Comments: A molybdohemoprotein.
References: [3726]

[EC 1.8.1.3 created 1972]

EC 1.8.1.4

Accepted name: dihydrolipoyl dehydrogenase
Reaction: protein N⁶-(dihydrolipoyl)lysine + NAD⁺ = protein N⁶-(lipoyl)lysine + NADH + H⁺
Other name(s): LDP-Glc; LDP-Val; dehydrolipoate dehydrogenase; diaphorase; dihydrolipoamide dehydrogenase; dihydrolipoamide:NAD⁺ oxidoreductase; dihydrolipoic dehydrogenase; dihydrothioctic dehydrogenase; lipoamide dehydrogenase (NADH); lipoamide oxidoreductase (NADH); lipoamide reductase; lipoamide reductase (NADH); lipoate dehydrogenase; lipoic acid dehydrogenase; lipoyl dehydrogenase; protein-6-N-(dihydrolipoyl)lysine:NAD⁺ oxidoreductase
Systematic name: protein-N⁶-(dihydrolipoyl)lysine:NAD⁺ oxidoreductase
Comments: A flavoprotein (FAD). A component of the multienzyme 2-oxo-acid dehydrogenase complexes. In the pyruvate dehydrogenase complex, it binds to the core of EC 2.3.1.12, dihydrolipoyllysine-residue acetyltransferase, and catalyses oxidation of its dihydrolipoyl groups. It plays a similar role in the oxoglutarate and 3-methyl-2-oxobutanoate dehydrogenase complexes. Another substrate is the dihydrolipoyl group in the H-protein of the glycine-cleavage system (click here for diagram), in which it acts, together with EC 1.4.4.2, glycine dehydrogenase (decarboxylating), and EC 2.1.2.10, aminomethyltransferase, to break down glycine. It can also use free dihydrolipoate, dihydrolipoamide or dihydrolipoyllysine as substrate. This enzyme was first shown to catalyse the oxidation of NADH by methylene blue; this activity was called diaphorase. The glycine cleavage system 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), the L protein (EC 1.8.1.4) and the lipoyl-bearing H protein [2764].
References: [2432, 2433, 3328, 3670, 2983, 2764]

[EC 1.8.1.4 created 1961 as EC 1.6.4.3, modified 1976, transferred 1983 to EC 1.8.1.4, modified 2003, modified 2006]

EC 1.8.1.5

Accepted name: 2-oxopropyl-CoM reductase (carboxylating)
Reaction: 2-mercaptoethanesulfonate + acetoacetate + NADP⁺ = 2-(2-oxopropylthio)ethanesulfonate + CO₂ + NADPH
Other name(s): NADPH:2-(2-ketopropylthio)ethanesulfonate oxidoreductase/carboxylase; NADPH:2-ketopropyl-coenzyme M oxidoreductase/carboxylase
Systematic name: 2-mercaptoethanesulfonate,acetoacetate:NADP⁺ oxidoreductase (decarboxylating)
Comments: Also acts on thioethers longer in chain length on the oxo side, e.g. 2-oxobutyl-CoM, but this portion must be attached to CoM (2-mercaptoethanesulfonate); no CoM analogs will substitute. This enzyme forms component II of a four-component enzyme system comprising EC 4.4.1.23 (2-hydroxypropyl-CoM lyase; component I), EC 1.8.1.5 [2-oxopropyl-CoM reductase (carboxylating); component II], EC 1.1.1.268 [2-(R)-hydroxypropyl-CoM dehydrogenase; component III] and EC 1.1.1.269 [2-(S)-hydroxypropyl-CoM dehydrogenase; component IV] that is involved in epoxyalkane carboxylation in *Xanthobacter* sp. strain Py2.
References: [62, 626]

[EC 1.8.1.5 created 2001]

EC 1.8.1.6

Accepted name: cystine reductase
Reaction: 2 L-cysteine + NAD⁺ = L-cystine + NADH + H⁺
Other name(s): cystine reductase (NADH); NADH-dependent cystine reductase; cystine reductase (NADH₂); NADH₂:L-cystine oxidoreductase

Systematic name: L-cysteine:NAD⁺ oxidoreductase

References: [3224, 512, 2397]

[EC 1.8.1.6 created 1961 as EC 1.6.4.1, transferred 2002 to EC 1.8.1.6]

EC 1.8.1.7

Accepted name: glutathione-disulfide reductase

Reaction: 2 glutathione + NADP⁺ = glutathione disulfide + NADPH + H⁺

Other name(s): glutathione reductase; glutathione reductase (NADPH); NADPH-glutathione reductase; GSH reductase; GSSG reductase; NADPH-GSSG reductase; glutathione *S*-reductase; NADPH:oxidized-glutathione oxidoreductase

Systematic name: glutathione:NADP⁺ oxidoreductase

Comments: A dimeric flavoprotein (FAD); activity is dependent on a redox-active disulfide in each of the active centres.

References: [2923, 3010, 3098, 4005, 4254, 335, 2244]

[EC 1.8.1.7 created 1961 as EC 1.6.4.2, modified 1989, transferred 2002 to EC 1.8.1.7]

EC 1.8.1.8

Accepted name: protein-disulfide reductase

Reaction: protein-dithiol + NAD(P)⁺ = protein-disulfide + NAD(P)H + H⁺

Other name(s): protein disulphide reductase; insulin-glutathione transhydrogenase; disulfide reductase; NAD(P)H₂:protein-disulfide oxidoreductase

Systematic name: protein-dithiol:NAD(P)⁺ oxidoreductase

References: [1417]

[EC 1.8.1.8 created 1965 as EC 1.6.4.4, transferred 2002 to EC 1.8.1.8]

EC 1.8.1.9

Accepted name: thioredoxin-disulfide reductase

Reaction: thioredoxin + NADP⁺ = thioredoxin disulfide + NADPH + H⁺

Other name(s): NADP-thioredoxin reductase; NADPH-thioredoxin reductase; thioredoxin reductase (NADPH); NADPH₂:oxidized thioredoxin oxidoreductase

Systematic name: thioredoxin:NADP⁺ oxidoreductase

Comments: A flavoprotein (FAD).

References: [2606, 3596, 121]

[EC 1.8.1.9 created 1972 as EC 1.6.4.5, transferred 2002 to EC 1.8.1.9]

EC 1.8.1.10

Accepted name: CoA-glutathione reductase

Reaction: CoA + glutathione + NADP⁺ = CoA-glutathione + NADPH + H⁺

Other name(s): coenzyme A glutathione disulfide reductase; NADPH-dependent coenzyme A-SS-glutathione reductase; coenzyme A disulfide-glutathione reductase; NADPH₂:CoA-glutathione oxidoreductase

Systematic name: glutathione:NADP⁺ oxidoreductase (CoA-acylating)

Comments: A flavoprotein. The substrate is a mixed disulfide. May be identical to EC 1.8.1.9, thioredoxin-disulfide reductase.

References: [2886, 2887, 505]

[EC 1.8.1.10 created 1972 as EC 1.6.4.6, transferred 2002 to EC 1.8.1.10]

EC 1.8.1.11

Accepted name: asparagusate reductase
Reaction: 3-mercapto-2-mercaptomethylpropanoate + NAD⁺ = asparagusate + NADH + H⁺
Other name(s): asparagusate dehydrogenase; asparagusic dehydrogenase; asparagusate reductase (NADH₂); NADH₂:asparagusate oxidoreductase
Systematic name: 3-mercapto-2-mercaptomethylpropanoate:NAD⁺ oxidoreductase
Comments: Also acts on lipoate.
References: [4333, 4334]

[EC 1.8.1.11 created 1978 as EC 1.6.4.7, transferred 2002 to EC 1.8.1.11]

EC 1.8.1.12

Accepted name: trypanothione-disulfide reductase
Reaction: trypanothione + NADP⁺ = trypanothione disulfide + NADPH + H⁺
Other name(s): trypanothione reductase; NADPH₂:trypanothione oxidoreductase
Systematic name: trypanothione:NADP⁺ oxidoreductase
Comments: Trypanothione disulfide is the oxidized form of *N*¹,*N*⁸-bis(glutathionyl)-spermidine from the insect-parasitic trypanosomatid *Crithidia fasciculata*. The enzyme from *Crithidia fasciculata* is a flavoprotein (FAD), whose activity is dependent on a redox-active cystine at the active centre. (*cf.* EC 1.8.1.7, glutathione-disulfide reductase)
References: [3458, 2407, 708]

[EC 1.8.1.12 created 1989 as EC 1.6.4.8, transferred 2002 to EC 1.8.1.12]

EC 1.8.1.13

Accepted name: bis- γ -glutamylcystine reductase
Reaction: 2 γ -glutamylcystine + NADP⁺ = bis- γ -glutamylcystine + NADPH + H⁺
Other name(s): NADPH₂:bis- γ -glutamylcystine oxidoreductase; GSR
Systematic name: γ -glutamylcystine:NADP⁺ oxidoreductase
Comments: Contains FAD. The enzyme, which is found only in halobacteria, maintains the concentration of γ -glutamylcystine, the major low molecular weight thiol in halobacteria. Not identical with EC 1.8.1.7 (glutathione-disulfide reductase) or EC 1.8.1.14 (CoA-disulfide reductase).
References: [3741, 3742, 1907]

[EC 1.8.1.13 created 1992 as EC 1.6.4.9, transferred 2002 to EC 1.8.1.13, modified 2013]

EC 1.8.1.14

Accepted name: CoA-disulfide reductase
Reaction: 2 CoA + NADP⁺ = CoA-disulfide + NADPH + 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 [2309], while the bacterium *Bacillus megaterium* contains both NADH and NADPH-dependent enzymes [3445].
References: [3445, 787, 2309]

[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 1.8.1.15

Accepted name: mycothione reductase
Reaction: 2 mycothiol + NAD(P)⁺ = mycothione + NAD(P)H + H⁺
Other name(s): mycothiol-disulfide reductase

Systematic name: mycothiol:NAD(P)⁺ oxidoreductase
Comments: Contains FAD. No activity with glutathione, trypanothione or coenzyme A as substrate.
References: [2955, 2956]

[EC 1.8.1.15 created 2002]

EC 1.8.1.16

Accepted name: glutathione amide reductase
Reaction: 2 glutathione amide + NAD⁺ = glutathione amide disulfide + NADH + H⁺
Other name(s): GAR
Systematic name: glutathione amide:NAD⁺ oxidoreductase
Comments: A dimeric flavoprotein (FAD). The enzyme restores glutathione amide disulfide, which is produced during the reduction of peroxide by EC 1.11.1.17 (glutathione amide-dependent peroxidase), back to glutathione amide (it catalyses the reaction in the opposite direction to that shown). The enzyme belongs to the family of flavoprotein disulfide oxidoreductases, but unlike other members of the family, which are specific for NADPH, it prefers NADH [4032].
References: [4032, 4033]

[EC 1.8.1.16 created 2010]

EC 1.8.1.17

Accepted name: dimethylsulfone reductase
Reaction: dimethyl sulfoxide + H₂O + NAD⁺ = dimethyl sulfone + NADH + H⁺
Comments: A molybdoprotein.
References: [355, 356]

[EC 1.8.1.17 created 2011]

EC 1.8.1.18

Accepted name: NAD(P)H sulfur oxidoreductase (CoA-dependent)
Reaction: hydrogen sulfide + NAD(P)⁺ = sulfur + NAD(P)H + H⁺
Other name(s): NADPH NSR; S⁰ reductase; coenzyme A-dependent NADPH sulfur oxidoreductase
Systematic name: hydrogen sulfide:NAD(P)⁺ oxidoreductase (CoA-dependent)
Comments: This FAD-dependent enzyme, characterized from the archaeon *Pyrococcus furiosus*, is responsible for NAD(P)H-linked sulfur reduction. The activity with NADH is about half of that with NADPH. The reaction is dependent on CoA, although the nature of this dependency is not well understood.
References: [3408, 399, 1397]

[EC 1.8.1.18 created 2013]

EC 1.8.1.19

Accepted name: sulfide dehydrogenase
Reaction: hydrogen sulfide + (sulfide)_n + NADP⁺ = (sulfide)_{n+1} + NADPH + 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: [2328, 1339]

[EC 1.8.1.19 created 2013]

EC 1.8.1.20

- Accepted name:** 4,4'-dithiodibutanoate disulfide reductase
Reaction: 2 4-sulfanylbutanoate + NAD⁺ = 4,4'-disulfanediyldibutanoate + NADH + H⁺
Systematic name: 4-sulfanylbutanoate:NAD⁺ oxidoreductase
Comments: The enzyme, characterized from the bacterium *Rhodococcus erythropolis* MI2, contains an FMN cofactor.
References: [1892, 1893]

[EC 1.8.1.20 created 2017]

EC 1.8.2 With a cytochrome as acceptor

EC 1.8.2.1

- Accepted name:** sulfite dehydrogenase (cytochrome)
Reaction: sulfite + 2 ferricytochrome *c* + H₂O = sulfate + 2 ferrocyclochrome *c* + 2 H⁺
Other name(s): sulfite cytochrome *c* reductase; sulfite-cytochrome *c* oxidoreductase; sulfite oxidase (ambiguous); sulfite dehydrogenase (ambiguous); *sorAB* (gene names)
Systematic name: sulfite:ferricytochrome-*c* oxidoreductase
Comments: Associated with cytochrome *c*-551. The enzyme from the bacterium *Starkeya novella* contains a molybdopyranopterin cofactor and a smaller monoheme cytochrome *c* subunit. *cf.* EC 1.8.5.6, sulfite dehydrogenase (quinone).
References: [548, 2327, 4323, 2307, 1812]

[EC 1.8.2.1 created 1972, modified 2016]

EC 1.8.2.2

- Accepted name:** thiosulfate dehydrogenase
Reaction: 2 thiosulfate + 2 ferricytochrome *c* = tetrathionate + 2 ferrocyclochrome *c*
Other name(s): *tsdA* (gene name); tetrathionate synthase; thiosulfate oxidase; thiosulfate-oxidizing enzyme; thiosulfate-acceptor oxidoreductase
Systematic name: thiosulfate:ferricytochrome-*c* oxidoreductase
Comments: The enzyme catalyses the reversible formation of a sulfur-sulfur bond between the sulfane atoms of two thiosulfate molecules, yielding tetrathionate and releasing two electrons. In many bacterial species the enzyme is a diheme *c*-type cytochrome. In a number of organisms, including *Thiomonas intermedia* and *Sideroxydans lithotrophicus*, a second diheme cytochrome (TsdB) acts as the electron acceptor. However, some organisms, such as *Allochroamatium vinosum*, lack TsdB. The electron acceptor in these organisms may be the high-potential iron-sulfur protein (HiPIP).
References: [2308, 1109, 2286, 404, 2093]

[EC 1.8.2.2 created 1990]

EC 1.8.2.3

- Accepted name:** sulfide-cytochrome-*c* reductase (flavocytochrome *c*)
Reaction: hydrogen sulfide + 2 ferricytochrome *c* = sulfur + 2 ferrocyclochrome *c* + 2 H⁺
Systematic name: hydrogen-sulfide:flavocytochrome *c* oxidoreductase
Comments: The enzyme from *Allochroamatium vinosum* contains covalently bound FAD and covalently-bound *c*-type hemes.
References: [2094, 1110, 1265, 579, 3588, 2039]

[EC 1.8.2.3 created 2011]

EC 1.8.2.4

Accepted name: dimethyl sulfide:cytochrome *c*₂ reductase
Reaction: dimethyl sulfide + 2 ferricytochrome *c*₂ + H₂O = dimethyl sulfoxide + 2 ferrocyclochrome *c*₂ + 2 H⁺
Other name(s): Ddh (gene name)
Systematic name: dimethyl sulfide:cytochrome-*c*₂ oxidoreductase
Comments: The enzyme from the bacterium *Rhodovulum sulfidophilum* binds molybdopterin guanine dinucleotide, heme *b* and [4Fe-4S] clusters.
References: [1369, 2482]

[EC 1.8.2.4 created 2011]

EC 1.8.2.5

Accepted name: thiosulfate reductase (cytochrome)
Reaction: sulfite + hydrogen sulfide + 2 ferricytochrome *c*₃ = thiosulfate + 2 ferrocyclochrome *c*₃
Systematic name: sulfite,hydrogen sulfide:ferricytochrome-*c*₃ oxidoreductase (thiosulfate-forming)
Comments: The enzyme is found in sulfate-reducing bacteria. The source of the electrons is molecular hydrogen, via EC 1.12.2.1, cytochrome-*c*₃ hydrogenase. The organisms utilize the sulfite that is produced for energy generation by EC 1.8.99.5, dissimilatory sulfite reductase.
References: [1671, 1670, 2720, 1406, 1418, 47]

[EC 1.8.2.5 created 2017]

EC 1.8.2.6

Accepted name: *S*-disulfanyl-L-cysteine oxidoreductase
Reaction: [SoxY protein]-*S*-disulfanyl-L-cysteine + 6 ferricytochrome *c* + 3 H₂O = [SoxY protein]-*S*-sulfosulfanyl-L-cysteine + 6 ferrocyclochrome *c* + 6 H⁺
Other name(s): SoxCD; sulfur dehydrogenase
Systematic name: [SoxY protein]-*S*-disulfanyl-L-cysteine:cytochrome-*c* oxidoreductase
Comments: The enzyme is part of the Sox enzyme system, which participates in a bacterial thiosulfate oxidation pathway that produces sulfate. The enzyme from the bacterium *Paracoccus pantotrophus* contains a molybdoprotein component and a diheme *c*-type cytochrome component. The enzyme successively oxidizes the outer sulfur atom in [SoxY protein]-*S*-disulfanyl-L-cysteine, using three water molecules and forming [SoxY protein]-*S*-sulfosulfanyl-L-cysteine. During the process, six electrons are transferred to the electron chain via cytochrome *c*.
References: [1075, 200, 1255]

[EC 1.8.2.6 created 2018]

EC 1.8.3 With oxygen as acceptor

EC 1.8.3.1

Accepted name: sulfite oxidase
Reaction: sulfite + O₂ + H₂O = sulfate + H₂O₂
Systematic name: sulfite:oxygen oxidoreductase
Comments: A molybdohemoprotein.
References: [1890, 2349, 3774]

[EC 1.8.3.1 created 1961]

EC 1.8.3.2

Accepted name: thiol oxidase
Reaction: 2 R'C(R)SH + O₂ = R'C(R)S-S(R)CR' + H₂O₂
Other name(s): sulfhydryl oxidase

Systematic name: thiol:oxygen oxidoreductase
Comments: R may be =S or =O, or a variety of other groups. The enzyme is not specific for R'.
References: [141, 2765, 2905, 1555, 1711, 3450, 716, 990, 1296, 765, 3186]

[EC 1.8.3.2 created 1961, modified 2010, modified 2011]

EC 1.8.3.3

Accepted name: glutathione oxidase
Reaction: 2 glutathione + O₂ = glutathione disulfide + H₂O₂
Systematic name: glutathione:oxygen oxidoreductase
Comments: A flavoprotein (FAD). Also acts, more slowly, on L-cysteine and several other thiols.
References: [2096]

[EC 1.8.3.3 created 1989]

EC 1.8.3.4

Accepted name: methanethiol oxidase
Reaction: methanethiol + O₂ + H₂O = formaldehyde + hydrogen sulfide + H₂O₂
Other name(s): methylmercaptan oxidase; methyl mercaptan oxidase; (MM)-oxidase; MT-oxidase
Systematic name: methanethiol:oxygen oxidoreductase
References: [3747]

[EC 1.8.3.4 created 1990]

EC 1.8.3.5

Accepted name: prenylcysteine oxidase
Reaction: an *S*-prenyl-L-cysteine + O₂ + H₂O = a prenal + L-cysteine + H₂O₂
Other name(s): prenylcysteine lyase
Systematic name: *S*-prenyl-L-cysteine:oxygen oxidoreductase
Comments: A flavoprotein (FAD). Cleaves the thioether bond of *S*-prenyl-L-cysteines, such as *S*-farnesylcysteine and *S*-geranylgeranyl-L-cysteine. *N*-Acetyl-prenylcysteine and prenylcysteiny peptides are not substrates. May represent the final step in the degradation of prenylated proteins in mammalian tissues. Originally thought to be a simple lyase so it had been classified as EC 4.4.1.18.
References: [4443, 3934]

[EC 1.8.3.5 created 2000 as EC 4.4.1.18, transferred 2002 to EC 1.8.3.5]

EC 1.8.3.6

Accepted name: farnesylcysteine lyase
Reaction: *S*-(2*E*,6*E*)-farnesyl-L-cysteine + O₂ + H₂O = (2*E*,6*E*)-farnesal + L-cysteine + H₂O₂
Other name(s): FC lyase; FCLY
Systematic name: *S*-(2*E*,6*E*)-farnesyl-L-cysteine oxidase
Comments: A flavoprotein (FAD). In contrast to mammalian EC 1.8.3.5 (prenylcysteine oxidase) the farnesylcysteine lyase from *Arabidopsis* is specific for *S*-farnesyl-L-cysteine and shows no activity with *S*-geranylgeranyl-L-cysteine.
References: [1607, 698]

[EC 1.8.3.6 created 2011]

EC 1.8.3.7

Accepted name: formylglycine-generating enzyme
Reaction: a [sulfatase]-L-cysteine + O₂ + 2 a thiol = a [sulfatase]-3-oxo-L-alanine + hydrogen sulfide + a disulfide + H₂O

Other name(s): sulfatase-modifying factor 1; C α -formylglycine-generating enzyme 1; SUMF1 (gene name)
Systematic name: [sulfatase]-L-cysteine:oxygen oxidoreductase (3-oxo-L-alanine-forming)
Comments: Requires a copper cofactor and Ca²⁺. The enzyme, which is found in both prokaryotes and eukaryotes, catalyses a modification of a conserved L-cysteine residue in the active site of sulfatases, generating a unique 3-oxo-L-alanine residue that is essential for sulfatase activity. The exact nature of the thiol involved is still not clear - dithiothreitol and cysteamine are the most efficiently used thiols *in vitro*. Glutathione also acts *in vitro*, but it is not known whether it is used *in vivo*.
References: [822, 821, 3060, 3218, 507, 1540, 1978, 1977, 2516]

[EC 1.8.3.7 created 2014]

EC 1.8.4 With a disulfide as acceptor

EC 1.8.4.1

Accepted name: glutathione—homocystine transhydrogenase
Reaction: 2 glutathione + homocystine = glutathione disulfide + 2 homocystine
Systematic name: glutathione:homocystine oxidoreductase
Comments: The reactions catalysed by this enzyme and by others in this subclass may be similar to those catalysed by EC 2.5.1.18 glutathione transferase.
References: [3097]

[EC 1.8.4.1 created 1961]

EC 1.8.4.2

Accepted name: protein-disulfide reductase (glutathione)
Reaction: 2 glutathione + protein-disulfide = glutathione-disulfide + protein-dithiol
Other name(s): glutathione-insulin transhydrogenase; insulin reductase; reductase, protein disulfide (glutathione); protein disulfide transhydrogenase; glutathione-protein disulfide oxidoreductase; protein disulfide reductase (glutathione); GSH-insulin transhydrogenase; protein-disulfide interchange enzyme; protein-disulfide isomerase/oxidoreductase; thiol:protein-disulfide oxidoreductase; thiol-protein disulfide oxidoreductase
Systematic name: glutathione:protein-disulfide oxidoreductase
Comments: Reduces insulin and some other proteins.
References: [1847, 2009]

[EC 1.8.4.2 created 1965]

EC 1.8.4.3

Accepted name: glutathione—CoA-glutathione transhydrogenase
Reaction: CoA + glutathione disulfide = CoA-glutathione + glutathione
Other name(s): glutathione-coenzyme A glutathione disulfide transhydrogenase; glutathione-coenzyme A glutathione disulfide transhydrogenase; glutathione coenzyme A-glutathione transhydrogenase; glutathione:coenzyme A-glutathione transhydrogenase; coenzyme A:oxidized-glutathione oxidoreductase; coenzyme A:glutathione-disulfide oxidoreductase
Systematic name: CoA:glutathione-disulfide oxidoreductase
References: [541]

[EC 1.8.4.3 created 1972]

EC 1.8.4.4

Accepted name: glutathione—cystine transhydrogenase
Reaction: 2 glutathione + cystine = glutathione disulfide + 2 cysteine

Other name(s): GSH-cystine transhydrogenase; NADPH-dependent GSH-cystine transhydrogenase
Systematic name: glutathione:cystine oxidoreductase
References: [2681]

[EC 1.8.4.4 created 1972]

[1.8.4.5 *Transferred entry. methionine-S-oxide reductase. Now EC 1.8.4.13, L-methionine (S)-S-oxide reductase and EC 1.8.4.14, L-methionine (R)-S-oxide reductase*]

[EC 1.8.4.5 created 1984, deleted 2006]

[1.8.4.6 *Transferred entry. protein-methionine-S-oxide reductase. Proved to be due to EC 1.8.4.11, peptide-methionine (S)-S-oxide reductase*]

[EC 1.8.4.6 created 1984, deleted 2006]

EC 1.8.4.7

Accepted name: enzyme-thiol transhydrogenase (glutathione-disulfide)
Reaction: [xanthine dehydrogenase] + glutathione disulfide = [xanthine oxidase] + 2 glutathione
Other name(s): [xanthine-dehydrogenase]:oxidized-glutathione *S*-oxidoreductase; enzyme-thiol transhydrogenase (oxidized-glutathione); glutathione-dependent thiol:disulfide oxidoreductase; thiol:disulphide oxidoreductase
Systematic name: [xanthine-dehydrogenase]:glutathione-disulfide *S*-oxidoreductase
Comments: Converts EC 1.17.1.4 xanthine dehydrogenase into EC 1.17.3.2 xanthine oxidase in the presence of glutathione disulfide; also reduces the disulfide bond of ricin. Not inhibited by Cu²⁺ or thiol reagents.
References: [213]

[EC 1.8.4.7 created 1989, modified 2002]

EC 1.8.4.8

Accepted name: phosphoadenylyl-sulfate reductase (thioredoxin)
Reaction: adenosine 3',5'-bisphosphate + sulfite + thioredoxin disulfide = 3'-phosphoadenylyl sulfate + thioredoxin
Other name(s): PAPS reductase, thioredoxin-dependent; PAPS reductase; thioredoxin:adenosine 3'-phosphate 5'-phosphosulfate reductase; 3'-phosphoadenylylsulfate reductase; thioredoxin:3'-phosphoadenylylsulfate reductase; phosphoadenosine-phosphosulfate reductase; adenosine 3',5'-bisphosphate,sulfite:oxidized-thioredoxin oxidoreductase (3'-phosphoadenosine-5'-phosphosulfate-forming)
Systematic name: adenosine 3',5'-bisphosphate,sulfite:thioredoxin-disulfide oxidoreductase (3'-phosphoadenosine-5'-phosphosulfate-forming)
Comments: Specific for PAPS. The enzyme from *Escherichia coli* will use thioredoxins from other species.
References: [262]

[EC 1.8.4.8 created 1999 as EC 1.8.99.4, transferred 2000 to EC 1.8.4.8]

EC 1.8.4.9

Accepted name: adenylyl-sulfate reductase (glutathione)
Reaction: AMP + sulfite + glutathione disulfide = adenylyl sulfate + 2 glutathione
Other name(s): 5'-adenylylsulfate reductase (also used for EC 1.8.99.2); AMP,sulfite:oxidized-glutathione oxidoreductase (adenosine-5'-phosphosulfate-forming); plant-type 5'-adenylylsulfate reductase
Systematic name: AMP,sulfite:glutathione-disulfide oxidoreductase (adenosine-5'-phosphosulfate-forming)

Comments: This enzyme differs from EC 1.8.99.2, adenylyl-sulfate reductase, in using glutathione as the reductant. Glutathione can be replaced by γ -glutamylcysteine or dithiothreitol, but not by thioredoxin, glutaredoxin or mercaptoethanol. The enzyme from the mouse ear cress, *Arabidopsis thaliana*, contains a glutaredoxin-like domain. The enzyme is also found in other photosynthetic eukaryotes, e.g., the Madagascar periwinkle, *Catharanthus roseus* and the hollow green seaweed, *Enteromorpha intestinalis*.

References: [1325, 3446, 295]

[EC 1.8.4.9 created 2000, modified 2002]

EC 1.8.4.10

Accepted name: adenylyl-sulfate reductase (thioredoxin)
Reaction: AMP + sulfite + thioredoxin disulfide = 5'-adenylyl sulfate + thioredoxin
Other name(s): thioredoxin-dependent 5'-adenylylsulfate reductase
Systematic name: AMP,sulfite:thioredoxin-disulfide oxidoreductase (adenosine-5'-phosphosulfate-forming)
Comments: Uses adenylyl sulfate, not phosphoadenylyl sulfate, distinguishing this enzyme from EC 1.8.4.8, phosphoadenylyl-sulfate reductase (thioredoxin). Uses thioredoxin as electron donor, not glutathione or other donors, distinguishing it from EC 1.8.4.9 [adenylyl-sulfate reductase (glutathione)] and EC 1.8.99.2 (adenylyl-sulfate reductase).
References: [296, 5, 4222, 2772]

[EC 1.8.4.10 created 2003]

EC 1.8.4.11

Accepted name: peptide-methionine (S)-S-oxide reductase
Reaction: (1) peptide-L-methionine + thioredoxin disulfide + H₂O = peptide-L-methionine (S)-S-oxide + thioredoxin
(2) L-methionine + thioredoxin disulfide + H₂O = L-methionine (S)-S-oxide + thioredoxin
Other name(s): MsrA; methionine sulfoxide reductase (ambiguous); methionine sulphoxide reductase A; methionine S-oxide reductase (ambiguous); methionine S-oxide reductase (S-form oxidizing); methionine sulfoxide reductase A; peptide methionine sulfoxide reductase
Systematic name: peptide-L-methionine:thioredoxin-disulfide S-oxidoreductase [L-methionine (S)-S-oxide-forming]
Comments: The reaction occurs in the reverse direction to that shown above. The enzyme exhibits high specificity for the reduction of the S-form of L-methionine S-oxide, acting faster on the residue in a peptide than on the free amino acid [2878]. On the free amino acid, it can also reduce D-methionine (S)-S-oxide but more slowly [2878]. The enzyme plays a role in preventing oxidative-stress damage caused by reactive oxygen species by reducing the oxidized form of methionine back to methionine and thereby reactivating peptides that had been damaged. In some species, e.g. *Neisseria meningitidis*, both this enzyme and EC 1.8.4.12, peptide-methionine (R)-S-oxide reductase, are found within the same protein whereas, in other species, they are separate proteins [2639, 360]. The reaction proceeds via a sulfenic-acid intermediate [975, 412].
References: [2639, 3832, 3538, 360, 975, 4167, 1848, 4067, 2878, 412]

[EC 1.8.4.11 created 2006]

EC 1.8.4.12

Accepted name: peptide-methionine (R)-S-oxide reductase
Reaction: peptide-L-methionine + thioredoxin disulfide + H₂O = peptide-L-methionine (R)-S-oxide + thioredoxin
Other name(s): MsrB; methionine sulfoxide reductase (ambiguous); pMSR; methionine S-oxide reductase (ambiguous); selenoprotein R; methionine S-oxide reductase (R-form oxidizing); methionine sulfoxide reductase B; SelR; SelX; PilB; pRMsr
Systematic name: peptide-methionine:thioredoxin-disulfide S-oxidoreductase [methionine (R)-S-oxide-forming]

- Comments:** The reaction occurs in the reverse direction to that shown above. The enzyme exhibits high specificity for reduction of the *R*-form of methionine *S*-oxide, with higher activity being observed with L-methionine *S*-oxide than with D-methionine *S*-oxide [2878]. While both free and protein-bound methionine (*R*)-*S*-oxide act as substrates, the activity with the peptide-bound form is far greater [3280]. The enzyme plays a role in preventing oxidative-stress damage caused by reactive oxygen species by reducing the oxidized form of methionine back to methionine and thereby reactivating peptides that had been damaged. In some species, e.g. *Neisseria meningitidis*, both this enzyme and EC 1.8.4.11, peptide-methionine (*S*)-*S*-oxide reductase, are found within the same protein whereas in other species, they are separate proteins [3538, 975]. The reaction proceeds via a sulfenic-acid intermediate [975, 3280]. For MsrB2 and MsrB3, thioredoxin is a poor reducing agent but thionein works well []. The enzyme from some species contains selenocysteine and Zn²⁺.
- References:** [2639, 3832, 3538, 360, 975, 4167, 1848, 4067, 2878, 3280]

[EC 1.8.4.12 created 2006]

EC 1.8.4.13

- Accepted name:** L-methionine (*S*)-*S*-oxide reductase
- Reaction:** L-methionine + thioredoxin disulfide + H₂O = L-methionine (*S*)-*S*-oxide + thioredoxin
- Other name(s):** fSMsr; methyl sulfoxide reductase I and II; acetylmethionine sulfoxide reductase; methionine sulfoxide reductase; L-methionine:oxidized-thioredoxin *S*-oxidoreductase; methionine-*S*-oxide reductase; free-methionine (*S*)-*S*-oxide reductase
- Systematic name:** L-methionine:thioredoxin-disulfide *S*-oxidoreductase
- Comments:** Requires NADPH [933]. The reaction occurs in the opposite direction to that given above. Dithiothreitol can replace reduced thioredoxin. L-Methionine (*R*)-*S*-oxide is not a substrate [see EC 1.8.4.14, L-methionine (*R*)-*S*-oxide reductase].
- References:** [308, 933, 934, 4167]

[EC 1.8.4.13 created 1984 as EC 1.8.4.5, part transferred 2006 to EC 1.8.4.13]

EC 1.8.4.14

- Accepted name:** L-methionine (*R*)-*S*-oxide reductase
- Reaction:** L-methionine + thioredoxin disulfide + H₂O = L-methionine (*R*)-*S*-oxide + thioredoxin
- Other name(s):** fRMsr; FRMsr; free met-R-(o) reductase; free-methionine (*R*)-*S*-oxide reductase
- Systematic name:** L-methionine:thioredoxin-disulfide *S*-oxidoreductase [L-methionine (*R*)-*S*-oxide-forming]
- Comments:** Requires NADPH. Unlike EC 1.8.4.12, peptide-methionine (*R*)-*S*-oxide reductase, this enzyme cannot use peptide-bound methionine (*R*)-*S*-oxide as a substrate [969]. Differs from EC 1.8.4.13, L-methionine (*S*)-*S*-oxide in that L-methionine (*S*)-*S*-oxide is not a substrate.
- References:** [969]

[EC 1.8.4.14 created 1984 as EC 1.8.4.5, part transferred 2006 to EC 1.8.4.14]

EC 1.8.5 With a quinone or similar compound as acceptor

EC 1.8.5.1

- Accepted name:** glutathione dehydrogenase (ascorbate)
- Reaction:** 2 glutathione + dehydroascorbate = glutathione disulfide + ascorbate
- Other name(s):** dehydroascorbic reductase; dehydroascorbic acid reductase; glutathione dehydroascorbate reductase; DHA reductase ; dehydroascorbate reductase; GDOR; glutathione:dehydroascorbic acid oxidoreductase
- Systematic name:** glutathione:dehydroascorbate oxidoreductase
- References:** [694]

[EC 1.8.5.1 created 1961]

EC 1.8.5.2

- Accepted name:** thiosulfate dehydrogenase (quinone)
Reaction: 2 thiosulfate + 6-decylubiquinone = tetrathionate + 6-decylubiquinol
Other name(s): thiosulfate:quinone oxidoreductase; thiosulphate:quinone oxidoreductase; thiosulfate oxidoreductase, tetrathionate-forming; TQO
Systematic name: thiosulfate:6-decylubiquinone oxidoreductase
Comments: The reaction can also proceed with ferricyanide as the electron acceptor, but more slowly. Unlike EC 1.8.2.2, thiosulfate dehydrogenase, this enzyme cannot utilize cytochrome *c* as an acceptor.
References: [2651]

[EC 1.8.5.2 created 2004]

EC 1.8.5.3

- Accepted name:** dimethylsulfoxide reductase
Reaction: dimethylsulfide + menaquinone + H₂O = dimethylsulfoxide + menaquinol
Other name(s): DMSO reductase
Systematic name: dimethyl sulfide:menaquinone oxidoreductase
Comments: Contains molybdopterin and [4Fe-4S] clusters. Also reduces pyridine *N*-oxide and trimethylamine *N*-oxide, with lower activity, to the corresponding amines.
References: [3531, 746, 2532, 3239]

[EC 1.8.5.3 created 2011]

EC 1.8.5.4

- Accepted name:** bacterial sulfide:quinone reductase
Reaction: $n \text{ HS}^- + n \text{ quinone} = \text{polysulfide} + n \text{ quinol}$
Other name(s): *sqr* (gene name); sulfide:quinone reductase (ambiguous)
Systematic name: sulfide:quinone oxidoreductase
Comments: Contains FAD. Ubiquinone, plastoquinone or menaquinone can act as acceptor in different species. This enzyme catalyses the formation of sulfur globules. It repeats the catalytic cycle without releasing the product, producing a polysulfide of up to 10 sulfur atoms. The reaction stops when the maximum length of the polysulfide that can be accommodated in the sulfide oxidation pocket is achieved. The enzyme also plays an important role in anoxygenic bacterial photosynthesis. *cf.* EC 1.8.5.8, eukaryotic sulfide quinone oxidoreductase.
References: [120, 3160, 2826, 405, 586, 2393]

[EC 1.8.5.4 created 2011, modified 2017]

EC 1.8.5.5

- Accepted name:** thiosulfate reductase (quinone)
Reaction: sulfite + hydrogen sulfide + a quinone = thiosulfate + a quinol
Other name(s): *phsABC* (gene names)
Systematic name: sulfite,hydrogen sulfide:quinone oxidoreductase
Comments: The enzyme, characterized from the bacterium *Salmonella enterica*, is similar to EC 1.17.5.3, formate dehydrogenase-N. It contains a molybdopterin-guanine dinucleotide, five [4Fe-4S] clusters and two heme *b* groups. The reaction occurs *in vivo* in the direction of thiosulfate disproportionation, which is highly endergonic. It is driven by the proton motive force that occurs across the cytoplasmic membrane.
References: [2106, 628, 50, 1464, 3658]

[EC 1.8.5.5 created 2016, modified 2017]

EC 1.8.5.6

Accepted name: sulfite dehydrogenase (quinone)
Reaction: sulfite + a quinone + H₂O = sulfate + a quinol
Other name(s): *soeABC* (gene name)
Systematic name: sulfite:quinone oxidoreductase
Comments: This membrane-bound bacterial enzyme catalyses the direct oxidation of sulfite to sulfate in the cytoplasm. The enzyme, characterized from the bacteria *Ruegeria pomeroyi* and *Allochromatium vinosum*, is a complex that consists of a membrane anchor (SoeC) and two cytoplasmic subunits: an iron-sulfur protein (SoeB) and a molybdoprotein that contains a [4Fe-4S] iron-sulfur cluster (SoeA). *cf.* EC 1.8.2.1, sulfite dehydrogenase (cytochrome).
References: [718]

[EC 1.8.5.6 created 2016]

EC 1.8.5.7

Accepted name: glutathionyl-hydroquinone reductase
Reaction: glutathione + 2-(glutathione-*S*-yl)-hydroquinone = glutathione disulfide + hydroquinone
Other name(s): *pcpF* (gene name); *yqjG* (gene name)
Systematic name: 2-(glutathione-*S*-yl)-hydroquinone:glutathione oxidoreductase
Comments: This type of enzymes, which are found in bacteria, halobacteria, fungi, and plants, catalyse the glutathione-dependent reduction of glutathionyl-hydroquinones. The enzyme from the bacterium *Sphingobium chlorophenicum* can act on halogenated substrates such as 2,6-dichloro-3-(glutathione-*S*-yl)-hydroquinone and 2,3,5-trichloro-6-(glutathione-*S*-yl)-hydroquinone. Substrates for these enzymes are often formed spontaneously by interaction of benzoquinones with glutathione.
References: [1597, 4290, 2116, 1270]

[EC 1.8.5.7 created 2017]

EC 1.8.5.8

Accepted name: eukaryotic sulfide quinone oxidoreductase
Reaction: hydrogen sulfide + glutathione + a quinone = *S*-sulfanylglutathione + a quinol
Other name(s): SQR; SQOR; SQRDL (gene name)
Systematic name: sulfide:glutathione,quinone oxidoreductase
Comments: Contains FAD. This eukaryotic enzyme, located at the inner mitochondrial membrane, catalyses the first step in the metabolism of sulfide. While both sulfite and glutathione have been shown to act as sulfane sulfur acceptors *in vitro*, it is thought that the latter acts as the main acceptor *in vivo*. The electrons are transferred via FAD and quinones to the electron transfer chain. Unlike the bacterial homolog (EC 1.8.5.4, bacterial sulfide:quinone reductase), which repeats the catalytic cycle without releasing the product, producing a polysulfide, the eukaryotic enzyme transfers the persulfide to an acceptor at the end of each catalytic cycle.
References: [4158, 1500, 1704, 2243]

[EC 1.8.5.8 created 2017]

EC 1.8.6 With a nitrogenous group as acceptor (deleted sub-subclass)

[1.8.6.1 Deleted entry. Nitrate-ester reductase. Now included with EC 2.5.1.18 glutathione transferase]

[EC 1.8.6.1 created 1961, deleted 1976]

EC 1.8.7 With an iron-sulfur protein as acceptor

EC 1.8.7.1

Accepted name: assimilatory sulfite reductase (ferredoxin)
Reaction: hydrogen sulfide + 6 oxidized ferredoxin [iron-sulfur] cluster + 3 H₂O = sulfite + 6 reduced ferredoxin [iron-sulfur] cluster + 6 H⁺
Other name(s): ferredoxin-sulfite reductase; SIR (gene name); sulfite reductase (ferredoxin)
Systematic name: hydrogen-sulfide:ferredoxin oxidoreductase
Comments: An iron protein. The enzyme participates in sulfate assimilation. While it is usually found in cyanobacteria, plants and algae, it has also been reported in bacteria [2772]. Different from EC 1.8.99.5, dissimilatory sulfite reductase, which is involved in prokaryotic sulfur-based energy metabolism. *cf.* EC 1.8.1.2, assimilatory sulfite reductase (NADPH).
References: [3372, 1210, 354, 2772]

[EC 1.8.7.1 created 1972, modified 2015]

EC 1.8.7.2

Accepted name: ferredoxin:thioredoxin reductase
Reaction: 2 reduced ferredoxin + thioredoxin disulfide = 2 oxidized ferredoxin + thioredoxin + 2 H⁺
Systematic name: ferredoxin:thioredoxin disulfide oxidoreductase
Comments: The enzyme contains a [4Fe-4S] cluster and internal disulfide. It forms a mixed disulfide with thioredoxin on one side, and docks ferredoxin on the other side, enabling two one-electron transfers. The reduced thioredoxins generated by the enzyme activate the Calvin cycle enzymes EC 3.1.3.11 (fructose-bisphosphatase), EC 3.1.3.37 (sedoheptulose-bisphosphatase) and EC 2.7.1.19 (phosphoribulokinase) as well as other chloroplast enzymes by disulfide reduction.
References: [437, 615, 3621]

[EC 1.8.7.2 created 2010]

EC 1.8.7.3

Accepted name: ferredoxin:CoB-CoM heterodisulfide reductase
Reaction: 2 oxidized ferredoxin [iron-sulfur] cluster + CoB + CoM = 2 reduced ferredoxin [iron-sulfur] cluster + CoM-S-S-CoB + 2 H⁺
Other name(s): *hdrABC* (gene names); *hdrA1B1C1* (gene names); *hdrA2B2C2* (gene names)
Systematic name: CoB,CoM:ferredoxin oxidoreductase
Comments: HdrABC is an enzyme complex that is found in most methanogens and catalyses the reduction of the CoB-CoM heterodisulfide back to CoB and CoM. HdrA contains a FAD cofactor that acts as the entry point for electrons, which are transferred via HdrC to the HdrB catalytic subunit. One form of the enzyme from *Methanosarcina acetivorans* (HdrA2B2C2) can also catalyse EC 1.8.98.4, coenzyme F₄₂₀:CoB-CoM heterodisulfide,ferredoxin reductase. *cf.* EC 1.8.98.5, H₂:CoB-CoM heterodisulfide,ferredoxin reductase, EC 1.8.98.6, formate:CoB-CoM heterodisulfide,ferredoxin reductase, and EC 1.8.98.1, dihydromethanophenazine:CoB-CoM heterodisulfide reductase.
References: [434, 4332]

[EC 1.8.7.3 created 2017]

EC 1.8.98 With other, known, physiological acceptors

EC 1.8.98.1

Accepted name: dihydromethanophenazine:CoB-CoM heterodisulfide reductase
Reaction: CoB + CoM + methanophenazine = CoM-S-S-CoB + dihydromethanophenazine
Other name(s): *hdrDE* (gene names); CoB—CoM heterodisulfide reductase (ambiguous); heterodisulfide reductase (ambiguous); coenzyme B:coenzyme M:methanophenazine oxidoreductase
Systematic name: CoB:CoM:methanophenazine oxidoreductase

Comments: This enzyme, found in methanogenic archaea that belong to the *Methanosarcinales* order, regenerates CoM and CoB after the action of EC 2.8.4.1, coenzyme-B sulfoethylthiotransferase. It is a membrane-bound enzyme that contains (per heterodimeric unit) two distinct *b*-type hemes and two [4Fe-4S] clusters. *cf.* EC 1.8.7.3, ferredoxin:CoB-CoM heterodisulfide reductase, EC 1.8.98.5, H₂:CoB-CoM heterodisulfide,ferredoxin reductase, EC 1.8.98.6, formate:CoB-CoM heterodisulfide,ferredoxin reductase and EC 1.8.98.4, coenzyme F₄₂₀:CoB-CoM heterodisulfide,ferredoxin reductase.

References: [1451, 4, 3532, 2664]

[EC 1.8.98.1 created 2003, modified 2017]

EC 1.8.98.2

Accepted name: sulfiredoxin

Reaction: peroxiredoxin-(*S*-hydroxy-*S*-oxocysteine) + ATP + 2 R-SH = peroxiredoxin-(*S*-hydroxycysteine) + ADP + phosphate + R-S-S-R

Other name(s): Srx1; sulphiredoxin; peroxiredoxin-(*S*-hydroxy-*S*-oxocysteine) reductase

Systematic name: peroxiredoxin-(*S*-hydroxy-*S*-oxocysteine):thiol oxidoreductase [ATP-hydrolysing; peroxiredoxin-(*S*-hydroxycysteine)-forming]

Comments: In the course of the reaction of EC 1.11.1.15, peroxiredoxin, its cysteine residue is alternately oxidized to the sulfenic acid, *S*-hydroxycysteine, and reduced back to cysteine. Occasionally the *S*-hydroxycysteine residue is further oxidized to the sulfinic acid *S*-hydroxy-*S*-oxocysteine, thereby inactivating the enzyme. The reductase provides a mechanism for regenerating the active form of peroxiredoxin, i.e. the peroxiredoxin-(*S*-hydroxycysteine) form. Apparently the reductase first catalyses the phosphorylation of the -S(O)-OH group by ATP to give -S(O)-O-P, which is attached to the peroxiredoxin by a cysteine residue, forming an -S(O)-S- link between the two enzymes. Attack by a thiol splits this bond, leaving the peroxiredoxin as the sulfenic acid and the reductase as the thiol.

References: [302, 543, 4247]

[EC 1.8.98.2 created 2005]

EC 1.8.98.3

Accepted name: sulfite reductase (coenzyme F₄₂₀)

Reaction: hydrogen sulfide + 3 oxidized coenzyme F₄₂₀ + 3 H₂O = sulfite + 3 reduced coenzyme F₄₂₀

Other name(s): coenzyme F₄₂₀-dependent sulfite reductase; Fsr

Systematic name: hydrogen sulfide:coenzyme F₄₂₀ oxidoreductase

Comments: The enzyme, isolated from the archaeon *Methanocaldococcus jannaschii*, is involved in sulfite detoxification and assimilation.

References: [1754, 1755]

[EC 1.8.98.3 created 2014]

EC 1.8.98.4

Accepted name: coenzyme F₄₂₀:CoB-CoM heterodisulfide,ferredoxin reductase

Reaction: 2 oxidized coenzyme F₄₂₀ + 2 reduced ferredoxin [iron-sulfur] cluster + CoB + CoM + 2 H⁺ = 2 reduced coenzyme F₄₂₀ + 2 oxidized ferredoxin [iron-sulfur] cluster + CoM-S-S-CoB

Other name(s): *hdrA2B2C2* (gene names)

Systematic name: CoB,CoM,ferredoxin:coenzyme F₄₂₀ oxidoreductase

Comments: The enzyme, characterized from the archaeon *Methanosarcina acetivorans*, catalyses the reduction of CoB-CoM heterodisulfide back to CoB and CoM. The enzyme consists of three components, HdrA, HdrB and HdrC, all of which contain [4Fe-4S] clusters. Electrons enter at HdrA, which also contains FAD, and are transferred via HdrC to the catalytic component, HdrB. During methanogenesis from acetate the enzyme catalyses the activity of EC 1.8.7.3, ferredoxin:CoB-CoM heterodisulfide reductase. However, it can also use electron bifurcation to direct electron pairs from reduced coenzyme F₄₂₀ towards the reduction of both ferredoxin and CoB-CoM heterodisulfide. This activity is proposed to take place during Fe(III)-dependent anaerobic methane oxidation. *cf.* EC 1.8.98.5, H₂:CoB-CoM heterodisulfide,ferredoxin reductase, EC 1.8.98.6, formate:CoB-CoM heterodisulfide,ferredoxin reductase, and EC 1.8.98.1, dihydromethanophenazine:CoB-CoM heterodisulfide reductase.

References: [4332]

[EC 1.8.98.4 created 2017]

EC 1.8.98.5

Accepted name: H₂:CoB-CoM heterodisulfide,ferredoxin reductase

Reaction: 2 reduced ferredoxin [iron-sulfur] cluster + CoB + CoM + 2 H⁺ = 2 H₂ + 2 oxidized ferredoxin [iron-sulfur] cluster + CoM-S-S-CoB

Systematic name: CoB,CoM,ferredoxin:H₂ oxidoreductase

Comments: This enzyme complex is found in H₂-oxidizing CO₂-reducing methanogenic archaea such as *Methanothermobacter thermautotrophicus*. It consists of a cytoplasmic complex of HdrABC reductase and MvhAGD hydrogenase. Electron pairs donated by the hydrogenase are transferred via its δ subunit to the HdrA subunit of the reductase, where they are bifurcated, reducing both ferredoxin and CoB-CoM heterodisulfide. The reductase can also form a similar complex with formate dehydrogenase, see EC 1.8.98.6, formate:CoB-CoM heterodisulfide,ferredoxin reductase. *cf.* EC 1.8.7.3, ferredoxin:CoB-CoM heterodisulfide reductase, EC 1.8.98.4, coenzyme F₄₂₀:CoB-CoM heterodisulfide,ferredoxin reductase, and EC 1.8.98.1, dihydromethanophenazine:CoB-CoM heterodisulfide reductase.

References: [3154, 1452, 3448, 3660, 1826, 670]

[EC 1.8.98.5 created 2017]

EC 1.8.98.6

Accepted name: formate:CoB-CoM heterodisulfide,ferredoxin reductase

Reaction: 2 CO₂ + 2 reduced ferredoxin [iron-sulfur] cluster + CoB + CoM + 2 H⁺ = 2 formate + 2 oxidized ferredoxin [iron-sulfur] cluster + CoM-S-S-CoB

Systematic name: coenzyme B,coenzyme M,ferredoxin:formate oxidoreductase

Comments: The enzyme is found in formate-oxidizing CO₂-reducing methanogenic archaea such as *Methanococcus maripaludis*. It consists of a cytoplasmic complex of HdrABC reductase and formate dehydrogenase. Electron pairs donated by formate dehydrogenase are transferred to the HdrA subunit of the reductase, where they are bifurcated, reducing both ferredoxin and CoB-CoM heterodisulfide. *cf.* EC 1.8.7.3, ferredoxin:CoB-CoM heterodisulfide reductase, EC 1.8.98.4, coenzyme F₄₂₀:CoB-CoM heterodisulfide,ferredoxin reductase, EC 1.8.98.5, H₂:CoB-CoM heterodisulfide,ferredoxin reductase, and EC 1.8.98.1, dihydromethanophenazine:CoB-CoM heterodisulfide reductase.

References: [671, 670]

[EC 1.8.98.6 created 2017]

EC 1.8.99 With unknown physiological acceptors

[1.8.99.1 Deleted entry. sulfite reductase. Now covered by EC 1.8.1.2, assimilatory sulfite reductase (NADPH) and EC 1.8.7.1, assimilatory sulfite reductase (ferredoxin).]

[EC 1.8.99.1 created 1972, deleted 2015]

EC 1.8.99.2

- Accepted name:** adenylyl-sulfate reductase
Reaction: AMP + sulfite + acceptor = adenylyl sulfate + reduced acceptor
Other name(s): adenosine phosphosulfate reductase; adenosine 5'-phosphosulfate reductase; APS-reductase; APS reductase; AMP, sulfite:(acceptor) oxidoreductase (adenosine-5'-phosphosulfate-forming)
Systematic name: AMP,sulfite:acceptor oxidoreductase (adenosine-5'-phosphosulfate-forming)
Comments: An iron flavoprotein (FAD). Methylviologen can act as acceptor.
References: [2520]

[EC 1.8.99.2 created 1972]

[1.8.99.3 Deleted entry. *hydrogensulfite reductase, now known to be an in vitro artifact of EC 1.8.99.5, dissimilatory sulfite reductase*]

[EC 1.8.99.3 created 1986, deleted 2016]

[1.8.99.4 Transferred entry. *phosphoadenosine-phosphosulfate reductase. Now EC 1.8.4.8, phosphoadenylyl-sulfate reductase (thioredoxin)*]

[EC 1.8.99.4 created 1999, deleted 2000]

EC 1.8.99.5

- Accepted name:** dissimilatory sulfite reductase
Reaction: (1) hydrogen sulfide + a [DsrC protein]-disulfide + 2 acceptor + 3 H₂O = sulfite + a [DsrC protein]-dithiol + 2 reduced acceptor + 2 H⁺ (overall reaction)
(1a) hydrogen sulfide + a [DsrC protein]-disulfide = a [DsrC protein]-S-sulfanyl-L-cysteine
(1b) a [DsrC protein]-S-sulfanyl-L-cysteine + 2 acceptor + 3 H₂O = sulfite + a [DsrC protein]-dithiol + 2 reduced acceptor + 2 H⁺
(2) a [DsrC protein]-S-sulfanyl-L-cysteine + 3 acceptor + 3 H₂O = sulfite + a [DsrC protein]-disulfide + 3 reduced acceptor + 2 H⁺ (overall reaction)
(2a) a [DsrC protein]-S-sulfanyl-L-cysteine + 3 acceptor + 3 H₂O = a [DsrC]-S-sulfo-L-cysteine + 3 reduced acceptor + H⁺
(2b) a [DsrC]-S-sulfo-L-cysteine = sulfite + a [DsrC protein]-disulfide
Other name(s): siroheme sulfite reductase; hydrogen-sulfide:(acceptor) oxidoreductase (ambiguous); DsrAB
Systematic name: hydrogen-sulfide:[DsrC sulfur-carrier protein],acceptor oxidoreductase
Comments: Contain siroheme. The enzyme is essential in prokaryotic sulfur-based energy metabolism, including sulfate/sulfite reducing organisms, sulfur-oxidizing bacteria, and organosulfonate reducers. In sulfur reducers it catalyses the reduction of sulfite to sulfide (reaction 1 in the right to left direction), while in sulfur oxidizers it catalyses the opposite reaction (reaction 2 in the left to right direction) [3354]. The reaction involves the small protein DsrC, which is present in all the organisms that contain dissimilatory sulfite reductase. During the process an intramolecular disulfide bond is formed between two L-cysteine residues of DsrC. This disulfide can be reduced by a number of proteins including DsrK and TcmB [4029]. This enzyme is different from EC 1.8.1.2, assimilatory sulfite reductase (NADPH), and EC 1.8.7.1, assimilatory sulfite reductase (ferredoxin), which are involved in sulfate assimilation.
References: [3354, 3435, 3043, 2873, 4029]

[EC 1.8.99.5 created 2015]

EC 1.9 Acting on a heme group of donors

This subclass contains the cytochrome oxidases and nitrate reductases. Sub-subclasses are based on the acceptor: oxygen (EC 1.9.3), a nitrogenous group (EC 1.9.6), or some other acceptor (EC 1.9.99).

EC 1.9.3 With oxygen as acceptor

EC 1.9.3.1

- Accepted name:** cytochrome-*c* oxidase
Reaction: $4 \text{ ferrocyanochrome } c + \text{O}_2 + 4 \text{ H}^+ = 4 \text{ ferricyanochrome } c + 2 \text{ H}_2\text{O}$
Other name(s): cytochrome oxidase; cytochrome *a*₃; cytochrome aa₃; Warburg's respiratory enzyme; indophenol oxidase; indophenolase; complex IV (mitochondrial electron transport); ferrocyanochrome *c* oxidase; NADH cytochrome *c* oxidase
Systematic name: ferrocyanochrome-*c*:oxygen oxidoreductase
Comments: A cytochrome of the *a* type containing copper. The reduction of O₂ to water is accompanied by the extrusion of four protons from the intramitochondrial compartment. Several bacteria appear to contain analogous oxidases.
References: [1870, 1871, 4080, 4367, 4368]

[EC 1.9.3.1 created 1961, modified 2000]

[1.9.3.2 *Transferred entry. Pseudomonas cytochrome oxidase. Now included with EC 1.7.2.1, nitrite reductase (NO-forming)*]

[EC 1.9.3.2 created 1965, deleted 2002]

EC 1.9.6 With a nitrogenous group as acceptor

EC 1.9.6.1

- Accepted name:** nitrate reductase (cytochrome)
Reaction: $2 \text{ ferrocyanochrome } + 2 \text{ H}^+ + \text{nitrate} = 2 \text{ ferricyanochrome } + \text{nitrite}$
Other name(s): respiratory nitrate reductase; benzyl viologen-nitrate reductase
Systematic name: ferrocyanochrome:nitrate oxidoreductase
References: [3275]

[EC 1.9.6.1 created 1961]

EC 1.9.98 With other, known, physiological acceptors

EC 1.9.98.1

- Accepted name:** iron—cytochrome-*c* reductase
Reaction: $\text{ferrocyanochrome } c + \text{Fe}^{3+} = \text{ferricyanochrome } c + \text{Fe}^{2+}$
Other name(s): iron-cytochrome *c* reductase
Systematic name: ferrocyanochrome-*c*:Fe³⁺ oxidoreductase
Comments: An iron protein.
References: [4353]

[EC 1.9.98.1 created 1972 as EC 1.9.99.1, transferred 2014 to EC 1.9.98.1]

EC 1.9.99 With unknown physiological acceptors

[1.9.99.1 *Transferred entry. iron—cytochrome-*c* reductase. Now EC 1.9.98.1, iron—cytochrome-*c* reductase*]

[EC 1.9.99.1 created 1972, deleted 2014]

EC 1.10 Acting on diphenols and related substances as donors

This subclass contains enzymes that catalyse the oxidation of diphenols or ascorbate. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.10.1), a cytochrome (EC 1.10.2), oxygen (EC 1.10.3), or some other acceptor (EC 1.10.99). Some enzymes that catalyse the oxidation of phenols are oxygenases (EC 1.14.18).

EC 1.10.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.10.1.1

Accepted name: *trans*-acenaphthene-1,2-diol dehydrogenase
Reaction: (±)-*trans*-acenaphthene-1,2-diol + 2 NADP⁺ = acenaphthenequinone + 2 NADPH + 2 H⁺
Other name(s): *trans*-1,2-acenaphthenediol dehydrogenase
Systematic name: (±)-*trans*-acenaphthene-1,2-diol:NADP⁺ oxidoreductase
Comments: Some preparations also utilize NAD⁺.
References: [1559]

[EC 1.10.1.1 created 1976]

EC 1.10.2 With a cytochrome as acceptor

EC 1.10.2.1

Accepted name: L-ascorbate—cytochrome-*b*₅ reductase
Reaction: L-ascorbate + ferricytochrome *b*₅ = monodehydroascorbate + ferrocyclochrome *b*₅ + H⁺
Other name(s): ascorbate-cytochrome *b*₅ reductase
Systematic name: L-ascorbate:ferricytochrome-*b*₅ oxidoreductase
References: [971]

[EC 1.10.2.1 created 1972, modified 2000]

[1.10.2.2 *Transferred entry. quinol—cytochrome-c reductase. Now EC 7.1.1.8, quinol—cytochrome-c reductase*]

[EC 1.10.2.2 created 1978, modified 2013, deleted 2018]

EC 1.10.3 With oxygen as acceptor

EC 1.10.3.1

Accepted name: catechol oxidase
Reaction: 2 catechol + O₂ = 2 1,2-benzoquinone + 2 H₂O
Other name(s): diphenol oxidase; *o*-diphenolase; polyphenol oxidase; pyrocatechol oxidase; dopa oxidase; catecholase; *o*-diphenol:oxygen oxidoreductase; *o*-diphenol oxidoreductase
Systematic name: 1,2-benzenediol:oxygen oxidoreductase
Comments: A type 3 copper protein that catalyses exclusively the oxidation of catechol (i.e., *o*-diphenol) to the corresponding *o*-quinone. The enzyme also acts on a variety of substituted catechols. It is different from tyrosinase, EC 1.14.18.1, which can catalyse both the monooxygenation of monophenols and the oxidation of catechols.
References: [417, 757, 1279, 2429, 2472, 2961, 3035, 3200, 1183]

[EC 1.10.3.1 created 1961, deleted 1972, reinstated 1978]

EC 1.10.3.2

Accepted name: laccase
Reaction: $4 \text{ benzenediol} + \text{O}_2 = 4 \text{ benzosemiquinone} + 2 \text{ H}_2\text{O}$
Other name(s): urishiol oxidase; urushiol oxidase; *p*-diphenol oxidase
Systematic name: benzenediol:oxygen oxidoreductase
Comments: A group of multi-copper proteins of low specificity acting on both *o*- and *p*-quinols, and often acting also on aminophenols and phenylenediamine. The semiquinone may react further either enzymically or non-enzymically.
References: [757, 1874, 2382, 2472, 2704, 2705, 2975, 3163]

[EC 1.10.3.2 created 1961, deleted 1972, reinstated 1978]

EC 1.10.3.3

Accepted name: L-ascorbate oxidase
Reaction: $4 \text{ L-ascorbate} + \text{O}_2 = 4 \text{ monodehydroascorbate} + 2 \text{ H}_2\text{O}$
Other name(s): ascorbase; ascorbic acid oxidase; ascorbate oxidase; ascorbic oxidase; ascorbate dehydrogenase; L-ascorbic acid oxidase; AAO; L-ascorbate:O₂ oxidoreductase; AA oxidase
Systematic name: L-ascorbate:oxygen oxidoreductase
Comments: A multicopper protein.
References: [4327, 3623, 2511]

[EC 1.10.3.3 created 1961, modified 2011]

EC 1.10.3.4

Accepted name: *o*-aminophenol oxidase
Reaction: $4 \text{ 2-aminophenol} + 3 \text{ O}_2 = 2 \text{ 2-aminophenoxazin-3-one} + 6 \text{ H}_2\text{O}$
Other name(s): isophenoxazine synthase; *o*-aminophenol:O₂ oxidoreductase; 2-aminophenol:O₂ oxidoreductase
Systematic name: 2-aminophenol:oxygen oxidoreductase
Comments: A flavoprotein which catalyses a 6-electron oxidation. The enzyme from the plant *Tecoma stans* requires Mn²⁺ and FAD [2695] whereas the fungus *Pycnoporus coccineus* requires Mn²⁺ and riboflavin 5'-phosphate [2697], the bacteria *Streptomyces antibioticus* requires Cu²⁺ [206] and the plant *Bauhinia monandra* does not require any co-factors [3126].
References: [2695, 2697, 3126, 206]

[EC 1.10.3.4 created 1972, modified 2006]

EC 1.10.3.5

Accepted name: 3-hydroxyanthranilate oxidase
Reaction: $3\text{-hydroxyanthranilate} + \text{O}_2 = 6\text{-imino-5-oxocyclohexa-1,3-dienecarboxylate} + \text{H}_2\text{O}_2$
Other name(s): 3-hydroxyanthranilic acid oxidase
Systematic name: 3-hydroxyanthranilate:oxygen oxidoreductase
References: [2616]

[EC 1.10.3.5 created 1972]

EC 1.10.3.6

Accepted name: rifamycin-B oxidase
Reaction: $\text{rifamycin B} + \text{O}_2 = \text{rifamycin O} + \text{H}_2\text{O}_2$
Other name(s): rifamycin B oxidase
Systematic name: rifamycin-B:oxygen oxidoreductase
Comments: Acts also on benzene-1,4-diol and, more slowly, on some other *p*-quinols. Not identical with EC 1.10.3.1 (catechol oxidase), EC 1.10.3.2 (laccase), EC 1.10.3.4 (*o*-aminophenol oxidase) or EC 1.10.3.5 (3-hydroxyanthranilate oxidase).
References: [1364]

[EC 1.10.3.6 created 1986]

[1.10.3.7 *Transferred entry. sulochrin oxidase [(+)-bisdechlorogeodin-forming]. Now EC 1.21.3.4, sulochrin oxidase [(+)-bisdechlorogeodin-forming]]*

[EC 1.10.3.7 created 1986, deleted 2002]

[1.10.3.8 *Transferred entry. sulochrin oxidase [(+)-bisdechlorogeodin-forming]. Now EC 1.21.3.5, sulochrin oxidase [(-)-bisdechlorogeodin-forming]]*

[EC 1.10.3.8 created 1986, deleted 2002]

EC 1.10.3.9

Accepted name: photosystem II
Reaction: $2 \text{H}_2\text{O} + 2 \text{ plastoquinone} + 4 h\nu = \text{O}_2 + 2 \text{ plastoquinol}$
Systematic name: H₂O:plastoquinone reductase (light-dependent)
Comments: Contains chlorophyll *a*, β -carotene, pheophytin, plastoquinone, a Mn₄Ca cluster, heme and non-heme iron. Four successive photoreactions, resulting in a storage of four positive charges, are required to oxidize two water molecules to one oxygen molecule.
References: [1971, 1322]

[EC 1.10.3.9 created 2011]

[1.10.3.10 *Transferred entry. ubiquinol oxidase (H⁺-transporting). Now EC 7.1.1.3, ubiquinol oxidase (H⁺-transporting)]*

[EC 1.10.3.10 created 2011, modified 2014, deleted 2018]

EC 1.10.3.11

Accepted name: ubiquinol oxidase (non-electrogenic)
Reaction: $2 \text{ ubiquinol} + \text{O}_2 = 2 \text{ ubiquinone} + 2 \text{ H}_2\text{O}$
Other name(s): plant alternative oxidase; cyanide-insensitive oxidase; AOX (gene name); ubiquinol oxidase; ubiquinol:O₂ oxidoreductase (non-electrogenic)
Systematic name: ubiquinol:oxygen oxidoreductase (non-electrogenic)
Comments: The enzyme, described from the mitochondria of plants and some fungi and protists, is *an* alternative terminal oxidase that is not sensitive to cyanide inhibition and does not generate a proton motive force. Unlike the electrogenic terminal oxidases that contain hemes (*cf.* EC 1.10.3.10 and EC 1.10.3.14), this enzyme contains a dinuclear non-heme iron complex. The function of this oxidase is believed to be dissipating excess reducing power, minimizing oxidative stress, and optimizing photosynthesis in response to changing conditions.
References: [258, 3528, 281, 4215, 1151]

[EC 1.10.3.11 created 2011, modified 2014]

[1.10.3.12 *Transferred entry. menaquinol oxidase (H⁺-transporting). Now EC 7.1.1.5, menaquinol oxidase (H⁺-transporting)]*

[EC 1.10.3.12 created 2011, deleted 2018]

[1.10.3.13 *Transferred entry. caldariellaquinol oxidase (H⁺-transporting). Now EC 7.1.1.4, caldariellaquinol oxidase (H⁺-transporting)]*

[EC 1.10.3.13 created 2013, deleted 2018]

[1.10.3.14 *Transferred entry. ubiquinol oxidase (electrogenic, non H⁺-transporting). Now EC 7.1.1.7, ubiquinol oxidase (electrogenic, proton-motive force generating)]*

[EC 1.10.3.14 created 2014, modified 2017, deleted 2018]

EC 1.10.3.15

Accepted name: grixazone synthase
Reaction: 2 3-amino-4-hydroxybenzoate + *N*-acetyl-L-cysteine + 2 O₂ = grixazone B + 4 H₂O + CO₂
Other name(s): GriF
Systematic name: 3-amino-4-hydroxybenzoate:*N*-acetyl-L-cysteine:oxygen oxidoreductase
Comments: A type 3 multi copper protein. The enzyme, isolated from the bacterium *Streptomyces griseus*, catalyses an 8 electron oxidation. Activation of the enzyme requires a copper chaperone (GriE). It also acts on 3-amino-4-hydroxybenzaldehyde, giving grixazone A. The second aldehyde group is presumably lost as formate. The enzyme also catalyses the reaction of EC 1.10.3.4 *o*-aminophenol oxidase.
References: [3748, 3217]

[EC 1.10.3.15 created 2014]

EC 1.10.3.16

Accepted name: dihydrophenazinedicarboxylate synthase
Reaction: (1) (1*R*,6*R*)-1,4,5,5a,6,9-hexahydrophenazine-1,6-dicarboxylate + O₂ = (1*R*,10a*S*)-1,4,10,10a-tetrahydrophenazine-1,6-dicarboxylate + H₂O₂
 (2) (1*R*,10a*S*)-1,4,10,10a-tetrahydrophenazine-1,6-dicarboxylate + O₂ = (5a*S*)-5,5a-dihydrophenazine-1,6-dicarboxylate + H₂O₂
 (3) (1*R*,10a*S*)-1,4,10,10a-tetrahydrophenazine-1-carboxylate + O₂ = (10a*S*)-10,10a-dihydrophenazine-1-carboxylate + H₂O₂
 (4) (1*R*)-1,4,5,10-tetrahydrophenazine-1-carboxylate + O₂ = (10a*S*)-5,10-dihydrophenazine-1-carboxylate + H₂O₂
Other name(s): *phzG* (gene name)
Systematic name: 1,4,5a,6,9,10a-hexahydrophenazine-1,6-dicarboxylate:oxygen oxidoreductase
Comments: Requires FMN. The enzyme, isolated from the bacteria *Pseudomonas fluorescens* 2-79 and *Burkholderia lata* 383, is involved in biosynthesis of the reduced forms of phenazine, phenazine-1-carboxylate, and phenazine-1,6-dicarboxylate, where it catalyses multiple reactions.
References: [4285]

[EC 1.10.3.16 created 2016]

EC 1.10.5 With a quinone or related compound as acceptor

EC 1.10.5.1

Accepted name: ribosyldihydronicotinamide dehydrogenase (quinone)
Reaction: 1-(β-D-ribofuranosyl)-1,4-dihydronicotinamide + a quinone = 1-(β-D-ribofuranosyl)nicotinamide + a quinol
Other name(s): NRH:quinone oxidoreductase 2; NQO₂; NAD(P)H:quinone oxidoreductase-2 (misleading); QR2; quinone reductase 2; *N*-ribosyldihydronicotinamide dehydrogenase (quinone); NAD(P)H:quinone oxidoreductase2 (misleading)
Systematic name: 1-(β-D-ribofuranosyl)-1,4-dihydronicotinamide:quinone oxidoreductase
Comments: A flavoprotein. Unlike EC 1.6.5.2, NAD(P)H dehydrogenase (quinone), this quinone reductase cannot use NADH or NADPH; instead it uses *N*-ribofuranosyl- and *N*-alkyldihydronicotinamides. Polycyclic aromatic hydrocarbons, such as benz[*a*]anthracene, and the estrogens 17β-estradiol and diethylstilbestrol are potent inhibitors, but dicoumarol is only a very weak inhibitor [4461]. This enzyme can catalyse both 2-electron and 4-electron reductions, but one-electron acceptors, such as potassium ferricyanide, cannot be reduced [4260].
References: [2242, 4461, 4260, 1709]

[EC 1.10.5.1 created 2005 as EC 1.10.99.2, transferred 2015 to EC 1.10.5.1]

EC 1.10.9 With a copper protein as acceptor

[1.10.9.1 Transferred entry. *plastoquinol—plastocyanin reductase*. Now EC 7.1.1.6, *plastoquinol—plastocyanin reductase*]

[EC 1.10.9.1 created 1984 as EC 1.10.99.1, transferred 2011 to EC 1.10.9.1, deleted 2018]

EC 1.10.99 With unknown physiological acceptors

[1.10.99.1 Transferred entry. Now EC 1.10.9.1 *plastoquinol—plastocyanin reductase*]

[EC 1.10.99.1 created 1984, deleted 2011]

[1.10.99.2 Transferred entry. *ribosyldihyronicotinamide dehydrogenase (quinone)*. Now classified as EC 1.10.5.1, *ribosyldihyronicotinamide dehydrogenase (quinone)*.]

[EC 1.10.99.2 created 2005, deleted 2014]

[1.10.99.3 Transferred entry. *violaxanthin de-epoxidase*. Now classified as EC 1.23.5.1, *violaxanthin de-epoxidase*.]

[EC 1.10.99.3 created 2005, deleted 2014]

EC 1.11 Acting on a peroxide as acceptor

This subclass contains two sub-subclasses: the peroxidases (EC 1.11.1) and the peroxygenases (EC 1.11.2).

EC 1.11.1 Peroxidases

Acting on a peroxide as acceptor (peroxidases)

EC 1.11.1.1

Accepted name: NADH peroxidase

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

Other name(s): DPNH peroxidase; NAD peroxidase; diphosphopyridine nucleotide peroxidase; NADH-peroxidase; nicotinamide adenine dinucleotide peroxidase; NADH₂ peroxidase

Systematic name: NADH:hydrogen-peroxide oxidoreductase

Comments: A flavoprotein (FAD). Ferricyanide, quinones, etc., can replace H₂O₂.

References: [850, 2582, 4087]

[EC 1.11.1.1 created 1961]

EC 1.11.1.2

Accepted name: NADPH peroxidase

Reaction: $\text{NADPH} + \text{H}^+ + \text{H}_2\text{O}_2 = \text{NADP}^+ + 2 \text{H}_2\text{O}$

Other name(s): TPNH peroxidase; NADP peroxidase; nicotinamide adenine dinucleotide phosphate peroxidase; TPN peroxidase; triphosphopyridine nucleotide peroxidase; NADPH₂ peroxidase

Systematic name: NADPH:hydrogen-peroxide oxidoreductase

References: [648]

[EC 1.11.1.2 created 1961]

EC 1.11.1.3

Accepted name: fatty-acid peroxidase

Reaction: $\text{palmitate} + 2 \text{H}_2\text{O}_2 = \text{pentadecanal} + \text{CO}_2 + 3 \text{H}_2\text{O}$

Other name(s): long chain fatty acid peroxidase
Systematic name: hexadecanoate:hydrogen-peroxide oxidoreductase
Comments: Acts on long-chain fatty acids from dodecanoic to octadecanoic acid.
References: [2415]

[EC 1.11.1.3 created 1961]

[1.11.1.4 *Transferred entry. now EC 1.13.11.11 tryptophan 2,3-dioxygenase*]

[EC 1.11.1.4 created 1961, deleted 1964, reinstated 1965 as EC 1.13.1.12, deleted 1972]

EC 1.11.1.5

Accepted name: cytochrome-*c* peroxidase
Reaction: $2 \text{ ferrocyclochrome } c + \text{H}_2\text{O}_2 = 2 \text{ ferricytochrome } c + 2 \text{H}_2\text{O}$
Other name(s): cytochrome peroxidase; cytochrome *c*-551 peroxidase; apocytochrome *c* peroxidase; mesocytochrome *c* peroxidase azide; mesocytochrome *c* peroxidase cyanide; mesocytochrome *c* peroxidase cyanate; cytochrome *c*-H₂O oxidoreductase; cytochrome *c* peroxidase
Systematic name: ferrocyclochrome-*c*:hydrogen-peroxide oxidoreductase
Comments: A hemoprotein.
References: [67, 4322, 4369]

[EC 1.11.1.5 created 1961]

EC 1.11.1.6

Accepted name: catalase
Reaction: $2 \text{H}_2\text{O}_2 = \text{O}_2 + 2 \text{H}_2\text{O}$
Other name(s): equilase; caperase; optidase; catalase-peroxidase; CAT
Systematic name: hydrogen-peroxide:hydrogen-peroxide oxidoreductase
Comments: A hemoprotein. A manganese protein containing Mn^{III} in the resting state, which also belongs here, is often called pseudocatalase. The enzymes from some organisms, such as *Penicillium simplicissimum*, can also act as a peroxidase (EC 1.11.1.7) for which several organic substances, especially ethanol, can act as a hydrogen donor. Enzymes that exhibit both catalase and peroxidase activity belong under EC 1.11.1.21, catalase-peroxidase.
References: [1479, 1480, 1869, 2025, 2782, ?]

[EC 1.11.1.6 created 1961, modified 1986, modified 1999, modified 2013]

EC 1.11.1.7

Accepted name: peroxidase
Reaction: $2 \text{ phenolic donor} + \text{H}_2\text{O}_2 = 2 \text{ phenoxyl radical of the donor} + 2 \text{H}_2\text{O}$
Other name(s): lactoperoxidase; guaiacol peroxidase; plant peroxidase; Japanese radish peroxidase; horseradish peroxidase (HRP); soybean peroxidase (SBP); extensin peroxidase; heme peroxidase; oxyperoxidase; protoheme peroxidase; pyrocatechol peroxidase; scopoletin peroxidase; *Coprinus cinereus* peroxidase; *Arthromyces ramosus* peroxidase
Systematic name: phenolic donor:hydrogen-peroxide oxidoreductase
Comments: Heme proteins with histidine as proximal ligand. The iron in the resting enzyme is Fe(III). They also peroxidize non-phenolic substrates such as 3,3',5,5'-tetramethylbenzidine (TMB) and 2,2'-azinobis(3-ethylbenzthiazoline-6-sulfonic acid) (ABTS). Certain peroxidases (e.g. lactoperoxidase, SBP) oxidize bromide, iodide and thiocyanate.
References: [1882, 2632, 2964, 3773, 3859, 986, 41, 888, 3915]

[EC 1.11.1.7 created 1961, modified 2011]

EC 1.11.1.8

Accepted name: iodide peroxidase
Reaction: (1) $2 \text{I}^- + \text{H}_2\text{O}_2 + 2 \text{H}^+ = \text{I}_2 + 2 \text{H}_2\text{O}$
 (2) [thyroglobulin]-L-tyrosine + iodide + $\text{H}_2\text{O}_2 =$ [thyroglobulin]-3-iodo-L-tyrosine + $2 \text{H}_2\text{O}$
 (3) [thyroglobulin]-3-iodo-L-tyrosine + iodide + $\text{H}_2\text{O}_2 =$ [thyroglobulin]-3,5-diiodo-L-tyrosine + $2 \text{H}_2\text{O}$
 (4) 2 [thyroglobulin]-3,5-diiodo-L-tyrosine + $\text{H}_2\text{O}_2 =$ [thyroglobulin]-L-thyroxine + [thyroglobulin]-aminoacrylate + $2 \text{H}_2\text{O}$
 (5) [thyroglobulin]-3-iodo-L-tyrosine + [thyroglobulin]-3,5-diiodo-L-tyrosine + $\text{H}_2\text{O}_2 =$ [thyroglobulin]-3,5,3'-triiodo-L-thyronine + [thyroglobulin]-aminoacrylate + $2 \text{H}_2\text{O}$
Other name(s): thyroid peroxidase; iodotyrosine deiodase; iodinase; iodoperoxidase (heme type); iodide peroxidase-tyrosine iodinase; iodotyrosine deiodinase; moniodotyrosine deiodinase; thyroperoxidase; tyrosine iodinase; TPO
Systematic name: iodide:hydrogen-peroxide oxidoreductase
Comments: Thyroid peroxidase catalyses the biosynthesis of the thyroid hormones L-thyroxine and triiodo-L-thyronine. It catalyses both the iodination of tyrosine residues in thyroglobulin (forming mono- and di-iodinated forms) and their coupling to form either L-thyroxine or triiodo-L-thyronine.
References: [706, 1582, 678, 1171, 2855, 2364, 4047, 3138, 3733, 3828, 3257]

[EC 1.11.1.8 created 1961, modified 2012]

EC 1.11.1.9

Accepted name: glutathione peroxidase
Reaction: $2 \text{GSH} + \text{H}_2\text{O}_2 = \text{GSH disulfide} + 2 \text{H}_2\text{O}$
Other name(s): GSH peroxidase; selenium-glutathione peroxidase; reduced glutathione peroxidase
Systematic name: glutathione:hydrogen-peroxide oxidoreductase
Comments: A protein containing a selenocysteine residue. Steroid and lipid hydroperoxides, but not the product of reaction of EC 1.13.11.12 lipoxygenase on phospholipids, can act as acceptor, but more slowly than H_2O_2 (*cf.* EC 1.11.1.12 phospholipid-hydroperoxide glutathione peroxidase).
References: [558, 1303, 2708]

[EC 1.11.1.9 created 1965, modified 1989]

EC 1.11.1.10

Accepted name: chloride peroxidase
Reaction: $\text{RH} + \text{chloride} + \text{H}_2\text{O}_2 = \text{RCl} + 2 \text{H}_2\text{O}$
Other name(s): chloroperoxidase; CPO; vanadium haloperoxidase
Systematic name: chloride:hydrogen-peroxide oxidoreductase
Comments: Brings about the chlorination of a range of organic molecules, forming stable C-Cl bonds. Also oxidizes bromide and iodide. Enzymes of this type are either heme-thiolate proteins, or contain vanadate. A secreted enzyme produced by the ascomycetous fungus *Caldariomyces fumago* (*Leptoxyphium fumago*) is an example of the heme-thiolate type. It catalyses the production of hypochlorous acid by transferring one oxygen atom from H_2O_2 to chloride. At a separate site it catalyses the chlorination of activated aliphatic and aromatic substrates, via HClO and derived chlorine species. In the absence of halides, it shows peroxidase (e.g. phenol oxidation) and peroxygenase activities. The latter inserts oxygen from H_2O_2 into, for example, styrene (side chain epoxidation) and toluene (benzylic hydroxylation), however, these activities are less pronounced than its activity with halides. Has little activity with non-activated substrates such as aromatic rings, ethers or saturated alkanes. The chlorinating peroxidase produced by ascomycetous fungi (e.g. *Curvularia inaequalis*) is an example of a vanadium chloroperoxidase, and is related to bromide peroxidase (EC 1.11.1.18). It contains vanadate and oxidizes chloride, bromide and iodide into hypohalous acids. In the absence of halides, it peroxygenates organic sulfides and oxidizes ABTS [2,2'-azinobis(3-ethylbenzthiazoline-6-sulfonic acid)] but no phenols.
References: [2631, 1340, 3855, 3737, 3846, 3845, 2385, 2071, 2386]

[EC 1.11.1.10 created 1972, modified 2011]

EC 1.11.1.11

- Accepted name:** L-ascorbate peroxidase
Reaction: $2 \text{ L-ascorbate} + \text{H}_2\text{O}_2 + 2 \text{ H}^+ = \text{L-ascorbate} + \text{L-dehydroascorbate} + 2 \text{ H}_2\text{O}$ (overall reaction)
(1a) $2 \text{ L-ascorbate} + \text{H}_2\text{O}_2 + 2 \text{ H}^+ = 2 \text{ monodehydroascorbate} + 2 \text{ H}_2\text{O}$
(1b) $2 \text{ monodehydroascorbate} = \text{L-ascorbate} + \text{L-dehydroascorbate}$ (spontaneous)
Other name(s): L-ascorbic acid peroxidase; L-ascorbic acid-specific peroxidase; ascorbate peroxidase; ascorbic acid peroxidase
Systematic name: L-ascorbate:hydrogen-peroxide oxidoreductase
Comments: A heme protein. Oxidizes ascorbate and low molecular weight aromatic substrates. The monodehydroascorbate radical produced is either directly reduced back to ascorbate by EC 1.6.5.4 [monodehydroascorbate reductase (NADH)] or undergoes non-enzymic disproportionation to ascorbate and dehydroascorbate.
References: [3488, 3487, 2716, 2963, 3465, 2341]

[EC 1.11.1.11 created 1983, modified 2010, modified 2011]

EC 1.11.1.12

- Accepted name:** phospholipid-hydroperoxide glutathione peroxidase
Reaction: $2 \text{ glutathione} + \text{a hydroperoxy-fatty-acyl-[lipid]} = \text{glutathione disulfide} + \text{a hydroxy-fatty-acyl-[lipid]} + \text{H}_2\text{O}$
Other name(s): peroxidation-inhibiting protein; PHGPX; peroxidation-inhibiting protein:peroxidase,glutathione (phospholipid hydroperoxide-reducing); phospholipid hydroperoxide glutathione peroxidase; hydroperoxide glutathione peroxidase
Systematic name: glutathione:lipid-hydroperoxide oxidoreductase
Comments: A protein containing a selenocysteine residue. The products of action of EC 1.13.11.12 lipoxygenase on phospholipids can act as acceptors; H_2O_2 can also act, but much more slowly (*cf.* EC 1.11.1.9 glutathione peroxidase).
References: [3977, 3385]

[EC 1.11.1.12 created 1989, modified 2015]

EC 1.11.1.13

- Accepted name:** manganese peroxidase
Reaction: $2 \text{ Mn(II)} + 2 \text{ H}^+ + \text{H}_2\text{O}_2 = 2 \text{ Mn(III)} + 2 \text{ H}_2\text{O}$
Other name(s): peroxidase-M2; Mn-dependent (NADH-oxidizing) peroxidase
Systematic name: Mn(II):hydrogen-peroxide oxidoreductase
Comments: A hemoprotein. The enzyme from white rot basidiomycetes is involved in the oxidative degradation of lignin. The enzyme oxidizes a bound Mn^{2+} ion to Mn^{3+} in the presence of hydrogen peroxide. The product, Mn^{3+} , is released from the active site in the presence of a chelator (mostly oxalate and malate) that stabilizes it against disproportionation to Mn^{2+} and insoluble Mn^{4+} [2064]. The complexed Mn^{3+} ion can diffuse into the lignified cell wall, where it oxidizes phenolic components of lignin and other organic substrates [1222]. It is inactive with veratryl alcohol or nonphenolic substrates.
References: [1222, 2953, 4131, 2064]

[EC 1.11.1.13 created 1992]

EC 1.11.1.14

- Accepted name:** lignin peroxidase
Reaction: (1) $1\text{-}(3,4\text{-dimethoxyphenyl})\text{-2-}(2\text{-methoxyphenoxy})\text{propane-1,3-diol} + \text{H}_2\text{O}_2 = 3,4\text{-dimethoxybenzaldehyde} + 2\text{-methoxyphenol} + \text{glycolaldehyde} + \text{H}_2\text{O}$
(2) $2 \text{ (3,4-dimethoxyphenyl)methanol} + \text{H}_2\text{O}_2 = 2 \text{ (3,4-dimethoxyphenyl)methanol radical} + 2 \text{ H}_2\text{O}$

Other name(s): diarylpropane oxygenase; ligninase I; diarylpropane peroxidase; LiP; diarylpropane:oxygen,hydrogen-peroxide oxidoreductase (C-C-bond-cleaving); 1,2-bis(3,4-dimethoxyphenyl)propane-1,3-diol:hydrogen-peroxide oxidoreductase (incorrect); (3,4-dimethoxyphenyl)methanol:hydrogen-peroxide oxidoreductase

Systematic name: 1-(3,4-dimethoxyphenyl)-2-(2-methoxyphenoxy)propane-1,3-diol:hydrogen-peroxide oxidoreductase

Comments: A hemoprotein, involved in the oxidative breakdown of lignin by white-rot basidiomycete fungi. The reaction involves an initial oxidation of the heme iron by hydrogen peroxide, forming compound I (Fe^{IV}=O radical cation) at the active site. A single one-electron reduction of compound I by an electron derived from a substrate molecule yields compound II (Fe^{IV}=O non-radical cation), followed by a second one-electron transfer that returns the enzyme to the ferric oxidation state. The electron transfer events convert the substrate molecule into a transient cation radical intermediate that fragments spontaneously. The enzyme can act on a wide range of aromatic compounds, including methoxybenzenes and nonphenolic β -O-4 linked arylglycerol β -aryl ethers, but cannot act directly on the lignin molecule, which is too large to fit into the active site. However larger lignin molecules can be degraded in the presence of veratryl alcohol. It has been suggested that the free radical that is formed when the enzyme acts on veratryl alcohol can diffuse into the lignified cell wall, where it oxidizes lignin and other organic substrates. In the presence of high concentration of hydrogen peroxide and lack of substrate, the enzyme forms a catalytically inactive form (compound III). This form can be rescued by interaction with two molecules of the free radical products. In the case of veratryl alcohol, such an interaction yields two molecules of veratryl aldehyde.

References: [1887, 2953, 1404, 4132, 475, 1899, 1900, 1898, 866, 3031]

[EC 1.11.1.14 created 1992, modified 2006, modified 2011, modified 2016]

EC 1.11.1.15

Accepted name: peroxiredoxin

Reaction: $2 R'-SH + ROOH = R'-S-S-R' + H_2O + ROH$

Other name(s): thioredoxin peroxidase; tryparedoxin peroxidase; alkyl hydroperoxide reductase C22; AhpC; TrxPx; TXNPx; Prx; PRDX

Systematic name: thiol-containing-reductant:hydroperoxide oxidoreductase

Comments: Peroxiredoxins (Prxs) are a ubiquitous family of antioxidant proteins. They can be divided into three classes: typical 2-Cys, atypical 2-Cys and 1-Cys peroxiredoxins [4251]. The peroxidase reaction comprises two steps centred around a redox-active cysteine called the peroxidatic cysteine. All three peroxiredoxin classes have the first step in common, in which the peroxidatic cysteine attacks the peroxide substrate and is oxidized to *S*-hydroxycysteine (a sulfenic acid) (see mechanism). The second step of the peroxidase reaction, the regeneration of cysteine from *S*-hydroxycysteine, distinguishes the three peroxiredoxin classes. For typical 2-Cys Prxs, in the second step, the peroxidatic *S*-hydroxycysteine from one subunit is attacked by the 'resolving' cysteine located in the C-terminus of the second subunit, to form an intersubunit disulfide bond, which is then reduced by one of several cell-specific thiol-containing reductants (R'-SH) (e.g. thioredoxin, AhpF, tryparedoxin or AhpD), completing the catalytic cycle. In the atypical 2-Cys Prxs, both the peroxidatic cysteine and its resolving cysteine are in the same polypeptide, so their reaction forms an intrachain disulfide bond [4251]. To recycle the disulfide, known atypical 2-Cys Prxs appear to use thioredoxin as an electron donor [3444]. The 1-Cys Prxs conserve only the peroxidatic cysteine, so that its oxidized form is directly reduced to cysteine by the reductant molecule [608].

References: [4251, 1533, 3444, 608]

[EC 1.11.1.15 created 2004]

EC 1.11.1.16

Accepted name: versatile peroxidase

Reaction: (1) 1-(4-hydroxy-3-methoxyphenyl)-2-(2-methoxyphenoxy)propane-1,3-diol + H₂O₂ = 4-hydroxy-3-methoxybenzaldehyde + 2-methoxyphenol + glycolaldehyde + H₂O
(2) 2 manganese(II) + 2 H⁺ + H₂O₂ = 2 manganese(III) + 2 H₂O

Other name(s): VP; hybrid peroxidase; polyvalent peroxidase; reactive-black-5:hydrogen-peroxide oxidoreductase

Systematic name: 1-(4-hydroxy-3-methoxyphenyl)-2-(2-methoxyphenoxy)propane-1,3-diol:hydrogen-peroxide oxidoreductase

Comments: A hemoprotein. This ligninolytic peroxidase combines the substrate-specificity characteristics of the two other ligninolytic peroxidases, EC 1.11.1.13, manganese peroxidase and EC 1.11.1.14, lignin peroxidase. Unlike these two enzymes, it is also able to oxidize phenols, hydroquinones and both low- and high-redox-potential dyes, due to a hybrid molecular architecture that involves multiple binding sites for substrates [1463, 483].

References: [2418, 1463, 2739, 483, 2738, 482, 2737, 190, 2982, 500]

[EC 1.11.1.16 created 2006, modified 2016]

EC 1.11.1.17

Accepted name: glutathione amide-dependent peroxidase

Reaction: 2 glutathione amide + H₂O₂ = glutathione amide disulfide + 2 H₂O

Systematic name: glutathione amide:hydrogen-peroxide oxidoreductase

Comments: This enzyme, which has been characterized from the proteobacterium *Marichromatium gracile*, is a chimeric protein, containing a peroxiredoxin-like N-terminus and a glutaredoxin-like C terminus. The enzyme has peroxidase activity towards hydrogen peroxide and several small alkyl hydroperoxides, and is thought to represent an early adaptation for fighting oxidative stress [4032]. The glutathione amide disulfide produced by this enzyme can be restored to glutathione amide by EC 1.8.1.16 (glutathione amide reductase).

References: [4032]

[EC 1.11.1.17 created 2010]

EC 1.11.1.18

Accepted name: bromide peroxidase

Reaction: RH + HBr + H₂O₂ = RBr + 2 H₂O

Other name(s): bromoperoxidase; haloperoxidase (ambiguous); eosinophil peroxidase

Systematic name: bromide:hydrogen-peroxide oxidoreductase

Comments: Bromoperoxidases of red and brown marine algae (Rhodophyta and Phaeophyta) contain vanadate. They catalyse the bromination of a range of organic molecules such as sesquiterpenes, forming stable C-Br bonds. Bromoperoxidases also oxidize iodides.

References: [330, 3931, 1677, 513, 2853]

[EC 1.11.1.18 created 2010]

EC 1.11.1.19

Accepted name: dye decolorizing peroxidase

Reaction: Reactive Blue 5 + 2 H₂O₂ = phthalate + 2,2'-disulfonyl azobenzene + 3-[(4-amino-6-chloro-1,3,5-triazin-2-yl)amino]benzenesulfonate + 2 H₂O

Other name(s): DyP; DyP-type peroxidase

Systematic name: Reactive-Blue-5:hydrogen-peroxide oxidoreductase

Comments: Heme proteins with proximal histidine secreted by basidiomycetous fungi and eubacteria. They are similar to EC 1.11.1.16 versatile peroxidase (oxidation of Reactive Black 5, phenols, veratryl alcohol), but differ from the latter in their ability to efficiently oxidize a number of recalcitrant anthraquinone dyes, and inability to oxidize Mn(II). The model substrate Reactive Blue 5 is converted with high efficiency via a so far unique mechanism that combines oxidative and hydrolytic steps and leads to the formation of phthalic acid. Bacterial TfuDyP catalyses sulfoxidation.

References: [1919, 3708, 4493, 3709, 3707, 2844, 3994, 2250, 1534]

[EC 1.11.1.19 created 2011, modified 2015]

EC 1.11.1.20

- Accepted name:** prostamide/prostaglandin F_{2α} synthase
Reaction: thioredoxin + (5Z,9α,11α,13E,15S)-9,11-epidioxy-15-hydroxy-prosta-5,13-dienoate = thioredoxin disulfide + (5Z,9α,11α,13E,15S)-9,11,15-trihydroxyprosta-5,13-dienoate
Other name(s): prostamide/PGF synthase; prostamide F synthase; prostamide/prostaglandin F synthase; tPGF synthase
Systematic name: thioredoxin:(5Z,9α,11α,13E,15S)-9,11-epidioxy-15-hydroxy-prosta-5,13-dienoate oxidoreductase
Comments: The enzyme contains a thioredoxin-type disulfide as a catalytic group. Prostamide H₂ and prostaglandin H₂ are the best substrates; the latter is converted to prostaglandin F_{2α}. The enzyme also reduces *tert*-butyl hydroperoxide, cumene hydroperoxide and H₂O₂, but not prostaglandin D₂ or prostaglandin E₂.
References: [2629, 4384]

[EC 1.11.1.20 created 2011]

EC 1.11.1.21

- Accepted name:** catalase-peroxidase
Reaction: (1) donor + H₂O₂ = oxidized donor + 2 H₂O
(2) 2 H₂O₂ = O₂ + 2 H₂O
Other name(s): *katG* (gene name)
Systematic name: donor:hydrogen-peroxide oxidoreductase
Comments: Differs from EC 1.11.1.7, peroxidase in having a relatively high catalase (EC 1.11.1.6) activity with H₂O₂ as donor, releasing O₂; both activities use the same heme active site. In *Mycobacterium tuberculosis* it is responsible for activation of the commonly used antitubercular drug, isoniazid.
References: [2291, 1526, 1046, 284, 4049]

[EC 1.11.1.21 created 2011]

EC 1.11.1.22

- Accepted name:** hydroperoxy fatty acid reductase
Reaction: a hydroperoxy fatty acid + NADPH + H⁺ = a hydroxy fatty acid + NADP⁺ + H₂O
Other name(s): slr1171 (gene name); slr1992 (gene name); hydroperoxy fatty acid:NADPH oxidoreductase
Systematic name: NADPH:hydroperoxy fatty acid oxidoreductase
Comments: The enzyme, characterized from the cyanobacterium *Synechocystis* PCC 6803, can reduce unsaturated fatty acid hydroperoxides and alkyl hydroperoxides. The enzyme, which utilizes NADPH generated by the photosynthetic electron transfer system, protects the cells from lipid peroxidation.
References: [1129, 1130]

[EC 1.11.1.22 created 2013]

EC 1.11.1.23

- Accepted name:** (S)-2-hydroxypropylphosphonic acid epoxidase
Reaction: (S)-2-hydroxypropylphosphonate + H₂O₂ = (1R,2S)-1,2-epoxypropylphosphonate + 2 H₂O
Other name(s): HPP epoxidase; HppE; 2-hydroxypropylphosphonic acid epoxidase; Fom4; (S)-2-hydroxypropylphosphonate epoxidase
Systematic name: (S)-2-hydroxypropylphosphonate:hydrogen-peroxide epoxidase
Comments: This is the last enzyme in the biosynthetic pathway of fosfomicin, a broad-spectrum antibiotic produced by certain *Streptomyces* species. Contains non heme iron that forms a iron(IV)-oxo (ferryl) complex with hydrogen peroxide, which functions as a proton abstractor from the substrate [4103].
References: [2661, 4330, 1491, 2282, 1495, 484, 4103]

[EC 1.11.1.23 created 2011 as EC 1.14.19.7, transferred 2014 to EC 1.11.1.23]

EC 1.11.2 Peroxygenases

With a peroxide as acceptor, one oxygen atom of which is incorporated into the product

EC 1.11.2.1

- Accepted name:** unspecific peroxygenase
Reaction: $\text{RH} + \text{H}_2\text{O}_2 = \text{ROH} + \text{H}_2\text{O}$
Other name(s): aromatic peroxygenase; mushroom peroxygenase; haloperoxidase-peroxygenase; *Agrocybe aegerita* peroxidase
Systematic name: substrate:hydrogen-peroxide oxidoreductase (RH-hydroxylating or -epoxidising)
Comments: A heme-thiolate protein (*P*-450). Enzymes of this type include glycoproteins secreted by agaric basidiomycetes. They catalyse the insertion of an oxygen atom from H_2O_2 into a wide variety of substrates, including aromatic rings such as naphthalene, toluene, phenanthrene, pyrene and *p*-nitrophenol, recalcitrant heterocycles such as pyridine, dibenzofuran, various ethers (resulting in *O*-dealkylation) and alkanes such as propane, hexane and cyclohexane. Reactions catalysed include hydroxylation, epoxidation, *N*-oxidation, sulfoxidation, *O*- and *N*-dealkylation, bromination and one-electron oxidations. They have little or no activity toward chloride. Mechanistically, the catalytic cycle of unspecific (mono)-peroxygenases combines elements of the "shunt" pathway of cytochrome *P*-450s (a side activity that utilizes a peroxide in place of dioxygen and NAD[P]H) and the classic heme peroxidase cycle.
References: [3971, 3970, 93, 3969, 111, 1934, 1968, 1935, 2972]

[EC 1.11.2.1 created 2011]

EC 1.11.2.2

- Accepted name:** myeloperoxidase
Reaction: $\text{Cl}^- + \text{H}_2\text{O}_2 + \text{H}^+ = \text{HClO} + \text{H}_2\text{O}$
Other name(s): MPO; verdoperoxidase
Systematic name: chloride:hydrogen-peroxide oxidoreductase (hypochlorite-forming)
Comments: Contains calcium and covalently bound heme (proximal ligand histidine). It is present in phagosomes of neutrophils and monocytes, where the hypochlorite produced is strongly bactericidal. It differs from EC 1.11.1.10 chloride peroxidase in its preference for formation of hypochlorite over the chlorination of organic substrates under physiological conditions (pH 5-8). Hypochlorite in turn forms a number of antimicrobial products (Cl_2 , chloramines, hydroxyl radical, singlet oxygen). MPO also oxidizes bromide, iodide and thiocyanate. In the absence of halides, it oxidizes phenols and has a moderate peroxygenase activity toward styrene.
References: [33, 1400, 1120, 3952, 1959, 1010, 1168]

[EC 1.11.2.2 created 2011]

EC 1.11.2.3

- Accepted name:** plant seed peroxygenase
Reaction: $\text{R}^1\text{H} + \text{R}^2\text{OOH} = \text{R}^1\text{OH} + \text{R}^2\text{OH}$
Other name(s): plant peroxygenase, soybean peroxygenase
Systematic name: substrate:hydroperoxide oxidoreductase (RH-hydroxylating or epoxidising)
Comments: A heme protein with calcium binding motif (caleosin-type). Enzymes of this type include membrane-bound proteins found in seeds of different plants. They catalyse the direct transfer of one oxygen atom from an organic hydroperoxide, which is reduced into its corresponding alcohol to a substrate which will be oxidized. Reactions catalysed include hydroxylation, epoxidation and sulfoxidation. Preferred substrate and co-substrate are unsaturated fatty acids and fatty acid hydroperoxides, respectively. Plant seed peroxygenase is involved in the synthesis of cutin.
References: [1669, 320, 1352, 2201, 1366]

[EC 1.11.2.3 created 2011]

EC 1.11.2.4

- Accepted name:** fatty-acid peroxygenase
Reaction: fatty acid + H₂O₂ = 3- or 2-hydroxy fatty acid + H₂O
Other name(s): fatty acid hydroxylase (ambiguous); P450 peroxygenase; CYP152A1; P450BS; P450SP α
Systematic name: fatty acid:hydroperoxide oxidoreductase (RH-hydroxylating)
Comments: A cytosolic heme-thiolate protein with sequence homology to *P*-450 monooxygenases. Unlike the latter, it needs neither NAD(P)H, dioxygen nor specific reductases for function. Enzymes of this type are produced by bacteria (e.g. *Sphingomonas paucimobilis*, *Bacillus subtilis*). Catalytic turnover rates are high compared with those of monooxygenation reactions as well as peroxide shunt reactions catalysed by the common *P*-450s. A model substrate is myristate, but other saturated and unsaturated fatty acids are also hydroxylated. Oxidizes the peroxidase substrate 3,3',5,5'-tetramethylbenzidine (TMB) and peroxygenates aromatic substrates in a fatty-acid-dependent reaction.
References: [2452, 2451, 2449, 1643, 2450, 2167, 2448, 3518]

[EC 1.11.2.4 created 2011]

EC 1.11.2.5

- Accepted name:** 3-methyl-L-tyrosine peroxygenase
Reaction: 3-methyl-L-tyrosine + H₂O₂ = 3-hydroxy-5-methyl-L-tyrosine + H₂O
Other name(s): SfmD; SacD; 3-methyltyrosine peroxidase; 3-methyl-L-tyrosine peroxidase
Systematic name: 3-methyl-L-tyrosine:hydrogen-peroxide oxidoreductase (3-hydroxy-5-methyl-L-tyrosine-forming)
Comments: The heme-containing peroxygenase from the bacterium *Streptomyces lavendulae* is involved in biosynthesis of saframycin A, a potent antitumor antibiotic that belongs to the tetrahydroisoquinoline family.
References: [3810]

[EC 1.11.2.5 created 2014]

EC 1.12 Acting on hydrogen as donor

This subclass contains hydrogenases other than those that use iron-sulfur compounds as donor (EC 1.18) for the reduction of H⁺ to H₂. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.12.1), a cytochrome (EC 1.12.2), a quinone or similar compound (EC 1.12.5), an iron-sulfur protein (EC 1.12.7), other, known, acceptors (EC 1.12.9), or some other acceptor (EC 1.12.99).

EC 1.12.1 With NAD⁺ or NADP⁺ as acceptor

[1.12.1.1 Transferred entry. peroxidase. Now EC 1.12.7.2, ferredoxin hydrogenase]

[EC 1.12.1.1 created 1965, deleted 1972]

EC 1.12.1.2

- Accepted name:** hydrogen dehydrogenase
Reaction: H₂ + NAD⁺ = H⁺ + NADH
Other name(s): H₂:NAD⁺ oxidoreductase; NAD-linked hydrogenase; bidirectional hydrogenase; hydrogenase
Systematic name: hydrogen:NAD⁺ oxidoreductase
Comments: An iron-sulfur flavoprotein (FMN or FAD). Some forms of this enzyme contain nickel.
References: [343, 3382]

[EC 1.12.1.2 created 1972, modified 2002]

EC 1.12.1.3

Accepted name: hydrogen dehydrogenase (NADP⁺)
Reaction: H₂ + NADP⁺ = H⁺ + NADPH
Other name(s): NADP⁺-linked hydrogenase; NADP⁺-reducing hydrogenase; hydrogenase (ambiguous); hydrogenase I (ambiguous)
Systematic name: hydrogen:NADP⁺ oxidoreductase
Comments: The protein from the bacterium *Desulfovibrio fructosovorans* is an iron-sulfur protein that exclusively functions as a hydrogen dehydrogenase [767], while the enzyme from the archaeon *Pyrococcus furiosus* is a nickel, iron, iron-sulfur protein, that is part of a heterotetrameric complex where the α and δ subunits function as a hydrogenase while the β and γ subunits function as sulfur reductase (EC 1.12.98.4, sulfhydrogenase). Different from EC 1.12.1.5, hydrogen dehydrogenase [NAD(P)⁺].
References: [767, 432, 2330, 2334, 4002]

[EC 1.12.1.3 created 2002, modified 2013]

EC 1.12.1.4

Accepted name: hydrogenase (NAD⁺, ferredoxin)
Reaction: 2 H₂ + NAD⁺ + 2 oxidized ferredoxin = 5 H⁺ + NADH + 2 reduced ferredoxin
Other name(s): bifurcating [FeFe] hydrogenase
Systematic name: hydrogen:NAD⁺, ferredoxin oxidoreductase
Comments: The enzyme from *Thermotoga maritima* contains a [FeFe] cluster (*H*-cluster) and iron-sulfur clusters. It works in the direction evolving hydrogen as a means of eliminating excess reducing equivalents.
References: [4034, 3407]

[EC 1.12.1.4 created 2011]

EC 1.12.1.5

Accepted name: hydrogen dehydrogenase [NAD(P)⁺]
Reaction: H₂ + NAD(P)⁺ = H⁺ + NAD(P)H
Other name(s): hydrogenase II (ambiguous)
Systematic name: hydrogen:NAD(P)⁺ oxidoreductase
Comments: A nickel, iron, iron-sulfur protein. The enzyme from the archaeon *Pyrococcus furiosus* is part of a heterotetrameric complex where the α and δ subunits function as a hydrogenase while the β and γ subunits function as sulfur reductase (EC 1.12.98.4, sulfhydrogenase). Different from EC 1.12.1.3, hydrogen dehydrogenase (NADP⁺).
References: [2333]

[EC 1.12.1.5 created 2013]

EC 1.12.2 With a cytochrome as acceptor

EC 1.12.2.1

Accepted name: cytochrome-*c*₃ hydrogenase
Reaction: H₂ + 2 ferricytochrome *c*₃ = 2 H⁺ + 2 ferrocyclochrome *c*₃
Other name(s): H₂:ferricytochrome *c*₃ oxidoreductase; cytochrome *c*₃ reductase; cytochrome hydrogenase; hydrogenase [ambiguous]
Systematic name: hydrogen:ferricytochrome-*c*₃ oxidoreductase
Comments: An iron-sulfur protein. Some forms of the enzyme contain nickel ([NiFe]-hydrogenases) and, of these, some contain selenocysteine ([NiFeSe]-hydrogenases). Methylene blue and other acceptors can also be reduced.
References: [801, 1499, 3190, 3276, 4053, 1154]

[EC 1.12.2.1 created 1972, modified 2002]

EC 1.12.5 With a quinone or similar compound as acceptor

EC 1.12.5.1

- Accepted name:** hydrogen:quinone oxidoreductase
Reaction: $H_2 + \text{menaquinone} = \text{menaquinol}$
Other name(s): hydrogen-ubiquinone oxidoreductase; hydrogen:menaquinone oxidoreductase; membrane-bound hydrogenase; quinone-reactive Ni/Fe-hydrogenase
Systematic name: hydrogen:quinone oxidoreductase
Comments: Contains nickel, iron-sulfur clusters and cytochrome *b*. Also catalyses the reduction of water-soluble quinones (e.g. 2,3-dimethylnaphthoquinone) or viologen dyes (benzylviologen or methylviologen).
References: [873, 874, 1301, 272, 997, 1668]

[EC 1.12.5.1 created 1999 as EC 1.12.99.3, transferred 2002 to EC 1.12.5.1]

EC 1.12.7 With an iron-sulfur protein as acceptor

[1.12.7.1 *Transferred entry. ferredoxin hydrogenase. Now EC 1.12.7.2, ferredoxin hydrogenase*]

[EC 1.12.7.1 created 1972, deleted 1978]

EC 1.12.7.2

- Accepted name:** ferredoxin hydrogenase
Reaction: $H_2 + 2 \text{ oxidized ferredoxin} = 2 \text{ reduced ferredoxin} + 2 H^+$
Other name(s): H_2 oxidizing hydrogenase; H_2 producing hydrogenase [ambiguous]; bidirectional hydrogenase; hydrogen-lyase [ambiguous]; hydrogenase (ferredoxin); hydrogenase I; hydrogenase II; hydrogenlyase [ambiguous]; uptake hydrogenase [ambiguous]
Systematic name: hydrogen:ferredoxin oxidoreductase
Comments: Contains iron-sulfur clusters. The enzymes from some sources contains nickel. Can use molecular hydrogen for the reduction of a variety of substances.
References: [3523, 3772, 3987, 4498, 23, 2986]

[EC 1.12.7.2 created 1961 as EC 1.98.1.1, transferred 1965 to EC 1.12.1.1, transferred 1972 to EC 1.12.7.1, transferred 1978 to EC 1.18.3.1, transferred 1984 to EC 1.18.99.1, transferred 2002 to EC 1.12.7.2]

EC 1.12.98 With other, known, physiological acceptors

EC 1.12.98.1

- Accepted name:** coenzyme F_{420} hydrogenase
Reaction: $H_2 + \text{oxidized coenzyme } F_{420} = \text{reduced coenzyme } F_{420}$
Other name(s): 8-hydroxy-5-deazaflavin-reducing hydrogenase; F_{420} -reducing hydrogenase; coenzyme F_{420} -dependent hydrogenase
Systematic name: hydrogen:coenzyme F_{420} oxidoreductase
Comments: An iron-sulfur flavoprotein (FAD) containing nickel. The enzyme from some sources contains selenocysteine. The enzyme also reduces the riboflavin analogue of F_{420} , flavins and methylviologen, but to a lesser extent. The hydrogen acceptor coenzyme F_{420} is a deazaflavin derivative.
References: [24, 4328, 1045, 2677, 202]

[EC 1.12.98.1 created 1989 as EC 1.12.99.1, transferred 2002 to EC 1.12.98.1]

EC 1.12.98.2

- Accepted name:** 5,10-methenyltetrahydromethanopterin hydrogenase

Reaction: $\text{H}_2 + 5,10\text{-methylene tetrahydromethanopterin} = \text{H}^+ + 5,10\text{-methylene tetrahydromethanopterin}$
Other name(s): H_2 -forming N^5, N^{10} -methylene tetrahydromethanopterin dehydrogenase; nonmetal hydrogenase; N^5, N^{10} -methylene tetrahydromethanopterin hydrogenase; hydrogen: N^5, N^{10} -methylene tetrahydromethanopterin oxidoreductase
Systematic name: hydrogen:5,10-methylene tetrahydromethanopterin oxidoreductase
Comments: Does not catalyse the reduction of artificial dyes. Does not by itself catalyse a H_2/H^+ exchange reaction. Does not contain nickel or iron-sulfur clusters.
References: [4490, 1963]

[EC 1.12.98.2 created 1999 as EC 1.12.99.4, transferred 2002 to EC 1.12.98.2, modified 2004]

EC 1.12.98.3

Accepted name: *Methanosarcina*-phenazine hydrogenase
Reaction: $\text{H}_2 + 2\text{-}(2,3\text{-dihydro pentaprenyloxy})\text{phenazine} = 2\text{-dihydro pentaprenyloxyphenazine}$
Other name(s): methanophenazine hydrogenase; methylviologen-reducing hydrogenase
Systematic name: hydrogen:2-(2,3-dihydro pentaprenyloxy)phenazine oxidoreductase
Comments: Contains nickel, iron-sulfur clusters and cytochrome *b*. The enzyme from some sources contains selenocysteine.
References: [4, 800, 246]

[EC 1.12.98.3 created 2002]

EC 1.12.98.4

Accepted name: sulfhydrogenase
Reaction: $\text{H}_2 + (\text{sulfide})_n = \text{hydrogen sulfide} + (\text{sulfide})_{n-1}$
Other name(s): sulfur reductase
Systematic name: H_2 :polysulfide oxidoreductase
Comments: An iron-sulfur protein. The enzyme from the hyperthermophilic archaeon *Pyrococcus furiosus* is part of two heterotetrameric complexes where the β and γ subunits function as sulfur reductase and the α and δ subunits function as hydrogenases (EC 1.12.1.3, hydrogen dehydrogenase [NADP^+] and EC 1.12.1.4, hydrogen dehydrogenase [NAD(P)^+], respectively). Sulfur can also be used as substrate, but since it is insoluble in aqueous solution and polysulfide is generated abiotically by the reaction of hydrogen sulfide and sulfur, polysulfide is believed to be the true substrate [2330].
References: [4492, 2330, 2334, 2333]

[EC 1.12.98.4 created 1992 as EC 1.97.1.3, transferred 2013 to EC 1.12.98.4]

EC 1.12.99 With unknown physiological acceptors

[1.12.99.1 Transferred entry. coenzyme F_{420} hydrogenase. Now EC 1.12.98.1, coenzyme F_{420} hydrogenase]

[EC 1.12.99.1 created 1989, deleted 2002]

[1.12.99.2 Deleted entry. coenzyme-M-7-mercaptoheptanoylthreonine-phosphate-heterodisulfide hydrogenase. Now shown to be two enzymes, EC 1.12.98.3, *Methanosarcina*-phenazine hydrogenase and EC 1.8.98.1, CoB—CoM heterodisulfide reductase]

[EC 1.12.99.2 created 1992, deleted 2002]

[1.12.99.3 Transferred entry. hydrogen:quinone oxidoreductase. Now EC 1.12.5.1, hydrogen:quinone oxidoreductase]

[EC 1.12.99.3 created 1999, deleted 2002]

[1.12.99.4 Transferred entry. N^5, N^{10} -methylene tetrahydromethanopterin hydrogenase. Now EC 1.12.98.2, 5,10-methylene tetrahydromethanopterin hydrogenase]

[EC 1.12.99.4 created 1999, deleted 2002]

[1.12.99.5 Deleted entry. 3,4-dihydroxyquinoline 2,4-dioxygenase. Identical to EC 1.13.11.47, 3-hydroxy-4-oxoquinoline 2,4-dioxygenase]

[EC 1.12.99.5 created 1999, deleted 2001]

EC 1.12.99.6

Accepted name: hydrogenase (acceptor)
Reaction: H₂ + acceptor = reduced acceptor
Other name(s): H₂ producing hydrogenase (ambiguous); hydrogen-lyase (ambiguous); hydrogenlyase (ambiguous); uptake hydrogenase (ambiguous); hydrogen:(acceptor) oxidoreductase
Systematic name: hydrogen:acceptor oxidoreductase
Comments: Uses molecular hydrogen for the reduction of a variety of substances. Contains iron-sulfur clusters. The enzyme from some sources contains nickel.
References: [3523, 24, 4043]

[EC 1.12.99.6 created 2002, modified 2003]

EC 1.13 Acting on single donors with incorporation of molecular oxygen (oxygenases)

This subclass contains oxygenases that incorporate oxygen into the substrate. They differ from those in EC 1.14 in that a second hydrogen donor is not required. Sub-subclasses are based on the number of atoms of oxygen that are incorporated: two atoms of oxygen (EC 1.13.11), one atom of oxygen (EC 1.13.12), or other cases (EC 1.13.99). This classification replaces an earlier version. Common names in this subclass are usually of the form 'monooxygenase' and 'dioxygenase'.

EC 1.13.1 Acting on single donors with incorporation of molecular oxygen (oxygenases)

[1.13.1.1 Transferred entry. Now EC 1.13.11.1, catechol 1,2-dioxygenase]

[EC 1.13.1.1 created 1961 as EC 1.99.2.2, transferred 1965 to EC 1.13.1.1, deleted 1972]

[1.13.1.2 Transferred entry. Now EC 1.13.11.2, catechol 2,3-dioxygenase]

[EC 1.13.1.2 created 1965, deleted 1972]

[1.13.1.3 Transferred entry. Now EC 1.13.11.3, protocatechuate 3,4-dioxygenase]

[EC 1.13.1.3 created 1961 as EC 1.99.2.3, transferred 1965 to EC 1.13.1.3, deleted 1972]

[1.13.1.4 Transferred entry. Now EC 1.13.11.4, gentisate 1,2-dioxygenase]

[EC 1.13.1.4 created 1961 as EC 1.99.2.4, transferred 1965 to EC 1.13.1.4, deleted 1972]

[1.13.1.5 Transferred entry. Now EC 1.13.11.5, homogentisate 1,2-dioxygenase]

[EC 1.13.1.5 created 1961 as EC 1.99.2.5, transferred 1965 to EC 1.13.1.5, deleted 1972]

[1.13.1.6 Transferred entry. Now EC 1.13.11.6, 3-hydroxyanthranilate 3,4-dioxygenase]

[EC 1.13.1.6 created 1965, deleted 1972]

[1.13.1.7 Deleted entry. 3,4-dihydroxyphenylacetate 3,4-dioxygenase]

[EC 1.13.1.7 created 1965, transferred 1972 to EC 1.13.11.7, deleted 1980]

[1.13.1.8 Transferred entry. Now EC 1.13.11.8, protocatechuate 4,5-dioxygenase]

[EC 1.13.1.8 created 1965, deleted 1972]

[1.13.1.9 *Transferred entry. Now EC 1.13.11.9, 2,5-dihydroxypyridine 5,6-dioxygenase*]

[EC 1.13.1.9 created 1965, deleted 1972]

[1.13.1.10 *Transferred entry. Now EC 1.13.11.10, 7,8-dihydroxykynurenate 8,8a-dioxygenase*]

[EC 1.13.1.10 created 1965, deleted 1972]

[1.13.1.11 *Transferred entry. Now EC 1.13.99.1, inositol oxygenase*]

[EC 1.13.1.11 created 1961 as EC 1.99.2.6, transferred 1965 to EC 1.13.1.11, deleted 1972]

[1.13.1.12 *Transferred entry. Now EC 1.13.11.11, tryptophan 2,3-dioxygenase*]

[EC 1.13.1.12 created 1961 as EC 1.11.1.4, deleted 1964, reinstated 1965 as EC 1.13.1.12, deleted 1972]

[1.13.1.13 *Transferred entry. Now EC 1.13.11.12, lipoxygenase*]

[EC 1.13.1.13 created 1961 as EC 1.99.2.1, transferred 1965 to EC 1.13.1.13, deleted 1972]

EC 1.13.11 With incorporation of two atoms of oxygen

EC 1.13.11.1

- Accepted name:** catechol 1,2-dioxygenase
Reaction: catechol + O₂ = *cis,cis*-muconate
Other name(s): catechol-oxygen 1,2-oxidoreductase; 1,2-pyrocatechase; catechase; catechol 1,2-oxygenase; catechol dioxygenase; pyrocatechase; pyrocatechol 1,2-dioxygenase; CD I; CD II
Systematic name: catechol:oxygen 1,2-oxidoreductase
Comments: Requires Fe³⁺. Involved in the metabolism of nitro-aromatic compounds by a strain of *Pseudomonas putida*.
References: [1430, 1431, 3543, 4436]

[EC 1.13.11.1 created 1961 as EC 1.99.2.2, transferred 1965 to EC 1.13.1.1, transferred 1972 to EC 1.13.11.1]

EC 1.13.11.2

- Accepted name:** catechol 2,3-dioxygenase
Reaction: catechol + O₂ = 2-hydroxymuconate-6-semialdehyde
Other name(s): 2,3-pyrocatechase; catechol 2,3-oxygenase; catechol oxygenase; metapyrocatechase; pyrocatechol 2,3-dioxygenase; *xylE* (gene name); catechol:oxygen 2,3-oxidoreductase (decyclizing)
Systematic name: catechol:oxygen 2,3-oxidoreductase (ring-opening)
Comments: Requires Fe^{II}. The enzyme initiates the *meta*-cleavage pathway of catechol degradation.
References: [1430, 2012, 2825, 2700, 1786, 1788]

[EC 1.13.11.2 created 1965 as EC 1.13.1.2, transferred 1972 to EC 1.13.11.2, modified 1999, modified 2013]

EC 1.13.11.3

- Accepted name:** protocatechuate 3,4-dioxygenase
Reaction: 3,4-dihydroxybenzoate + O₂ = 3-carboxy-*cis,cis*-muconate
Other name(s): protocatechuate oxygenase; protocatechuic acid oxidase; protocatechuic 3,4-dioxygenase; protocatechuic 3,4-oxygenase; protocatechuate:oxygen 3,4-oxidoreductase (decyclizing)
Systematic name: protocatechuate:oxygen 3,4-oxidoreductase (ring-opening)
Comments: Requires Fe³⁺. The enzyme, which participates in the degradation of aromatic compounds, catalyses the intradiol addition of both oxygen atoms from molecular oxygen, resulting in *ortho*-cleavage of the aromatic ring. The type of cleavage leads to mineralization via the intermediate 3-oxoadipate.
References: [1095, 1302, 3619]

[EC 1.13.11.3 created 1961 as EC 1.99.2.3, transferred 1965 to EC 1.13.1.3, transferred 1972 to EC 1.13.11.3]

EC 1.13.11.4

Accepted name: gentisate 1,2-dioxygenase
Reaction: 2,5-dihydroxybenzoate + O₂ = maleylpyruvate
Other name(s): gentisate oxygenase; 2,5-dihydroxybenzoate dioxygenase; gentisate dioxygenase; gentisic acid oxidase; gentisate:oxygen 1,2-oxidoreductase (decyclizing)
Systematic name: gentisate:oxygen 1,2-oxidoreductase (ring-opening)
Comments: Requires Fe²⁺.
References: [1430, 3717, 3716]

[EC 1.13.11.4 created 1961 as EC 1.99.2.4, transferred 1965 to EC 1.13.1.4, transferred 1972 to EC 1.13.11.4]

EC 1.13.11.5

Accepted name: homogentisate 1,2-dioxygenase
Reaction: homogentisate + O₂ = 4-maleylacetoacetate
Other name(s): homogentisicase; homogentisate oxygenase; homogentisate dioxygenase; homogentisate oxidase; homogentisic acid oxidase; homogentisic acid oxygenase; homogentisic oxygenase; homogentisate:oxygen 1,2-oxidoreductase (decyclizing)
Systematic name: homogentisate:oxygen 1,2-oxidoreductase (ring-opening)
Comments: Requires Fe²⁺.
References: [10, 688, 1430, 1941, 1980, 3135]

[EC 1.13.11.5 created 1961 as EC 1.99.2.5, transferred 1965 to EC 1.13.1.5, transferred 1972 to EC 1.13.11.5]

EC 1.13.11.6

Accepted name: 3-hydroxyanthranilate 3,4-dioxygenase
Reaction: 3-hydroxyanthranilate + O₂ = 2-amino-3-carboxymuconate semialdehyde
Other name(s): 3-hydroxyanthranilate oxygenase; 3-hydroxyanthranilic acid oxygenase; 3-hydroxyanthranilic oxygenase; 3-hydroxyanthranilic acid oxidase; 3HAO; 3-hydroxyanthranilate:oxygen 3,4-oxidoreductase (decyclizing)
Systematic name: 3-hydroxyanthranilate:oxygen 3,4-oxidoreductase (ring-opening)
Comments: Requires Fe²⁺.
References: [775, 1430]

[EC 1.13.11.6 created 1965 as EC 1.13.1.6, transferred 1972 to EC 1.13.11.6]

[1.13.11.7 Deleted entry. 3,4-dihydroxyphenylacetate 3,4-dioxygenase]

[EC 1.13.11.7 created 1965 as EC 1.13.1.7, transferred 1972 to EC 1.13.11.7, deleted 1980]

EC 1.13.11.8

Accepted name: protocatechuate 4,5-dioxygenase
Reaction: 3,4-dihydroxybenzoate + O₂ = 4-carboxy-2-hydroxymuconate semialdehyde
Other name(s): protocatechuate 4,5-oxygenase; protocatechuic 4,5-dioxygenase; protocatechuic 4,5-oxygenase; protocatechuate:oxygen 4,5-oxidoreductase (decyclizing); protocatechuate:oxygen 4,5-oxidoreductase (ring-opening)
Systematic name: 3,4-dihydroxybenzoate:oxygen 4,5-oxidoreductase (ring-opening)
Comments: Requires Fe²⁺.
References: [3930]

[EC 1.13.11.8 created 1965 as EC 1.13.1.8, transferred 1972 to EC 1.13.11.8]

EC 1.13.11.9

Accepted name: 2,5-dihydroxypyridine 5,6-dioxygenase
Reaction: 2,5-dihydroxypyridine + O₂ = *N*-formylmaleamic acid
Other name(s): 2,5-dihydroxypyridine oxygenase; pyridine-2,5-diol dioxygenase; NicX
Systematic name: 2,5-dihydroxypyridine:oxygen 5,6-oxidoreductase
Comments: Requires Fe²⁺.
References: [245, 1169, 1170, 1743]

[EC 1.13.11.9 created 1965 as EC 1.13.1.9, transferred 1972 to EC 1.13.11.9, modified 2010]

EC 1.13.11.10

Accepted name: 7,8-dihydroxykynurenate 8,8a-dioxygenase
Reaction: 7,8-dihydroxykynurenate + O₂ = 5-(3-carboxy-3-oxopropenyl)-4,6-dihydroxypyridine-2-carboxylate
Other name(s): 7,8-dihydroxykynurenate oxygenase; 7,8-dihydroxykynurenate 8,8α-dioxygenase; 7,8-dihydroxykynurenate:oxygen 8,8a-oxidoreductase (decyclizing)
Systematic name: 7,8-dihydroxykynurenate:oxygen 8,8a-oxidoreductase (ring-opening)
Comments: Requires Fe²⁺.
References: [2081]

[EC 1.13.11.10 created 1965 as EC 1.13.1.10, transferred 1972 to EC 1.13.11.10]

EC 1.13.11.11

Accepted name: tryptophan 2,3-dioxygenase
Reaction: L-tryptophan + O₂ = *N*-formyl-L-kynurenine
Other name(s): tryptophan pyrrolase (ambiguous); tryptophanase; tryptophan oxygenase; tryptamine 2,3-dioxygenase; tryptophan peroxidase; indoleamine 2,3-dioxygenase (ambiguous); indolamine 2,3-dioxygenase (ambiguous); L-tryptophan pyrrolase; TDO; L-tryptophan 2,3-dioxygenase; L-tryptophan:oxygen 2,3-oxidoreductase (decyclizing)
Systematic name: L-tryptophan:oxygen 2,3-oxidoreductase (ring-opening)
Comments: A protohemoprotein. In mammals, the enzyme appears to be located only in the liver. This enzyme, together with EC 1.13.11.52, indoleamine 2,3-dioxygenase, catalyses the first and rate-limiting step in the kynurenine pathway, the major pathway of tryptophan metabolism [2274]. The enzyme is specific for tryptophan as substrate, but is far more active with L-tryptophan than with D-tryptophan [3166].
References: [3956, 3166, 2184, 740, 2274]

[EC 1.13.11.11 created 1961 as EC 1.11.1.4, deleted 1964, reinstated 1965 as EC 1.13.1.12, transferred 1972 to EC 1.13.11.11, modified 1989, modified 2006]

EC 1.13.11.12

Accepted name: linoleate 13*S*-lipoxygenase
Reaction: (1) linoleate + O₂ = (9*Z*,11*E*,13*S*)-13-hydroperoxyoctadeca-9,11-dienoate
(2) α-linolenate + O₂ = (9*Z*,11*E*,13*S*,15*Z*)-13-hydroperoxyoctadeca-9,11,15-trienoate
Other name(s): 13-lipoxidase; carotene oxidase; 13-lipoperoxidase; fat oxidase; 13-lipoxydase; lionoleate:O₂ 13-oxidoreductase
Systematic name: linoleate:oxygen 13-oxidoreductase
Comments: Contains nonheme iron. A common plant lipoxygenase that oxidizes linoleate and α-linolenate, the two most common polyunsaturated fatty acids in plants, by inserting molecular oxygen at the C-13 position with (*S*)-configuration. This enzyme produces precursors for several important compounds, including the plant hormone jasmonic acid. EC 1.13.11.58, linoleate 9*S*-lipoxygenase, catalyses a similar reaction at the second available position of these fatty acids.
References: [618, 3862, 4488, 3245, 156]

[EC 1.13.11.12 created 1961 as EC 1.99.2.1, transferred 1965 to EC 1.13.1.13, transferred 1972 to EC 1.13.11.12, modified 2011, modified

2012]

[1.13.11.13 Deleted entry. ascorbate 2,3-dioxygenase. The activity is the sum of several enzymatic and spontaneous reactions]

[EC 1.13.11.13 created 1972, deleted 2012]

EC 1.13.11.14

Accepted name: 2,3-dihydroxybenzoate 3,4-dioxygenase
Reaction: 2,3-dihydroxybenzoate + O₂ = 3-carboxy-2-hydroxymuconate semialdehyde
Other name(s): *o*-pyrocatechuate oxygenase; 2,3-dihydroxybenzoate 1,2-dioxygenase; 2,3-dihydroxybenzoic oxygenase; 2,3-dihydroxybenzoate oxygenase; 2,3-dihydroxybenzoate:oxygen 3,4-oxidoreductase (decyclizing)
Systematic name: 2,3-dihydroxybenzoate:oxygen 3,4-oxidoreductase (ring-opening)
References: [3178]

[EC 1.13.11.14 created 1972, modified 1976]

EC 1.13.11.15

Accepted name: 3,4-dihydroxyphenylacetate 2,3-dioxygenase
Reaction: 3,4-dihydroxyphenylacetate + O₂ = 2-hydroxy-5-carboxymethylmuconate semialdehyde
Other name(s): 3,4-dihydroxyphenylacetic acid 2,3-dioxygenase; HPC dioxygenase; homoprotocatechuate 2,3-dioxygenase; 3,4-dihydroxyphenylacetate:oxygen 2,3-oxidoreductase (decyclizing)
Systematic name: 3,4-dihydroxyphenylacetate:oxygen 2,3-oxidoreductase (ring-opening)
Comments: An iron protein.
References: [12, 199, 2100]

[EC 1.13.11.15 created 1972]

EC 1.13.11.16

Accepted name: 3-carboxyethylcatechol 2,3-dioxygenase
Reaction: (1) 3-(2,3-dihydroxyphenyl)propanoate + O₂ = (2*Z*,4*E*)-2-hydroxy-6-oxonona-2,4-diene-1,9-dioate
(2) (2*E*)-3-(2,3-dihydroxyphenyl)prop-2-enoate + O₂ = (2*Z*,4*E*,7*E*)-2-hydroxy-6-oxonona-2,4,7-triene-1,9-dioate
Other name(s): 2,3-dihydroxy-β-phenylpropionic dioxygenase; 2,3-dihydroxy-β-phenylpropionate oxygenase; 3-(2,3-dihydroxyphenyl)propanoate:oxygen 1,2-oxidoreductase; 3-(2,3-dihydroxyphenyl)propanoate:oxygen 1,2-oxidoreductase (decyclizing)
Systematic name: 3-(2,3-dihydroxyphenyl)propanoate:oxygen 1,2-oxidoreductase (ring-opening)
Comments: An iron protein. This enzyme catalyses a step in the pathway of phenylpropanoid compounds degradation.
References: [717, 2118, 813]

[EC 1.13.11.16 created 1972, modified 2011, modified 2012]

EC 1.13.11.17

Accepted name: indole 2,3-dioxygenase
Reaction: indole + O₂ = 2-formylaminobenzaldehyde
Other name(s): indole oxidase; indoleamine 2,3-dioxygenase (ambiguous); indole:O₂ oxidoreductase; indole-oxygen 2,3-oxidoreductase (decyclizing); IDO (ambiguous); indole:oxygen 2,3-oxidoreductase (decyclizing)
Systematic name: indole:oxygen 2,3-oxidoreductase (ring-opening)
Comments: Enzymes from the plants *Tecoma stans*, *Jasminum grandiflorum* and *Zea mays* are flavoproteins containing copper. They are part of enzyme systems that form either anthranil (2,1-benzisoxazole) (*Tecoma stans*), anthranilate (*Jasminum grandiflorum*) or both (*Zea mays*) as the final product. A second enzyme from *Tecoma stans* is not a flavoprotein, does not require copper, and is part of a system that forms anthranilate as the final product.

References: [2693, 559, 835, 2077]

[EC 1.13.11.17 created 1972, modified 1986]

EC 1.13.11.18

Accepted name: persulfide dioxygenase
Reaction: S -sulfanylgutathione + O₂ + H₂O = glutathione + sulfite + 2 H⁺ (overall reaction)
(1a) S -sulfanylgutathione + O₂ = S -sulfinatoglutathione + H⁺
(1b) S -sulfinatoglutathione + H₂O = glutathione + sulfite + H⁺ (spontaneous)
Other name(s): sulfur oxygenase (incorrect); sulfur:oxygen oxidoreductase (incorrect); sulfur dioxygenase (incorrect)
Systematic name: S -sulfanylgutathione:oxygen oxidoreductase
Comments: An iron protein. Perthiols, formed spontaneously by interactions between thiols and elemental sulfur or sulfide, are the only acceptable substrate to the enzyme. The sulfite that is formed by the enzyme can be further converted into sulfate, thiosulfate or S -sulfoglutathione (GSSO₃⁻) non-enzymically [3221].
References: [3749, 3221, 2278, 1541, 2995]

[EC 1.13.11.18 created 1972, modified 2015]

EC 1.13.11.19

Accepted name: cysteamine dioxygenase
Reaction: 2-aminoethanethiol + O₂ = hypotaurine
Other name(s): persulfurase; cysteamine oxygenase; cysteamine:oxygen oxidoreductase
Systematic name: 2-aminoethanethiol:oxygen oxidoreductase
Comments: A non-heme iron protein that is involved in the biosynthesis of taurine. Requires catalytic amounts of a cofactor-like compound, such as sulfur, sulfide, selenium or methylene blue for maximal activity. 3-Aminopropanethiol (homocysteamine) and 2-mercaptoethanol can also act as substrates, but glutathione, cysteine, and cysteine ethyl- and methyl esters are not good substrates [524, 525].
References: [524, 4248, 525, 3180]

[EC 1.13.11.19 created 1972, modified 2006]

EC 1.13.11.20

Accepted name: cysteine dioxygenase
Reaction: L-cysteine + O₂ = 3-sulfinoalanine
Other name(s): cysteine oxidase
Systematic name: L-cysteine:oxygen oxidoreductase
Comments: Requires Fe²⁺ and NAD(P)H.
References: [2294]

[EC 1.13.11.20 created 1972, modified 1976]

[1.13.11.21 Transferred entry. β -carotene 15,15'-dioxygenase. Now EC 1.14.99.36, β -carotene 15,15'-monooxygenase]

[EC 1.13.11.21 created 1972, deleted 2001]

EC 1.13.11.22

Accepted name: caffeate 3,4-dioxygenase
Reaction: 3,4-dihydroxy-*trans*-cinnamate + O₂ = 3-(2-carboxyethenyl)-*cis,cis*-muconate
Other name(s): 3,4-dihydroxy-*trans*-cinnamate:oxygen 3,4-oxidoreductase (decyclizing)
Systematic name: 3,4-dihydroxy-*trans*-cinnamate:oxygen 3,4-oxidoreductase (ring-opening)
References: [3431]

[EC 1.13.11.22 created 1972]

EC 1.13.11.23

Accepted name: 2,3-dihydroxyindole 2,3-dioxygenase
Reaction: 2,3-dihydroxyindole + O₂ = anthranilate + CO₂
Other name(s): 2,3-dihydroxyindole:oxygen 2,3-oxidoreductase (deacyclizing)
Systematic name: 2,3-dihydroxyindole:oxygen 2,3-oxidoreductase (ring-opening)
References: [1094]

[EC 1.13.11.23 created 1972]

EC 1.13.11.24

Accepted name: quercetin 2,3-dioxygenase
Reaction: quercetin + O₂ = 2-(3,4-dihydroxybenzoyloxy)-4,6-dihydroxybenzoate + CO + H⁺
Other name(s): quercetinase; flavonol 2,4-oxygenase; quercetin:oxygen 2,3-oxidoreductase (deacyclizing)
Systematic name: quercetin:oxygen 2,3-oxidoreductase (ring-opening)
Comments: The enzyme from *Aspergillus* sp. is a copper protein whereas that from *Bacillus subtilis* contains iron. Quercetin is a flavonol (5,7,3',4'-tetrahydroxyflavonol).
References: [2857, 3635, 370]

[EC 1.13.11.24 created 1972]

EC 1.13.11.25

Accepted name: 3,4-dihydroxy-9,10-secoandrosta-1,3,5(10)-triene-9,17-dione 4,5-dioxygenase
Reaction: 3,4-dihydroxy-9,10-secoandrosta-1,3,5(10)-triene-9,17-dione + O₂ = 3-hydroxy-5,9,17-trioxo-4,5:9,10-disecoandrosta-1(10),2-dien-4-oate
Other name(s): steroid 4,5-dioxygenase; 3-alkylcatechol 2,3-dioxygenase; 3,4-dihydroxy-9,10-secoandrosta-1,3,5(10)-triene-9,17-dione:oxygen 4,5-oxidoreductase (deacyclizing)
Systematic name: 3,4-dihydroxy-9,10-secoandrosta-1,3,5(10)-triene-9,17-dione:oxygen 4,5-oxidoreductase (ring-opening)
Comments: Requires Fe²⁺. Also acts on 3-isopropylcatechol and 3-*tert*-butyl-5-methylcatechol.
References: [1201]

[EC 1.13.11.25 created 1972]

EC 1.13.11.26

Accepted name: peptide-tryptophan 2,3-dioxygenase
Reaction: [protein]-L-tryptophan + O₂ = [protein]-*N*-formyl-L-kynurenine
Other name(s): pyrroloxygenase; peptidyltryptophan 2,3-dioxygenase; tryptophan pyrroloxygenase; [protein]-L-tryptophan:oxygen 2,3-oxidoreductase (deacyclizing)
Systematic name: [protein]-L-tryptophan:oxygen 2,3-oxidoreductase (ring-opening)
Comments: Also acts on tryptophan.
References: [1085, 488]

[EC 1.13.11.26 created 1972, modified 2011]

EC 1.13.11.27

Accepted name: 4-hydroxyphenylpyruvate dioxygenase
Reaction: 4-hydroxyphenylpyruvate + O₂ = homogentisate + CO₂
Other name(s): *p*-hydroxyphenylpyruvic hydroxylase; *p*-hydroxyphenylpyruvate hydroxylase; *p*-hydroxyphenylpyruvate oxidase; *p*-hydroxyphenylpyruvic oxidase; *p*-hydroxyphenylpyruvate dioxygenase; *p*-hydroxyphenylpyruvic acid hydroxylase; 4-hydroxyphenylpyruvic acid dioxygenase

Systematic name: 4-hydroxyphenylpyruvate:oxygen oxidoreductase (hydroxylating, decarboxylating)
Comments: The *Pseudomonas* enzyme contains one Fe³⁺ per mole of enzyme; the enzymes from other sources may contain essential iron or copper.
References: [2266, 3207]

[EC 1.13.11.27 created 1961 as EC 1.99.1.14, transferred 1965 to EC 1.14.2.2, transferred 1972 to EC 1.13.11.27]

EC 1.13.11.28

Accepted name: 2,3-dihydroxybenzoate 2,3-dioxygenase
Reaction: 2,3-dihydroxybenzoate + O₂ = 2-carboxy-*cis,cis*-muconate
Other name(s): 2,3-dihydroxybenzoate 2,3-oxygenase; 2,3-dihydroxybenzoate:oxygen 2,3-oxidoreductase (decyclizing)
Systematic name: 2,3-dihydroxybenzoate:oxygen 2,3-oxidoreductase (ring-opening)
Comments: Also acts, more slowly, with 2,3-dihydroxy-4-methylbenzoate and 2,3-dihydroxy-4-isopropylbenzoate.
References: [876, 3462]

[EC 1.13.11.28 created 1978]

EC 1.13.11.29

Accepted name: stizolobate synthase
Reaction: L-dopa + O₂ = 4-(L-alanin-3-yl)-2-hydroxy-*cis,cis*-muconate 6-semialdehyde
Systematic name: 3,4-dihydroxy-L-phenylalanine:oxygen 4,5-oxidoreductase (recyclizing)
Comments: The intermediate product undergoes ring closure and oxidation, with NAD(P)⁺ as acceptor, to stizolobic acid. The enzyme requires Zn²⁺.
References: [3283, 3284]

[EC 1.13.11.29 created 1978]

EC 1.13.11.30

Accepted name: stizolobinate synthase
Reaction: L-dopa + O₂ = 5-(L-alanin-3-yl)-2-hydroxy-*cis,cis*-muconate 6-semialdehyde
Systematic name: 3,4-dihydroxy-L-phenylalanine:oxygen 2,3-oxidoreductase (recyclizing)
Comments: The intermediate product undergoes ring closure and oxidation, with NAD(P)⁺ as acceptor, to stizolobinic acid. The enzyme requires Zn²⁺.
References: [3283, 3284]

[EC 1.13.11.30 created 1978]

EC 1.13.11.31

Accepted name: arachidonate 12-lipoxygenase
Reaction: arachidonate + O₂ = (5*Z*,8*Z*,10*E*,14*Z*)-(12*S*)-12-hydroperoxyicoso-5,8,10,14-tetraenoate
Other name(s): Δ¹²-lipoxygenase; 12-lipoxygenase; 12Δ-lipoxygenase; C-12 lipoxygenase; 12*S*-lipoxygenase; leukotriene A₄ synthase; LTA₄ synthase
Systematic name: arachidonate:oxygen 12-oxidoreductase
Comments: The product is rapidly reduced to the corresponding 12*S*-hydroxy compound.
References: [1353, 2829, 4093]

[EC 1.13.11.31 created 1983]

[1.13.11.32 Transferred entry. 2-nitropropane dioxygenase. Now EC 1.13.12.16, nitronate monooxygenase]

[EC 1.13.11.32 created 1984, modified 2006, deleted 2009]

EC 1.13.11.33

Accepted name: arachidonate 15-lipoxygenase
Reaction: arachidonate + O₂ = (5Z,8Z,11Z,13E)-(15S)-15-hydroperoxyicosanoic acid
Other name(s): 15-lipoxygenase; linoleic acid ω⁶-lipoxygenase; ω⁶ lipoxygenase
Systematic name: arachidonate:oxygen 15-oxidoreductase
Comments: The product is rapidly reduced to the corresponding 15S-hydroxy compound.
References: [433, 2736, 2874, 3484]

[EC 1.13.11.33 created 1984]

EC 1.13.11.34

Accepted name: arachidonate 5-lipoxygenase
Reaction: arachidonate + O₂ = leukotriene A₄ + H₂O (overall reaction)
(1a) arachidonate + O₂ = (6E,8Z,11Z,14Z)-(5S)-5-hydroperoxyicosanoic acid
(1b) (6E,8Z,11Z,14Z)-(5S)-5-hydroperoxyicosanoic acid = leukotriene A₄ + H₂O
Other name(s): leukotriene-A₄ synthase; Δ⁵-lipoxygenase; 5Δ-lipoxygenase; arachidonic 5-lipoxygenase; arachidonic acid 5-lipoxygenase; C-5-lipoxygenase; LTA synthase; leukotriene A₄ synthase
Systematic name: arachidonate:oxygen 5-oxidoreductase
References: [2447, 2847, 3501, 3502]

[EC 1.13.11.34 created 1984, modified 1990]

EC 1.13.11.35

Accepted name: pyrogallol 1,2-oxygenase
Reaction: 1,2,3-trihydroxybenzene + O₂ = (2Z,4E)-2-hydroxyhexa-2,4-dienedioate
Other name(s): pyrogallol 1,2-dioxygenase; 1,2,3-trihydroxybenzene:oxygen 1,2-oxidoreductase (decyclizing)
Systematic name: 1,2,3-trihydroxybenzene:oxygen 1,2-oxidoreductase (ring-opening)
References: [1295]

[EC 1.13.11.35 created 1984, modified 2012]

EC 1.13.11.36

Accepted name: chloridazon-catechol dioxygenase
Reaction: 5-amino-4-chloro-2-(2,3-dihydroxyphenyl)-3(2H)-pyridazinone + O₂ = 5-amino-4-chloro-2-(2-hydroxymuconoyl)-3(2H)-pyridazinone
Other name(s): 5-amino-4-chloro-2-(2,3-dihydroxyphenyl)-3(2H)-pyridazinone 1,2-oxidoreductase (decyclizing)
Systematic name: 5-amino-4-chloro-2-(2,3-dihydroxyphenyl)-3(2H)-pyridazinone 1,2-oxidoreductase (ring-opening)
Comments: An iron protein, requiring additional Fe²⁺. Not identical with EC 1.13.11.1 (catechol 1,2-dioxygenase), EC 1.13.11.2 (catechol 2,3-dioxygenase) or EC 1.13.11.5 (homogentisate 1,2-dioxygenase). Involved in the breakdown of the herbicide chloridazon.
References: [2653, 2654]

[EC 1.13.11.36 created 1984]

EC 1.13.11.37

Accepted name: hydroxyquinol 1,2-dioxygenase
Reaction: hydroxyquinol + O₂ = maleylacetate
Other name(s): hydroxyquinol dioxygenase; benzene-1,2,4-triol:oxygen 1,2-oxidoreductase (decyclizing); benzene-1,2,4-triol:oxygen 1,2-oxidoreductase (ring-opening)
Systematic name: hydroxyquinol:oxygen 1,2-oxidoreductase (ring-opening)
Comments: An iron protein. Highly specific; catechol and pyrogallol are acted on at less than 1% of the rate at which hydroxyquinol is oxidized.
References: [3767, 1002, 1423]

[EC 1.13.11.37 created 1989, modified 2013]

EC 1.13.11.38

Accepted name: 1-hydroxy-2-naphthoate 1,2-dioxygenase
Reaction: 1-hydroxy-2-naphthoate + O₂ = (3Z)-4-(2-carboxyphenyl)-2-oxobut-3-enoate
Other name(s): 1-hydroxy-2-naphthoate dioxygenase; 1-hydroxy-2-naphthoate-degrading enzyme; 1-hydroxy-2-naphthoic acid dioxygenase; 1-hydroxy-2-naphthoate:oxygen 1,2-oxidoreductase (deacyclizing)
Systematic name: 1-hydroxy-2-naphthoate:oxygen 1,2-oxidoreductase (ring-opening)
Comments: Requires Fe²⁺. Involved, with EC 4.1.2.34 4-(2-carboxyphenyl)-2-oxobut-3-enoate aldolase, in the metabolism of phenanthrene in bacteria.
References: [201]

[EC 1.13.11.38 created 1989]

EC 1.13.11.39

Accepted name: biphenyl-2,3-diol 1,2-dioxygenase
Reaction: biphenyl-2,3-diol + O₂ = 2-hydroxy-6-oxo-6-phenylhexa-2,4-dienoate
Other name(s): 2,3-dihydroxybiphenyl dioxygenase; biphenyl-2,3-diol dioxygenase; *bphC* (gene name); biphenyl-2,3-diol:oxygen 1,2-oxidoreductase (deacyclizing)
Systematic name: biphenyl-2,3-diol:oxygen 1,2-oxidoreductase (ring-opening)
Comments: Contains Fe²⁺ or Mn²⁺ [1422]. This enzyme participates in the degradation pathway of biphenyl and PCB (poly chlorinated biphenyls), and catalyses the first ring cleavage step by incorporating two oxygen atoms into the catechol ring formed by EC 1.3.1.56, *cis*-2,3-dihydrobiphenyl-2,3-diol dehydrogenase. The enzyme from the bacterium *Burkholderia xenovorans* LB400 can also process catechol, 3-methylcatechol, and 4-methylcatechol, but less efficiently [944]. The enzyme from the carbazole-degrader *Pseudomonas resinovorans* strain CA10 also accepts 2'-aminobiphenyl-2,3-diol [1696]. The enzyme from *Ralstonia* sp. SBUG 290 can also accept 1,2-dihydroxydibenzofuran and 1,2-dihydroxynaphthalene [4180]. The enzyme is strongly inhibited by the substrate [944]. Not identical with EC 1.13.11.2 catechol 2,3-dioxygenase.
References: [944, 3974, 1422, 4180, 1696]

[EC 1.13.11.39 created 1989]

EC 1.13.11.40

Accepted name: arachidonate 8-lipoxygenase
Reaction: arachidonate + O₂ = (5Z,9E,11Z,14Z)-(8R)-8-hydroperoxyicosa-5,9,11,14-tetraenoate
Other name(s): 8-lipoxygenase; 8(R)-lipoxygenase
Systematic name: arachidonate:oxygen 8-oxidoreductase
Comments: From the coral *Pseudoplexaura porosa*.
References: [444]

[EC 1.13.11.40 created 1989]

EC 1.13.11.41

Accepted name: 2,4'-dihydroxyacetophenone dioxygenase
Reaction: 2,4'-dihydroxyacetophenone + O₂ = 4-hydroxybenzoate + formate
Other name(s): (4-hydroxybenzoyl)methanol oxygenase
Systematic name: 2,4'-dihydroxyacetophenone oxidoreductase (C-C-bond-cleaving)
References: [1561]

[EC 1.13.11.41 created 1989]

[1.13.11.42 Deleted entry. indoleamine-pyrrole 2,3-dioxygenase. The enzyme was identical to EC 1.13.11.11, tryptophan

2,3-dioxygenase]

[EC 1.13.11.42 created 1992, deleted 2006]

EC 1.13.11.43

Accepted name: lignostilbene $\alpha\beta$ -dioxygenase
Reaction: 1,2-bis(4-hydroxy-3-methoxyphenyl)ethylene + O₂ = 2 vanillin
Systematic name: 1,2-bis(4-hydroxy-3-methoxyphenyl)ethylene:oxygen oxidoreductase ($\alpha\beta$ -bond-cleaving)
Comments: An iron protein. The enzyme catalyses oxidative cleavage of the interphenyl double bond in the synthetic substrate and lignin-derived stilbenes. It is responsible for the degradation of a diarylpropane-type structure in lignin.
References: [1807]

[EC 1.13.11.43 created 1992]

[1.13.11.44 Deleted entry. linoleate diol synthase. Activity is covered by EC 1.13.11.60, linoleate 8R-lipoxygenase and EC 5.4.4.6, 9,12-octadecadienoate 8-hydroperoxide 8S-isomerase.]

[EC 1.13.11.44 created 2000, deleted 2011]

EC 1.13.11.45

Accepted name: linoleate 11-lipoxygenase
Reaction: linoleate + O₂ = (9Z,12Z)-(11S)-11-hydroperoxyoctadeca-9,12-dienoate
Other name(s): linoleate dioxygenase, manganese lipoxygenase
Systematic name: linoleate:oxygen 11S-oxidoreductase
Comments: The product (9Z,12Z)-(11S)-11-hydroperoxyoctadeca-9,12-dienoate, is converted, more slowly, into (9Z,11E)-(13R)-13-hydroperoxyoctadeca-9,11-dienoate. The enzyme from the fungus *Gaeumannomyces graminis* requires Mn²⁺. It also acts on α -linolenate, whereas γ -linolenate is a poor substrate. Oleate and arachidonate are not substrates.
References: [1354, 2875, 3699]

[EC 1.13.11.45 created 2000]

EC 1.13.11.46

Accepted name: 4-hydroxymandelate synthase
Reaction: 4-hydroxyphenylpyruvate + O₂ = (S)-4-hydroxymandelate + CO₂
Other name(s): 4-hydroxyphenylpyruvate dioxygenase II
Systematic name: (S)-4-hydroxyphenylpyruvate:oxygen oxidoreductase (decarboxylating)
Comments: Requires Fe²⁺. Involved in the biosynthesis of the vancomycin group of glycopeptide antibiotics.
References: [1599, 614]

[EC 1.13.11.46 created 2001]

EC 1.13.11.47

Accepted name: 3-hydroxy-4-oxoquinoline 2,4-dioxygenase
Reaction: 3-hydroxy-1H-quinolin-4-one + O₂ = N-formylanthranilate + CO
Other name(s): (1H)-3-hydroxy-4-oxoquinoline 2,4-dioxygenase; 3-hydroxy-4-oxo-1,4-dihydroquinoline 2,4-dioxygenase; 3-hydroxy-4(1H)-one, 2,4-dioxygenase; quinoline-3,4-diol 2,4-dioxygenase
Systematic name: 3-hydroxy-1H-quinolin-4-one 2,4-dioxygenase (CO-forming)
Comments: Does not contain a metal centre or organic cofactor. Fission of two C-C bonds: 2,4-dioxygenolytic cleavage with concomitant release of carbon monoxide. The enzyme from *Pseudomonas putida* is highly specific for this substrate.
References: [217, 218, 1020]

[EC 1.13.11.47 created 1999 as EC 1.13.99.5, transferred 2001 to EC 1.13.11.47 (EC 1.12.99.5 created 1999 deleted 2001 as identical)]

EC 1.13.11.48

Accepted name: 3-hydroxy-2-methylquinolin-4-one 2,4-dioxygenase
Reaction: 3-hydroxy-2-methyl-1*H*-quinolin-4-one + O₂ = *N*-acetylanthranilate + CO
Other name(s): (1*H*)-3-hydroxy-4-oxoquinoline 2,4-dioxygenase
Systematic name: 3-hydroxy-2-methyl-1*H*-quinolin-4-one 2,4-dioxygenase (CO-forming)
Comments: Does not contain a metal centre or organic cofactor. Fission of two C-C bonds: 2,4-dioxygenolytic cleavage with concomitant release of carbon monoxide. The enzyme from *Arthrobacter sp.* can also act on 3-hydroxy-4-oxoquinoline, forming *N*-formylanthranilate and CO (*cf.* EC 1.13.11.47, 3-hydroxy-4-oxoquinoline 2,4-dioxygenase), but more slowly.
References: [217, 218, 1020]

[EC 1.13.11.48 created 2001]

EC 1.13.11.49

Accepted name: chlorite O₂-lyase
Reaction: chloride + O₂ = chlorite
Systematic name: chloride:oxygen oxidoreductase
Comments: Reaction occurs in the reverse direction in chlorate- and perchlorate-reducing bacteria. There is no activity when chlorite is replaced by hydrogen peroxide, perchlorate, chlorate or nitrite. The term 'chlorite dismutase' is misleading as the reaction does not involve dismutation/disproportionation. Contains iron and protoheme IX.
References: [4001, 3638]

[EC 1.13.11.49 created 2001]

EC 1.13.11.50

Accepted name: acetylacetone-cleaving enzyme
Reaction: pentane-2,4-dione + O₂ = acetate + 2-oxopropanal
Other name(s): Dke1; acetylacetone dioxygenase; diketone cleaving dioxygenase; diketone cleaving enzyme
Systematic name: acetylacetone:oxygen oxidoreductase
Comments: An Fe(II)-dependent enzyme. Forms the first step in the acetylacetone degradation pathway of *Acinetobacter johnsonii*. While acetylacetone is by far the best substrate, heptane-3,5-dione, octane-2,4-dione, 2-acetylcyclohexanone and ethyl acetoacetate can also act as substrates.
References: [3668]

[EC 1.13.11.50 created 2003]

EC 1.13.11.51

Accepted name: 9-*cis*-epoxycarotenoid dioxygenase
Reaction: (1) a 9-*cis*-epoxycarotenoid + O₂ = 2-*cis*,4-*trans*-xanthoxin + a 12'-apo-carotenal
(2) 9-*cis*-violaxanthin + O₂ = 2-*cis*,4-*trans*-xanthoxin + (3*S*,5*R*,6*S*)-5,6-epoxy-3-hydroxy-5,6-dihydro-12'-apo-β-caroten-12'-al
(3) 9'-*cis*-neoxanthin + O₂ = 2-*cis*,4-*trans*-xanthoxin + (3*S*,5*R*,6*R*)-5,6-dihydroxy-6,7-didehydro-5,6-dihydro-12'-apo-β-caroten-12'-al
Other name(s): nine-*cis*-epoxycarotenoid dioxygenase; NCED; AtNCED3; PvNCED1; VP14
Systematic name: 9-*cis*-epoxycarotenoid 11,12-dioxygenase
Comments: Requires iron(II). Acts on 9-*cis*-violaxanthin and 9'-*cis*-neoxanthin but not on the *all-trans* isomers [3800, 3079]. In vitro, it will cleave 9-*cis*-zeaxanthin. Catalyses the first step of abscisic-acid biosynthesis from carotenoids in chloroplasts, in response to water stress. The other enzymes involved in the abscisic-acid biosynthesis pathway are EC 1.1.1.288 (xanthoxin dehydrogenase), EC 1.2.3.14 (abscisic-aldehyde oxidase) and EC 1.14.13.93 [(+)-abscisic acid 8'-hydroxylase].
References: [3413, 3800, 3079, 3872, 1686, 1687]

[EC 1.13.11.51 created 2005]

EC 1.13.11.52

- Accepted name:** indoleamine 2,3-dioxygenase
Reaction: (1) D-tryptophan + O₂ = *N*-formyl-D-kynurenine
(2) L-tryptophan + O₂ = *N*-formyl-L-kynurenine
Other name(s): IDO (ambiguous); tryptophan pyrrolase (ambiguous); D-tryptophan:oxygen 2,3-oxidoreductase (decyclizing)
Systematic name: D-tryptophan:oxygen 2,3-oxidoreductase (ring-opening)
Comments: A protohemoprotein. Requires ascorbic acid and methylene blue for activity. This enzyme has broader substrate specificity than EC 1.13.11.11, tryptophan 2,3-dioxygenase [4318]. It is induced in response to pathological conditions and host-defense mechanisms and its distribution in mammals is not confined to the liver [4350]. While the enzyme is more active with D-tryptophan than L-tryptophan, its only known function to date is in the metabolism of L-tryptophan [4350, 2274]. Super-oxide radicals can replace O₂ as oxygen donor [1516, 3870].
References: [4318, 4350, 3794, 1516, 740, 2274, 3870, 3582]

[EC 1.13.11.52 created 2006]

EC 1.13.11.53

- Accepted name:** acireductone dioxygenase (Ni²⁺-requiring)
Reaction: 1,2-dihydroxy-5-(methylsulfanyl)pent-1-en-3-one + O₂ = 3-(methylsulfanyl)propanoate + formate + CO
Other name(s): ARD; 2-hydroxy-3-keto-5-thiomethylpent-1-ene dioxygenase (ambiguous); acireductone dioxygenase (ambiguous); E-2; 1,2-dihydroxy-5-(methylthio)pent-1-en-3-one:oxygen oxidoreductase (formate- and CO-forming)
Systematic name: 1,2-dihydroxy-5-(methylsulfanyl)pent-1-en-3-one:oxygen oxidoreductase (formate- and CO-forming)
Comments: Requires Ni²⁺. If iron(II) is bound instead of Ni²⁺, the reaction catalysed by EC 1.13.11.54, acireductone dioxygenase [iron(II)-requiring], occurs instead [4256]. The enzyme from the bacterium *Klebsiella oxytoca* (formerly *Klebsiella pneumoniae*) ATCC strain 8724 is involved in the methionine salvage pathway.
References: [4256, 4257, 1118, 723, 2584, 722, 48, 3024]

[EC 1.13.11.53 created 2006]

EC 1.13.11.54

- Accepted name:** acireductone dioxygenase [iron(II)-requiring]
Reaction: 1,2-dihydroxy-5-(methylsulfanyl)pent-1-en-3-one + O₂ = 4-(methylsulfanyl)-2-oxobutanoate + formate
Other name(s): ARD'; 2-hydroxy-3-keto-5-thiomethylpent-1-ene dioxygenase (ambiguous); acireductone dioxygenase (ambiguous); E-2'; E-3 dioxygenase; 1,2-dihydroxy-5-(methylthio)pent-1-en-3-one:oxygen oxidoreductase (formate-forming)
Systematic name: 1,2-dihydroxy-5-(methylsulfanyl)pent-1-en-3-one:oxygen oxidoreductase (formate-forming)
Comments: Requires iron(II). If Ni²⁺ is bound instead of iron(II), the reaction catalysed by EC 1.13.11.53, acireductone dioxygenase (Ni²⁺-requiring), occurs instead. The enzyme from the bacterium *Klebsiella oxytoca* (formerly *Klebsiella pneumoniae*) ATCC strain 8724 is involved in the methionine salvage pathway.
References: [4256, 4257, 1118, 723, 2584, 722, 48, 3024]

[EC 1.13.11.54 created 2006]

EC 1.13.11.55

- Accepted name:** sulfur oxygenase/reductase

Reaction: 4 sulfur + 4 H₂O + O₂ = 2 hydrogen sulfide + 2 sulfite
Other name(s): SOR; sulfur oxygenase; sulfur oxygenase reductase
Systematic name: sulfur:oxygen oxidoreductase (hydrogen-sulfide- and sulfite-forming)
Comments: This enzyme, which is found in thermophilic microorganisms, contains one mononuclear non-heme iron centre per subunit. Elemental sulfur is both the electron donor and one of the two known acceptors, the other being oxygen. Thiosulfate is also observed as a product, but is likely formed non-enzymically by a reaction between sulfite and sulfur [1965]. This enzyme differs from EC 1.13.11.18, sulfur dioxygenase and EC 1.12.98.4, sulfhydrogenase, in that both activities occur simultaneously.
References: [1965, 1966, 3731, 3976]

[EC 1.13.11.55 created 2006]

EC 1.13.11.56

Accepted name: 1,2-dihydroxynaphthalene dioxygenase
Reaction: naphthalene-1,2-diol + O₂ = 2-hydroxy-2*H*-chromene-2-carboxylate
Other name(s): 1,2-DHN dioxygenase; DHNDO; 1,2-dihydroxynaphthalene oxygenase; 1,2-dihydroxynaphthalene:oxygen oxidoreductase
Systematic name: naphthalene-1,2-diol:oxygen oxidoreductase
Comments: This enzyme is involved in naphthalene degradation. Requires Fe²⁺.
References: [2069, 1866, 2958]

[EC 1.13.11.56 created 2010, modified 2010]

EC 1.13.11.57

Accepted name: gallate dioxygenase
Reaction: 3,4,5-trihydroxybenzoate + O₂ = (1*E*)-4-oxobut-1-ene-1,2,4-tricarboxylate
Other name(s): GalA; gallate:oxygen oxidoreductase
Systematic name: 3,4,5-trihydroxybenzoate:oxygen oxidoreductase
Comments: Contains non-heme Fe²⁺. The enzyme is a ring-cleavage dioxygenase that acts specifically on 3,4,5-trihydroxybenzoate to produce the keto-tautomer of 4-oxalomesaconate [2808, 2807].
References: [2808, 2807]

[EC 1.13.11.57 created 2011]

EC 1.13.11.58

Accepted name: linoleate 9*S*-lipoxygenase
Reaction: linoleate + O₂ = (9*S*,10*E*,12*Z*)-9-hydroperoxy-10,12-octadecadienoate
Other name(s): 9-lipoxygenase; 9*S*-lipoxygenase; linoleate 9-lipoxygenase; LOX1 (gene name); 9*S*-LOX
Systematic name: linoleate:oxygen 9*S*-oxidoreductase
Comments: Contains nonheme iron. A common plant lipoxygenase that oxidizes linoleate and α-linolenate, the two most common polyunsaturated fatty acids in plants, by inserting molecular oxygen at the C₉ position with (*S*)-configuration. The enzyme plays a physiological role during the early stages of seedling growth. The enzyme from *Arabidopsis thaliana* shows comparable activity towards linoleate and linolenate [194]. EC 1.13.11.12 (linoleate 13*S*-lipoxygenase) catalyses a similar reaction at another position of these fatty acids.
References: [4027, 329, 88, 194]

[EC 1.13.11.58 created 2011]

EC 1.13.11.59

Accepted name: torulene dioxygenase
Reaction: torulene + O₂ = 4'-apo-β,ψ-caroten-4'-al + 3-methylbut-2-enal
Other name(s): CAO-2; CarT

Systematic name: torulene:oxygen oxidoreductase
Comments: It is assumed that 3-methylbut-2-enal is formed. The enzyme cannot cleave the saturated 3',4'-bond of γ -carotene which implies that a 3',4'-double bond is necessary for this reaction.
References: [3051, 3277, 967]

[EC 1.13.11.59 created 2011]

EC 1.13.11.60

Accepted name: linoleate 8*R*-lipoxygenase
Reaction: linoleate + O₂ = (8*R*,9*Z*,12*Z*)-8-hydroperoxyoctadeca-9,12-dienoate
Other name(s): linoleic acid 8*R*-dioxygenase; 5,8-LDS (bifunctional enzyme); 7,8-LDS (bifunctional enzyme); 5,8-linoleate diol synthase (bifunctional enzyme); 7,8-linoleate diol synthase (bifunctional enzyme); PpoA
Systematic name: linoleate:oxygen (8*R*)-oxidoreductase
Comments: The enzyme contains heme [410, 3698]. The bifunctional enzyme from *Aspergillus nidulans* uses different heme domains to catalyse two separate reactions. Linoleic acid is oxidized within the N-terminal heme peroxidase domain to (8*R*,9*Z*,12*Z*)-8-hydroperoxyoctadeca-9,12-dienoate, which is subsequently isomerized by the C-terminal *P*-450 heme thiolate domain to (5*S*,8*R*,9*Z*,12*Z*)-5,8-dihydroxyoctadeca-9,12-dienoate (cf. EC 5.4.4.5, 9,12-octadecadienoate 8-hydroperoxide 8*R*-isomerase) [410]. The bifunctional enzyme from *Gaeumannomyces graminis* also catalyses the oxidation of linoleic acid to (8*R*,9*Z*,12*Z*)-8-hydroperoxyoctadeca-9,12-dienoate, but its second domain isomerizes it to (7*S*,8*S*,9*Z*,12*Z*)-5,8-dihydroxyoctadeca-9,12-dienoate (cf. EC 5.4.4.6, 9,12-octadecadienoate 8-hydroperoxide 8*S*-isomerase) [3698].
References: [410, 1355, 1160, 3698]

[EC 1.13.11.60 created 2011]

EC 1.13.11.61

Accepted name: linolenate 9*R*-lipoxygenase
Reaction: α -linolenate + O₂ = (9*R*,10*E*,12*Z*,15*Z*)-9-hydroperoxyoctadeca-10,12,15-trienoate
Other name(s): NspLOX; (9*R*)-LOX; linoleate 9*R*-dioxygenase
Systematic name: α -linolenate:oxygen (9*R*)-oxidoreductase
Comments: In cyanobacteria the enzyme is involved in oxylipin biosynthesis. The enzyme also converts linoleate to (9*R*,10*E*,12*Z*)-9-hydroperoxyoctadeca-10,12-dienoate.
References: [1736, 89, 2128]

[EC 1.13.11.61 created 2011]

EC 1.13.11.62

Accepted name: linoleate 10*R*-lipoxygenase
Reaction: linoleate + O₂ = (8*E*,10*R*,12*Z*)-10-hydroperoxy-8,12-octadecadienoate
Other name(s): 10*R*-DOX; (10*R*)-dioxygenase; 10*R*-dioxygenase
Systematic name: linoleate:oxygen (10*R*)-oxidoreductase
Comments: The enzyme is involved in biosynthesis of oxylipins, which affect sporulation, development, and pathogenicity of *Aspergillus* spp.
References: [1161, 1735]

[EC 1.13.11.62 created 2011]

EC 1.13.11.63

Accepted name: β -carotene 15,15'-dioxygenase
Reaction: β -carotene + O₂ = 2 *all-trans*-retinal
Other name(s): *blh* (gene name); BCO1 (gene name); BCDO (gene name); carotene dioxygenase; carotene 15,15'-dioxygenase; BCMO1 (misleading); β -carotene 15,15'-monooxygenase (incorrect)

Systematic name: β -carotene:oxygen 15,15'-dioxygenase (bond-cleaving)
Comments: Requires Fe²⁺. The enzyme cleaves β -carotene symmetrically, producing two molecules of *all-trans*-retinal. Both atoms of the oxygen molecule are incorporated into the products [785]. The enzyme can also process β -cryptoxanthin, 8'-apo- β -carotenal, 4'-apo- β -carotenal, α -carotene and γ -carotene in decreasing order. The presence of at least one unsubstituted β -ionone ring in a substrate greater than C₃₀ is mandatory [1928]. A prokaryotic enzyme has been reported from the uncultured marine bacterium 66A03, where it is involved in the proteorhodopsin system, which uses retinal as its chromophore [1927, 1929].
References: [1243, 1242, 4331, 2206, 1928, 1927, 1929, 785]

[EC 1.13.11.63 created 2012 (EC 1.14.99.36 created 1972 as EC 1.13.11.21, transferred 2001 to EC 1.14.99.36, incorporated 2015), modified 2016]

EC 1.13.11.64

Accepted name: 5-nitrosalicylate dioxygenase
Reaction: 5-nitrosalicylate + O₂ = 2-oxo-3-(5-oxofuran-2-ylidene)propanoate + nitrite (overall reaction)
(1a) 5-nitrosalicylate + O₂ = 4-nitro-6-oxohepta-2,4-dienedioate
(1b) 4-nitro-6-oxohepta-2,4-dienedioate = 2-oxo-3-(5-oxofuran-2-ylidene)propanoate + nitrite (spontaneous)
Other name(s): *naaB* (gene name); 5-nitrosalicylate:oxygen 1,2-oxidoreductase (decyclizing)
Systematic name: 5-nitrosalicylate:oxygen 1,2-oxidoreductase (ring-opening)
Comments: The enzyme, characterized from the soil bacterium *Bradyrhizobium* sp. JS329, is involved in the pathway of 5-nitroanthranilate degradation. It is unusual in being able to catalyse the ring fission without the requirement for prior removal of the nitro group. The product undergoes spontaneous lactonization, with concurrent elimination of the nitro group.
References: [3086, 3087]

[EC 1.13.11.64 created 2012]

EC 1.13.11.65

Accepted name: carotenoid isomeroxygenase
Reaction: zeaxanthin + O₂ = (3*R*)-11-*cis*-3-hydroxyretinal + (3*R*)-*all-trans*-3-hydroxyretinal
Other name(s): *ninaB* (gene name)
Systematic name: zeaxanthin:oxygen 15,15'-oxidoreductase (bond-cleaving, *cis*-isomerizing)
Comments: The enzyme, characterized from the moth *Galleria mellonella* and the fruit fly *Drosophila melanogaster*, is involved in the synthesis of retinal from dietary carotenoids in insects. The enzyme accepts different *all-trans* carotenoids, including β -carotene, α -carotene and lutein, and catalyses the symmetrical cleavage of the carotenoid and the simultaneous isomerization of only one of the products to a *cis* configuration. When the substrate is hydroxylated only in one side (as in cryptoxanthin), the enzyme preferentially isomerizes the hydroxylated part of the molecule.
References: [2834]

[EC 1.13.11.65 created 2012 as EC 1.14.13.164, transferred 2012 to EC 1.13.11.65]

EC 1.13.11.66

Accepted name: hydroquinone 1,2-dioxygenase
Reaction: benzene-1,4-diol + O₂ = (2*Z*,4*E*)-4-hydroxy-6-oxohexa-2,4-dienoate
Other name(s): hydroquinone dioxygenase; benzene-1,4-diol:oxygen 1,2-oxidoreductase (decyclizing)
Systematic name: benzene-1,4-diol:oxygen 1,2-oxidoreductase (ring-opening)
Comments: The enzyme is an extradiol-type dioxygenase, and is a member of the nonheme-iron(II)-dependent dioxygenase family. It catalyses the ring cleavage of a wide range of hydroquinone substrates to produce the corresponding 4-hydroxymuconic semialdehydes.
References: [2574, 2603, 3475]

[EC 1.13.11.66 created 2012]

EC 1.13.11.67

Accepted name: 8'-apo- β -carotenoid 14',13'-cleaving dioxygenase
Reaction: 8'-apo- β -carotenol + O₂ = 14'-apo- β -carotenal + an uncharacterized product
Other name(s): 8'-apo- β -carotenol:O₂ oxidoreductase (14',13'-cleaving)
Systematic name: 8'-apo- β -carotenol:oxygen oxidoreductase (14',13'-cleaving)
Comments: A thiol-dependent enzyme isolated from rat and rabbit. Unlike EC 1.13.11.63, β -carotene-15,15'-dioxygenase, it is not active towards β -carotene. The secondary product has not been characterized, but may be (3*E*,5*E*)-7-hydroxy-6-methylhepta-3,5-dien-2-one.
References: [842]

[EC 1.13.11.67 created 2000 as EC 1.13.12.12, transferred 2012 to EC 1.13.11.67]

EC 1.13.11.68

Accepted name: 9-*cis*- β -carotene 9',10'-cleaving dioxygenase
Reaction: 9-*cis*- β -carotene + O₂ = 9-*cis*-10'-apo- β -carotenal + β -ionone
Other name(s): CCD7 (gene name); MAX3 (gene name); NCED7 (gene name)
Systematic name: 9-*cis*- β -carotene:oxygen oxidoreductase (9',10'-cleaving)
Comments: Requires Fe²⁺. The enzyme participates in a pathway leading to biosynthesis of strigolactones, plant hormones involved in promotion of symbiotic associations known as arbuscular mycorrhiza.
References: [349, 57]

[EC 1.13.11.68 created 2012]

EC 1.13.11.69

Accepted name: carlactone synthase
Reaction: 9-*cis*-10'-apo- β -carotenal + 2 O₂ = carlactone + (2*E*,4*E*,6*E*)-7-hydroxy-4-methylhepta-2,4,6-trienal
Other name(s): CCD8 (gene name); MAX4 (gene name); NCED8 (gene name)
Systematic name: 9-*cis*-10'-apo- β -carotenal:oxygen oxidoreductase (14,15-cleaving, carlactone-forming)
Comments: Requires Fe²⁺. The enzyme participates in a pathway leading to biosynthesis of strigolactones, plant hormones involved in promotion of symbiotic associations known as arbuscular mycorrhiza. Also catalyses EC 1.13.11.70, *all-trans*-10'-apo- β -carotenal 13,14-cleaving dioxygenase, but 10-fold slower.
References: [3587, 3412, 57]

[EC 1.13.11.69 created 2012]

EC 1.13.11.70

Accepted name: *all-trans*-10'-apo- β -carotenal 13,14-cleaving dioxygenase
Reaction: *all-trans*-10'-apo- β -carotenal + O₂ = 13-*apo*- β -carotenone + (2*E*,4*E*,6*E*)-4-methylocta-2,4,6-trienal
Other name(s): CCD8 (gene name); MAX4 (gene name); NCED8 (gene name); *all-trans*-10'-apo- β -carotenal:O₂ oxidoreductase (13,14-cleaving)
Systematic name: *all-trans*-10'-apo- β -carotenal:oxygen oxidoreductase (13,14-cleaving)
Comments: Requires Fe²⁺. The enzyme from the plant *Arabidopsis thaliana* also catalyses EC 1.13.11.69, carlactone synthase, 10-fold faster.
References: [3412]

[EC 1.13.11.70 created 2012]

EC 1.13.11.71

Accepted name: carotenoid-9',10'-cleaving dioxygenase

Reaction: *all-trans*- β -carotene + O₂ = *all-trans*-10'-apo- β -carotenal + β -ionone
Other name(s): BCO₂ (gene name); β -carotene 9',10'-monooxygenase (misleading); *all-trans*- β -carotene:O₂ oxidoreductase (9',10'-cleaving)
Systematic name: *all-trans*- β -carotene:oxygen oxidoreductase (9',10'-cleaving)
Comments: Requires Fe²⁺. The enzyme catalyses the asymmetric oxidative cleavage of carotenoids. The mammalian enzyme can also cleave *all-trans*-lycopene.
References: [1903, 2264]

[EC 1.13.11.71 created 2012]

EC 1.13.11.72

Accepted name: 2-hydroxyethylphosphonate dioxygenase
Reaction: 2-hydroxyethylphosphonate + O₂ = hydroxymethylphosphonate + formate
Other name(s): HEPD; *phpD* (gene name); 2-hydroxyethylphosphonate:O₂ 1,2-oxidoreductase (hydroxymethylphosphonate forming)
Systematic name: 2-hydroxyethylphosphonate:oxygen 1,2-oxidoreductase (hydroxymethylphosphonate forming)
Comments: Requires non-heme-Fe(II). Isolated from some bacteria including *Streptomyces hygroscopicus* and *Streptomyces viridochromogenes*. The *pro-R* hydrogen at C-2 of the ethyl group is retained by the formate ion. Any stereochemistry at C-1 of the ethyl group is lost. One atom from dioxygen is present in each product. Involved in phosphinothricin biosynthesis.
References: [624, 4199, 2971]

[EC 1.13.11.72 created 2012]

EC 1.13.11.73

Accepted name: methylphosphonate synthase
Reaction: 2-hydroxyethylphosphonate + O₂ = methylphosphonate + HCO₃⁻
Other name(s): *mpnS* (gene name); 2-hydroxyethylphosphonate:O₂ 1,2-oxidoreductase (methylphosphonate forming)
Systematic name: 2-hydroxyethylphosphonate:oxygen 1,2-oxidoreductase (methylphosphonate forming)
Comments: Isolated from the marine archaeon *Nitrosopumilus maritimus*.
References: [2513]

[EC 1.13.11.73 created 2012]

EC 1.13.11.74

Accepted name: 2-aminophenol 1,6-dioxygenase
Reaction: 2-aminophenol + O₂ = 2-aminomuconate 6-semialdehyde
Other name(s): *amnA* (gene name); *amnB* (gene name); 2-aminophenol:oxygen 1,6-oxidoreductase (decyclizing)
Systematic name: 2-aminophenol:oxygen 1,6-oxidoreductase (ring-opening)
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 also has some activity with 2-amino-5-methylphenol and 2-amino-4-methylphenol [3792]. The enzyme from the bacterium *Comamonas testosteroni* CNB-1 also has the activity of EC 1.13.11.76, 2-amino-5-chlorophenol 1,6-dioxygenase [4259].
References: [3792, 4259, 2222]

[EC 1.13.11.74 created 2013]

EC 1.13.11.75

Accepted name: *all-trans*-8'-apo- β -carotenal 15,15'-oxygenase
Reaction: *all-trans*-8'-apo- β -carotenal + O₂ = *all-trans*-retinal + (2*E*,4*E*,6*E*)-2,6-dimethylocta-2,4,6-trienedial
Other name(s): DioX1; ACO; 8'-apo- β -carotenal 15,15'-oxygenase
Systematic name: *all-trans*-8'-apo- β -carotenal:oxygen 15,15'-oxidoreductase (bond-cleaving)

Comments: Contains an Fe²⁺-4His arrangement. The enzyme is involved in retinal biosynthesis in bacteria [1967].
References: [3249, 1967]

[EC 1.13.11.75 created 2010 as EC 1.14.99.41, transferred 2013 to EC 1.13.11.75]

EC 1.13.11.76

Accepted name: 2-amino-5-chlorophenol 1,6-dioxygenase
Reaction: 2-amino-5-chlorophenol + O₂ = 2-amino-5-chloromuconate 6-semialdehyde
Other name(s): *cnbC* (gene name); 2-amino-5-chlorophenol:oxygen 1,6-oxidoreductase (decyclizing)
Systematic name: 2-amino-5-chlorophenol:oxygen 1,6-oxidoreductase (ring-opening)
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 1.13.11.74, 2-aminophenol 1,6-dioxygenase.
References: [4259]

[EC 1.13.11.76 created 2013]

EC 1.13.11.77

Accepted name: oleate 10S-lipoxygenase
Reaction: (1) oleate + O₂ = (8*E*,10*S*)-10-hydroperoxyoctadeca-8-enoate
(2) linoleate + O₂ = (8*E*,10*S*,12*Z*)-10-hydroperoxyoctadeca-8,12-dienoate
(3) α-linolenate + O₂ = (8*E*,10*S*,12*Z*,15*Z*)-10-hydroperoxyoctadeca-8,12,15-trienoate
Other name(s): 10S-DOX; (10*S*)-dioxygenase; 10*S*-dioxygenase
Systematic name: oleate:oxygen (10*S*)-oxidoreductase
Comments: Binds Fe²⁺. The enzyme isolated from the bacterium *Pseudomonas* sp. 42A2 has similar activity with all the three Δ⁹ fatty acids. *cf.* EC 1.13.11.62, linoleate 10*R*-lipoxygenase.
References: [461]

[EC 1.13.11.77 created 2013]

EC 1.13.11.78

Accepted name: 2-amino-1-hydroxyethylphosphonate dioxygenase (glycine-forming)
Reaction: (2-amino-1-hydroxyethyl)phosphonate + O₂ = glycine + phosphate
Other name(s): *phnZ* (gene name)
Systematic name: 2-amino-1-hydroxyethylphosphonate:oxygen 1-oxidoreductase (glycine-forming)
Comments: Requires Fe²⁺. The enzyme, characterized from a marine bacterium, is involved in a 2-aminoethylphosphonate degradation pathway.
References: [2493, 4253]

[EC 1.13.11.78 created 2014]

EC 1.13.11.79

Accepted name: 5,6-dimethylbenzimidazole synthase
Reaction: FMNH₂ + O₂ = 5,6-dimethylbenzimidazole + D-erythrose 4-phosphate + other product(s)
Other name(s): BluB
Systematic name: FMNH₂ oxidoreductase (5,6-dimethylbenzimidazole-forming)

Comments: The enzyme catalyses a complex oxygen-dependent conversion of reduced flavin mononucleotide to form 5,6-dimethylbenzimidazole, the lower ligand of vitamin B₁₂. This conversion involves many sequential steps in two distinct stages, and an alloxan intermediate that acts as a proton donor, a proton acceptor, and a hydride acceptor [4124]. The C-2 of 5,6-dimethylbenzimidazole is derived from C-1' of the ribityl group of FMNH₂ and 2-H from the ribityl 1'-*pro-S* hydrogen. While D-erythrose 4-phosphate has been shown to be one of the byproducts, the nature of the other product(s) has not been verified yet.

References: [1267, 907, 3771, 4124, 642]

[EC 1.13.11.79 created 2010 as EC 1.14.99.40, transferred 2014 to EC 1.13.11.79]

EC 1.13.11.80

Accepted name: (3,5-dihydroxyphenyl)acetyl-CoA 1,2-dioxygenase
Reaction: (3,5-dihydroxyphenyl)acetyl-CoA + O₂ = 2-(3,5-dihydroxyphenyl)-2-oxoacetate + CoA
Other name(s): DpgC
Systematic name: (3,5-dihydroxyphenyl)acetyl-CoA:oxygen oxidoreductase
Comments: The enzyme, characterized from bacteria *Streptomyces toyocaensis* and *Amycolatopsis orientalis*, is involved in the biosynthesis of (3,5-dihydroxyphenyl)glycine, a component of the glycopeptide antibiotic vancomycin.
References: [569, 4205, 1011]

[EC 1.13.11.80 created 2015]

EC 1.13.11.81

Accepted name: 7,8-dihydroneopterin oxygenase
Reaction: 7,8-dihydroneopterin + O₂ = 7,8-dihydroxanthopterin + formate + glycolaldehyde
Systematic name: 7,8-dihydroneopterin:oxygen oxidoreductase
Comments: The enzyme from the bacterium *Mycobacterium tuberculosis* is multifunctional and also catalyses the epimerisation of the 2'-hydroxy group of 7,8-dihydroneopterin (EC 5.1.99.8, 7,8-dihydroneopterin epimerase) and the reaction of EC 4.1.2.25 (dihydroneopterin aldolase).
References: [714]

[EC 1.13.11.81 created 2015]

EC 1.13.11.82

Accepted name: 8'-apo-carotenoid 13,14-cleaving dioxygenase
Reaction: 8'-apo-β-carotenal + O₂ = 13-apo-β-carotenone + 2,6-dimethyldeca-2,4,6,8-tetraenedial
Other name(s): NACOX1 (gene name)
Systematic name: 8'-apo-β-carotenal:oxygen 13,14-dioxygenase (bond-cleaving)
Comments: Isolated from the bacterium *Novosphingobium aromaticivorans*. It is less active with 4'-apo-β-carotenal and γ-carotene.
References: [1930]

[EC 1.13.11.82 created 2015]

EC 1.13.11.83

Accepted name: 4-hydroxy-3-prenylphenylpyruvate oxygenase
Reaction: 3-dimethylallyl-4-hydroxyphenylpyruvate + O₂ = 3-dimethylallyl-4-hydroxymandelate + CO₂
Other name(s): CloR
Systematic name: 3-dimethylallyl-4-hydroxyphenylpyruvate:oxygen 1,2-oxidoreductase (3-dimethylallyl-4-hydroxymandelate forming)
Comments: Requires non-heme-Fe(II). Isolated from the bacterium *Streptomyces roseochromogenes* DS 12976. A bifunctional enzyme involved in clorobiocin biosynthesis that also catalyses the activity of EC 1.13.12.23, 3-dimethylallyl-4-hydroxybenzoate synthase.

References: [3028]

[EC 1.13.11.83 created 2017]

EC 1.13.11.84

Accepted name: crocetin dialdehyde synthase
Reaction: zeaxanthin + 2 O₂ = crocetin dialdehyde + 2 3β-hydroxy-β-cyclocitral (overall reaction)
(1a) zeaxanthin + O₂ = 3β-hydroxy-8'-apo-β-carotenal + 3β-hydroxy-β-cyclocitral
(1b) 3β-hydroxy-8'-apo-β-carotenal + O₂ = crocetin dialdehyde + 3β-hydroxy-β-cyclocitral
Other name(s): CCD2; zeaxanthin 7,8-dioxygenase
Systematic name: zeaxanthin:oxygen 7',8'-oxidoreductase (bond-cleaving)
Comments: The enzyme, characterized from the plant *Crocus sativus* (saffron), acts twice, cleaving 3β-hydroxy-β-cyclocitral off each 3-hydroxy end group. It is part of the zeaxanthin degradation pathway in that plant, leading to the different compounds that impart the color, flavor and aroma of the saffron spice. The enzyme can similarly cleave the 7-8 double bond of other carotenoids with a 3-hydroxy-β-carotenoid end group.
References: [1084, 38, 37]

[EC 1.13.11.84 created 2011 as EC 1.14.99.42, modified 2014, transferred 2017 to EC 1.13.11.84]

EC 1.13.11.85

Accepted name: exo-cleaving rubber dioxygenase
Reaction: *cis*-1,4-polyisoprene + *n* O₂ = *n* (4*Z*,8*Z*)-4,8-dimethyl-12-oxotrideca-4,8-dienal
Other name(s): *roxA* (gene name); heme-dependent rubber oxygenase (ambiguous)
Systematic name: *cis*-1,4-polyisoprene:oxygen dioxygenase [(4*Z*,8*Z*)-4,8-dimethyl-12-oxotrideca-4,8-dienal-forming]
Comments: The enzyme, studied mainly from the bacterium *Xanthomonas* sp. 35Y, catalyses the cleavage of the double bonds in natural and synthetic rubber (*cis*-1,4-polyisoprene polymers), generating ends that contain ketone and aldehyde groups. The enzyme from *Xanthomonas* sp. 35Y contains two *c*-type cytochromes. It attacks the substrate from its end, producing a single product of 15 carbons.
References: [3936, 1730, 377, 376, 3430, 300]

[EC 1.13.11.85 created 2018]

EC 1.13.11.86

Accepted name: 5-aminosalicylate 1,2-dioxygenase
Reaction: 5-aminosalicylate + O₂ = (2*Z*,4*E*)-4-amino-6-oxohepta-2,4-dienedioate
Other name(s): *mabB* (gene name)
Systematic name: 5-aminosalicylate:oxygen 1,2-oxidoreductase (ring-opening)
Comments: Requires Fe(II). The enzyme, characterized from different bacteria, is a nonheme iron dioxygenase in the bicupin family.
References: [3662, 4401]

[EC 1.13.11.86 created 2018]

EC 1.13.11.87

Accepted name: endo-cleaving rubber dioxygenase
Reaction: Cleavage of *cis*-1,4-polyisoprene polymers into a mixture of compounds, including a C₂₀ compound ((4*Z*,8*Z*,12*Z*,16*Z*,20*Z*,24*Z*)-4,8,12,16,20,24-hexamethyl-28-oxononacos-4,8,12,16,20,24-hexaenal), a C₂₅ compound ((4*Z*,8*Z*,12*Z*,16*Z*,20*Z*)-4,8,12,16,20-pentamethyl-24-oxopentacos-4,8,12,16,20-pentaenal), a C₃₀ compound ((4*Z*,8*Z*,12*Z*,16*Z*)-4,8,12,16-tetramethyl-20-oxohenicosa-4,8,12,16-tetraenal), and larger isoprenologes such as C₃₅, C₄₀, C₄₅, and higher analogues.
Other name(s): latex clearing protein; *lcp* (gene name); *roxB* (gene name)
Systematic name: *cis*-1,4-polyisoprene:oxygen dioxygenase (endo-cleaving)

Comments: The enzyme catalyses the cleavage of the double bonds in natural and synthetic rubber, producing a mixture of C₂₀, C₂₅, C₃₀, and higher oligo-isoprenoids with ketone and aldehyde groups at their ends. Two unrelated bacterial enzymes are known to possess this activity - the enzyme from *Streptomyces* sp. K30 (Lcp) contains a *b*-type cytochrome, while the enzyme from *Xanthomonas* sp. 35Y, (RoxB) contains two *c*-type cytochromes. Both enzymes attack the substrate at random locations, and are not able to cleave the C₃₅ or smaller products into shorter fragments.

References: [3936, 1730, 377, 376, 3430, 300, 301]

[EC 1.13.11.87 created 2018]

EC 1.13.12 With incorporation of one atom of oxygen (internal monooxygenases or internal mixed-function oxidases)

EC 1.13.12.1

Accepted name: arginine 2-monooxygenase
Reaction: L-arginine + O₂ = 4-guanidinobutanamide + CO₂ + H₂O
Other name(s): arginine monooxygenase; arginine decarboxylase; arginine oxygenase (decarboxylating); arginine decarboxy-oxidase
Systematic name: L-arginine:oxygen 2-oxidoreductase (decarboxylating)
Comments: A flavoprotein. Also acts on canavanine and homoarginine.
References: [2877, 3863, 3864]

[EC 1.13.12.1 created 1972]

EC 1.13.12.2

Accepted name: lysine 2-monooxygenase
Reaction: L-lysine + O₂ = 5-aminopentanamide + CO₂ + H₂O
Other name(s): lysine oxygenase; lysine monooxygenase; L-lysine-2-monooxygenase
Systematic name: L-lysine:oxygen 2-oxidoreductase (decarboxylating)
Comments: A flavoprotein (FAD). Also acts on other diamino acids.
References: [2724, 3787, 3788]

[EC 1.13.12.2 created 1972]

EC 1.13.12.3

Accepted name: tryptophan 2-monooxygenase
Reaction: L-tryptophan + O₂ = (indol-3-yl)acetamide + CO₂ + H₂O
Other name(s): tms1 (gene name); *iaaM* (gene name)
Systematic name: L-tryptophan:oxygen 2-oxidoreductase (decarboxylating)
Comments: The enzyme, studied from phytopathogenic bacteria such as *Pseudomonas savastanoi*, is involved in a pathway for the production of (indol-3-yl)acetate (IAA), the main auxin hormone in plants.
References: [2040, 2084, 1614, 2885, 945]

[EC 1.13.12.3 created 1972]

EC 1.13.12.4

Accepted name: lactate 2-monooxygenase
Reaction: (*S*)-lactate + O₂ = acetate + CO₂ + H₂O
Other name(s): lactate oxidative decarboxylase; lactate oxidase; lactic oxygenase; lactate oxygenase; lactic oxidase; L-lactate monooxygenase; lactate monooxygenase; L-lactate-2-monooxygenase
Systematic name: (*S*)-lactate:oxygen 2-oxidoreductase (decarboxylating)
Comments: A flavoprotein (FMN).

References: [1435, 3745]

[EC 1.13.12.4 created 1961 as EC 1.1.3.2, transferred 1972 to EC 1.13.12.4]

EC 1.13.12.5

Accepted name: *Renilla*-type luciferase
Reaction: coelenterazine h + O₂ = excited coelenteramide h monoanion + CO₂ (over-all reaction)
(1a) coelenterazine h + O₂ = coelenterazine h dioxetanone
(1b) coelenterazine h dioxetanone = excited coelenteramide h monoanion + CO₂
Other name(s): *Renilla*-luciferin 2-monooxygenase; luciferase (*Renilla* luciferin); *Renilla*-luciferin:oxygen 2-oxidoreductase (decarboxylating)
Systematic name: coelenterazine h:oxygen 2-oxidoreductase (decarboxylating)
Comments: This enzyme has been studied from the soft coral *Renilla reniformis*. Before the reaction occurs the substrate is sequestered by a coelenterazine-binding protein. Elevation in the concentration of calcium ions releases the substrate, which then interacts with the luciferase. Upon binding the substrate, the enzyme catalyses an oxygenation, producing a very short-lived hydroperoxide that cyclizes into a dioxetanone structure, which collapses, releasing a CO₂ molecule. The spontaneous breakdown of the dioxetanone releases the energy (about 50 kcal/mole) that is necessary to generate the excited state of the coelenteramide product, which is the singlet form of the monoanion. *In vivo* the product undergoes the process of nonradiative energy transfer to an accessory protein, a green fluorescent protein (GFP), which results in green bioluminescence. *In vitro*, in the absence of GFP, the product emits blue light.
References: [664, 1567, 84, 3505, 547, 2299, 2290]

[EC 1.13.12.5 created 1976, modified 1981, modified 1982, modified 2004, modified 2017]

EC 1.13.12.6

Accepted name: *Cypridina*-luciferin 2-monooxygenase
Reaction: *Cypridina* luciferin + O₂ = oxidized *Cypridina* luciferin + CO₂ + *hν*
Other name(s): *Cypridina*-type luciferase; luciferase (*Cypridina* luciferin); *Cypridina* luciferase
Systematic name: *Cypridina*-luciferin:oxygen 2-oxidoreductase (decarboxylating)
Comments: *Cypridina* is a bioluminescent crustacea. The luciferins (and presumably the luciferases, since they cross-react) of some luminous fish (e.g. *Apogon*, *Parapriacanthus*, *Porichthys*) are apparently similar. The enzyme may be assayed by measurement of light emission.
References: [663, 1817, 1940, 3938]

[EC 1.13.12.6 created 1976, modified 1982]

EC 1.13.12.7

Accepted name: firefly luciferase
Reaction: D-firefly luciferin + O₂ + ATP = firefly oxyluciferin + CO₂ + AMP + diphosphate + *hν*
Other name(s): *Photinus*-luciferin 4-monooxygenase (ATP-hydrolysing); luciferase (firefly luciferin); *Photinus* luciferin 4-monooxygenase (adenosine triphosphate-hydrolyzing); firefly luciferin luciferase; *Photinus pyralis* luciferase; *Photinus*-luciferin:oxygen 4-oxidoreductase (decarboxylating, ATP-hydrolysing)
Systematic name: D-firefly luciferin:oxygen 4-oxidoreductase (decarboxylating, ATP-hydrolysing)
Comments: The enzyme, which is found in fireflies (*Lampyridae*), is responsible for their bioluminescence. The reaction begins with the formation of an acid anhydride between the carboxylic group of D-firefly luciferin and AMP, with the release of diphosphate. An oxygenation follows, with release of the AMP group and formation of a very short-lived peroxide that cyclizes into a dioxetanone structure, which collapses, releasing a CO₂ molecule. The spontaneous breakdown of the dioxetanone (rather than the hydrolysis of the adenylate) releases the energy (about 50 kcal/mole) that is necessary to generate the excited state of oxyluciferin. The excited luciferin then emits a photon, returning to its ground state. The enzyme has a secondary acyl-CoA ligase activity when acting on L-firefly luciferin (see EC 6.2.1.52).

References: [1269, 4188, 1560, 4189, 2028, 771, 2703, 3740]

[EC 1.13.12.7 created 1976, modified 1981, modified 1982, modified 2017]

EC 1.13.12.8

Accepted name: *Watasenia*-luciferin 2-monooxygenase
Reaction: *Watasenia* luciferin + O₂ = oxidized *Watasenia* luciferin + CO₂ + *hν*
Other name(s): *Watasenia*-type luciferase
Systematic name: *Watasenia*-luciferin:oxygen 2-oxidoreductase (decarboxylating)
Comments: The enzyme from the luminous squid *Watasenia* may be assayed by measurement of light emission.
References: [1654]

[EC 1.13.12.8 created 1982]

EC 1.13.12.9

Accepted name: phenylalanine 2-monooxygenase
Reaction: L-phenylalanine + O₂ = 2-phenylacetamide + CO₂ + H₂O
Other name(s): L-phenylalanine oxidase (deaminating and decarboxylating); phenylalanine (deaminating, decarboxylating)oxidase
Systematic name: L-phenylalanine:oxygen 2-oxidoreductase (decarboxylating)
Comments: The reaction shown above is about 80% of the reaction catalysed; the remaining 20% is: L-phenylalanine + O₂ + H₂O = 3-phenylpyruvic acid + ammonia + H₂O₂; a reaction similar to that of EC 1.4.3.2, L-amino-acid oxidase.
References: [2046, 2048, 2047, 2049]

[EC 1.13.12.9 created 1986, modified 2003]

[1.13.12.10 Deleted entry. lysine 6-monooxygenase. Reaction covered by EC 1.14.13.59, L-lysine 6-monooxygenase (NADPH)]

[EC 1.13.12.10 created 1989, modified 1999, deleted 2001]

[1.13.12.11 Deleted entry. methylphenyltetrahydropyridine N-monooxygenase. The activity is due to EC 1.14.13.8, flavin-containing monooxygenase]

[EC 1.13.12.11 created 1992, deleted 2006]

[1.13.12.12 Transferred entry. apo-β-carotenoid-14',13'-dioxygenase. The enzyme was misclassified and has been transferred to EC 1.13.11.67, 8-apo-β-carotenoid 14',13'-cleaving dioxygenase]

[EC 1.13.12.12 created 2000, modified 2001, deleted 2012]

EC 1.13.12.13

Accepted name: *Oplophorus*-luciferin 2-monooxygenase
Reaction: *Oplophorus* luciferin + O₂ = oxidized *Oplophorus* luciferin + CO₂ + *hν*
Other name(s): *Oplophorus* luciferase
Systematic name: *Oplophorus*-luciferin:oxygen 2-oxidoreductase (decarboxylating)
Comments: The luciferase from the deep sea shrimp *Oplophorus gracilirostris* is a complex composed of more than one protein. The enzyme's specificity is quite broad, with both coelenterazine and bisdeoxycoelenterazine being good substrates.
References: [3507, 1656]

[EC 1.13.12.13 created 2004]

[1.13.12.14 Transferred entry. chlorophyllide-a oxygenase. Now EC 1.14.13.122, chlorophyllide-a oxygenase]

[EC 1.13.12.14 created 2006, deleted 2011]

EC 1.13.12.15

- Accepted name:** 3,4-dihydroxyphenylalanine oxidative deaminase
Reaction: $2 \text{ L-dopa} + \text{O}_2 = 2 \text{ 3,4-dihydroxyphenylpyruvate} + 2 \text{ NH}_3$
Other name(s): 3,4-dihydroxy-L-phenylalanine: oxidative deaminase; oxidative deaminase; DOPA oxidative deaminase; DOPAODA
Systematic name: 3,4-dihydroxy-L-phenylalanine:oxygen oxidoreductase (deaminating)
Comments: This enzyme is one of the three enzymes involved in L-dopa (3,4-dihydroxy-L-phenylalanine) catabolism in the non-oxygenic phototrophic bacterium *Rubrivivax benzoatilyticus* OU5 (and not *Rhodobacter sphaeroides* OU5 as had been thought [3123]), the other two being EC 4.3.1.22 (dihydroxyphenylalanine reductive deaminase) and EC 2.6.1.49 (3,4-dihydroxyphenylalanine transaminase). In addition to L-dopa, the enzyme can also use L-tyrosine, L-phenylalanine, L-tryptophan and glutamate as substrate, but more slowly. The enzyme is inhibited by NADH and 2-oxoglutarate.
References: [3123]

[EC 1.13.12.15 created 2008]

EC 1.13.12.16

- Accepted name:** nitronate monooxygenase
Reaction: ethylnitronate + $\text{O}_2 = \text{acetaldehyde} + \text{nitrite} + \text{other products}$
Other name(s): NMO; 2-nitropropane dioxygenase (incorrect)
Systematic name: nitronate:oxygen 2-oxidoreductase (nitrite-forming)
Comments: Previously classified as 2-nitropropane dioxygenase (EC 1.13.11.32), but it is now recognized that this was the result of the slow ionization of nitroalkanes to their nitronate (anionic) forms. The enzymes from the fungus *Neurospora crassa* and the yeast *Williopsis saturnus* var. *mrakii* (formerly classified as *Hansenula mrakii*) contain non-covalently bound FMN as the cofactor. Neither hydrogen peroxide nor superoxide were detected during enzyme turnover. Active towards linear alkyl nitronates of lengths between 2 and 6 carbon atoms and, with lower activity, towards propyl-2-nitronate. The enzyme from *N. crassa* can also utilize neutral nitroalkanes, but with lower activity.
References: [1053, 1327, 1135, 1052]

[EC 1.13.12.16 created 1984 as EC 1.13.11.32, transferred 2009 to EC 1.13.12.16, modified 2011]

EC 1.13.12.17

- Accepted name:** dichloroarcyriaflavin A synthase
Reaction: dichlorochromopyrrolate + $4 \text{ O}_2 + 4 \text{ NADH} + 4 \text{ H}^+ = \text{dichloroarcyriaflavin A} + 2 \text{ CO}_2 + 6 \text{ H}_2\text{O} + 4 \text{ NAD}^+$
Systematic name: dichlorochromopyrrolate,NADH:oxygen 2,5-oxidoreductase (dichloroarcyriaflavin A-forming)
Comments: The conversion of dichlorochromopyrrolate to dichloroarcyriaflavin A is a complex process that involves two enzyme components. RebP is an NAD-dependent cytochrome *P*-450 oxygenase that performs an aryl-aryl bond formation yielding the six-ring indolocarbazole scaffold [2379]. Along with RebC, a flavin-dependent hydroxylase, it also catalyses the oxidative decarboxylation of both carboxyl groups. The presence of RebC ensures that the only product is the rebeccamycin aglycone dichloroarcyriaflavin A [1586]. The enzymes are similar, but not identical, to StaP and StaC, which are involved in the synthesis of staurosporine [3303].
References: [2379, 1586, 3303]

[EC 1.13.12.17 created 2010]

EC 1.13.12.18

- Accepted name:** dinoflagellate luciferase
Reaction: dinoflagellate luciferin + $\text{O}_2 = \text{oxidized dinoflagellate luciferin} + \text{H}_2\text{O} + h\nu$
Other name(s): (dinoflagellate luciferin) luciferase; *Gonyaulax* luciferase
Systematic name: dinoflagellate-luciferin:oxygen 13²-oxidoreductase

Comments: A luciferase from dinoflagelates such as *Gonyaulax polyedra*, *Lingulodinium polyedrum*, *Noctiluca scintillans*, and *Pyrocystis lunula*. It is a single protein with three luciferase domains. The luciferin is strongly bound by a luciferin binding protein above a pH of 7.

References: [889, 2634, 160, 2227, 2633, 3399]

[EC 1.13.12.18 created 2011]

EC 1.13.12.19

Accepted name: 2-oxoglutarate dioxygenase (ethene-forming)

Reaction: 2-oxoglutarate + O₂ = ethene + 3 CO₂ + H₂O

Other name(s): ethylene-forming enzyme; EFE; 2-oxoglutarate dioxygenase (ethylene-forming); 2-oxoglutarate:oxygen oxidoreductase (decarboxylating, ethylene-forming)

Systematic name: 2-oxoglutarate:oxygen oxidoreductase (decarboxylating, ethene-forming)

Comments: This is one of two simultaneous reactions catalysed by the enzyme, which is responsible for ethene production in bacteria of the *Pseudomonas syringae* group. In the other reaction [EC 1.14.20.7, 2-oxoglutarate/L-arginine monooxygenase/decarboxylase (succinate-forming)] the enzyme catalyses the mono-oxygenation of both 2-oxoglutarate and L-arginine, forming succinate, carbon dioxide and L-hydroxyarginine, which is subsequently cleaved into guanidine and (S)-1-pyrroline-5-carboxylate. The enzymes catalyse two cycles of the ethene-forming reaction for each cycle of the succinate-forming reaction, so that the stoichiometry of the products ethene and succinate is 2:1.

References: [2679, 1107, 1106]

[EC 1.13.12.19 created 2011]

EC 1.13.12.20

Accepted name: noranthrone monooxygenase

Reaction: norsolorinic acid anthrone + O₂ = norsolorinic acid + H₂O

Other name(s): norsolorinate anthrone oxidase

Systematic name: norsolorinic acid anthrone:oxygen 9-oxidoreductase (norsolorinic acid-forming)

Comments: Involved in the synthesis of aflatoxins in the fungus *Aspergillus parasiticus*.

References: [928]

[EC 1.13.12.20 created 2013]

EC 1.13.12.21

Accepted name: tetracenomycin-F1 monooxygenase

Reaction: tetracenomycin F1 + O₂ = tetracenomycin D3 + H₂O

Other name(s): *tcmH* (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: [3472]

[EC 1.13.12.21 created 2013]

EC 1.13.12.22

Accepted name: deoxynogalocate monooxygenase

Reaction: deoxynogalocate + O₂ = nogalocate + H₂O

Other name(s): SnoaB (gene name); 12-deoxynogalonic acid oxidoreductase; [4,5-dihydroxy-10-oxo-3-(3-oxobutanoyl)-9,10-dihydroanthracen-2-yl]acetate oxidase; [4,5-dihydroxy-10-oxo-3-(3-oxobutanoyl)-9,10-dihydroanthracen-2-yl]acetate monooxygenase; deoxynogalocate oxidoreductase

Systematic name: deoxynogalocate:oxygen oxidoreductase

Comments: The enzyme, characterized from the bacterium *Streptomyces nogalater*, is involved in the biosynthesis of the aromatic polyketide nogalamycin.

References: [2038, 1290]

[EC 1.13.12.22 created 2015]

EC 1.13.12.23

Accepted name: 4-hydroxy-3-prenylbenzoate synthase
Reaction: 3-dimethylallyl-4-hydroxymandelate + O₂ = 3-dimethylallyl-4-hydroxybenzoate + CO₂ + H₂O
Other name(s): CloR; *novR* (gene name)
Systematic name: 3-dimethylallyl-4-hydroxymandelate:oxygen oxidoreductase (3-dimethylallyl-4-hydroxybenzoate forming)
Comments: Isolated from the bacterium *Streptomyces roseochromogenes* DS 12976. A bifunctional enzyme involved in clorobiocin biosynthesis that also catalyses the activity of EC 1.13.11.83, 3-dimethylallyl-4-hydroxyphenylpyruvate oxygenase.
References: [3028]

[EC 1.13.12.23 created 2017]

EC 1.13.12.24

Accepted name: calcium-regulated photoprotein
Reaction: [apoaequorin] + coelenterazine + O₂ + 3 Ca²⁺ = [excited state blue fluorescent protein] + CO₂ (overall reaction)
(1a) [apoaequorin] + coelenterazine = [apoaequorin containing coelenterazine]
(1b) [apoaequorin containing coelenterazine] + O₂ = [aequorin]
(1c) [aequorin] + 3 Ca²⁺ = [aequorin] 1,2-dioxetan-3-one
(1d) [aequorin] 1,2-dioxetan-3-one = [excited state blue fluorescent protein] + CO₂
Other name(s): Ca²⁺-regulated photoprotein; calcium-activated photoprotein; aequorin; obelin; halistaurin; mitrocomin; phialidin; clytin; mnemiopsin; berovin
Systematic name: coelenterazine:oxygen 2-oxidoreductase (decarboxylating, calcium-dependent)
Comments: Ca²⁺-regulated photoproteins are found in a variety of bioluminescent marine organisms, mostly coelenterates, and are responsible for their light emission. The best studied enzyme is from the jellyfish *Aequorea victoria*. The enzyme tightly binds the imidazolopyrazinone derivative coelenterazine, which is then peroxidized by oxygen. The hydroperoxide is stably bound until three Ca²⁺ ions bind to the protein, inducing a structural change that results in the formation of a 1,2-dioxetan-3-one ring, followed by decarboxylation and generation of a protein-bound coelenteramide in an excited state. The calcium-bound protein-product complex is known as a blue fluorescent protein. *In vivo* the energy is transferred to a green fluorescent protein (GFP) by Förster resonance energy transfer. *In vitro*, in the absence of GFP, coelenteramide emits a photon of blue light while returning to its ground state.
References: [3503, 2624, 1655, 1447, 793]

[EC 1.13.12.24 created 2018]

EC 1.13.99 Miscellaneous

EC 1.13.99.1

Accepted name: inositol oxygenase
Reaction: *myo*-inositol + O₂ = D-glucuronate + H₂O
Other name(s): *meso*-inositol oxygenase; *myo*-inositol oxygenase; MOO
Systematic name: *myo*-inositol:oxygen oxidoreductase
Comments: An iron protein.
References: [545, 3146, 122]

[EC 1.13.99.1 created 1961 as EC 1.99.2.6, transferred 1965 to EC 1.13.1.11, transferred 1972 to EC 1.13.99.1, modified 2002]

[1.13.99.2 *Transferred entry. benzoate 1,2-dioxygenase. Now EC 1.14.12.10, benzoate 1,2-dioxygenase*]

[EC 1.13.99.2 created 1972, deleted 1992]

EC 1.13.99.3

Accepted name: tryptophan 2'-dioxygenase

Reaction: L-tryptophan + O₂ = (indol-3-yl)glycolaldehyde + CO₂ + NH₃

Other name(s): indole-3-alkane α -hydroxylase; tryptophan side-chain α,β -oxidase; tryptophan side chain oxidase II; tryptophan side-chain oxidase; TSO; indolyl-3-alkan α -hydroxylase; tryptophan side chain oxidase type I; TSO I ; TSO II; tryptophan side chain oxidase

Systematic name: L-tryptophan:oxygen 2'-oxidoreductase (side-chain-cleaving)

Comments: A hemoprotein. Acts on a number of indole-3-alkane derivatives, oxidizing the 3-side-chain in the 2'-position. Best substrates were L-tryptophan and 5-hydroxy-L-tryptophan.

References: [3203, 3783]

[EC 1.13.99.3 created 1984]

[1.13.99.4 *Transferred entry. 4-chlorophenylacetate 3,4-dioxygenase. Now EC 1.14.12.9, 4-chlorophenylacetate 3,4-dioxygenase*]

[EC 1.13.99.4 created 1989, deleted 1992]

[1.13.99.5 *Transferred entry. now EC 1.13.11.47, 3-hydroxy-4-oxoquinoline 2,4-dioxygenase*]

[EC 1.13.99.5 created 1999, deleted 2001]

EC 1.14 Acting on paired donors, with incorporation or reduction of molecular oxygen

This subclass contains enzymes that act on two hydrogen-donors, and oxygen is incorporated into one or both of them. Sub-subclasses are based on the second donor and the number of oxygen atoms that are incorporated into one or both donors: 2-oxoglutarate is one donor and one atom of oxygen is incorporated into each donor (EC 1.14.11), NADH or NADPH is one donor, and two atoms of oxygen are incorporated into the other donor (EC 1.14.12), NADH or NADPH is one donor, but only one atom of oxygen is incorporated into the other donor (EC 1.14.13). In sub-subclasses EC 1.14.14-1.14.18, one atom of oxygen is incorporated into one donor, the other donor being a reduced flavin or flavoprotein (EC 1.14.14), a reduced iron-sulfur protein (EC 1.14.15), a reduced pteridine (EC 1.14.16), reduced ascorbate (EC 1.14.17), or some other compound (EC 1.14.18). Sub-subclass EC 1.14.19 differs from others in subclass EC 1.14 in that hydrogen atoms removed from the two donors are combined with O₂ to form two molecules of water. Sub-subclass EC 1.14.20 has 2-oxoglutarate as one donor, and the other is dehydrogenated. Sub-subclass EC 1.14.21 has NADH or NADPH as one donor, and the other is dehydrogenated. Sub-subclass EC 1.14.99 is for cases where information about the second donor is incomplete.

EC 1.14.1 With NADH or NADPH as one donor (deleted sub-subclass)

[1.14.1.1 *Transferred entry. now EC 1.14.14.1, unspecific monooxygenase*]

[EC 1.14.1.1 created 1961 as EC 1.99.1.1, transferred 1965 to EC 1.14.14.1, deleted 1972]

[1.14.1.2 *Transferred entry. now EC 1.14.13.9, kynurenine 3-monooxygenase*]

[EC 1.14.1.2 created 1965, deleted 1972]

[1.14.1.3 *Deleted entry. squalene hydroxylase. Activity is covered by EC 1.14.99.7, squalene monooxygenase and EC 5.4.99.7, lanosterol synthase*]

[EC 1.14.1.3 created 1961 as EC 1.99.1.13, transferred 1965 to EC 1.14.1.3, deleted 1972]

[1.14.1.4 *Transferred entry. now EC 1.14.99.2, kynurenine 7,8-hydroxylase*]

[EC 1.14.1.4 created 1965, deleted 1972]

[1.14.1.5 *Transferred entry. now EC 1.14.13.5, imidazoleacetate 4-monooxygenase*]

[EC 1.14.1.5 created 1965, deleted 1972]

[1.14.1.6 *Transferred entry. now EC 1.14.15.4, steroid 11 β -monooxygenase*]

[EC 1.14.1.6 created 1961 as EC 1.99.1.7, transferred 1965 to EC 1.14.1.6, deleted 1972]

[1.14.1.7 *Transferred entry. now EC 1.14.99.9, steroid 17 α -monooxygenase*]

[EC 1.14.1.7 created 1965, deleted 1972]

[1.14.1.8 *Transferred entry. now EC 1.14.99.10, steroid 21-monooxygenase*]

[EC 1.14.1.8 created 1965, deleted 1972]

[1.14.1.9 *Deleted entry. cholesterol 20-hydroxylase*]

[EC 1.14.1.9 created 1965, deleted 1972]

[1.14.1.10 *Transferred entry. now EC 1.14.99.11, estradiol 6 β -monooxygenase*]

[EC 1.14.1.10 created 1965, deleted 1972]

[1.14.1.11 *Deleted entry. oestriol 2-hydroxylase*]

[EC 1.14.1.11 created 1965, deleted 1972]

EC 1.14.2 With ascorbate as one donor (deleted sub-subclass)

[1.14.2.1 *Transferred entry. now EC 1.14.17.1, dopamine β -monooxygenase*]

[EC 1.14.2.1 created 1965, deleted 1972]

[1.14.2.2 *Transferred entry. now EC 1.13.11.27, 4-hydroxyphenylpyruvate dioxygenase*]

[EC 1.14.2.2 created 1961 as EC 1.99.1.14, transferred 1965 to EC 1.14.2.2, deleted 1972]

EC 1.14.3 With reduced pteridine as one donor (deleted sub-subclass)

[1.14.3.1 *Transferred entry. now EC 1.14.16.1, phenylalanine 4-monooxygenase*]

[EC 1.14.3.1 created 1961 as EC 1.99.1.2, transferred 1965 to EC 1.14.3.1, deleted 1972]

EC 1.14.11 With 2-oxoglutarate as one donor, and incorporation of one atom of oxygen into each donor

EC 1.14.11.1

- Accepted name:** γ -butyrobetaine dioxygenase
Reaction: 4-trimethylammoniobutanoate + 2-oxoglutarate + O₂ = 3-hydroxy-4-trimethylammoniobutanoate + succinate + CO₂
Other name(s): α -butyrobetaine hydroxylase; γ -butyrobetaine hydroxylase; butyrobetaine hydroxylase
Systematic name: 4-trimethylammoniobutanoate,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Requires Fe²⁺ and ascorbate.
References: [2265]

[EC 1.14.11.1 created 1972]

EC 1.14.11.2

- Accepted name:** procollagen-proline 4-dioxygenase
Reaction: procollagen L-proline + 2-oxoglutarate + O₂ = procollagen *trans*-4-hydroxy-L-proline + succinate + CO₂
Other name(s): P4HA (gene name); P4HB (gene name); procollagen hydroxylase; proline hydroxylase; proline,2-oxoglutarate 4-dioxygenase; collagen proline hydroxylase; hydroxylase, collagen proline; peptidyl proline hydroxylase; proline procollagen hydroxylase; proline, 2-oxoglutarate dioxygenase; prolyl hydroxylase; prolylprocollagen dioxygenase; prolylprocollagen hydroxylase; procollagen proline 4-hydroxylase; procollagen proline dioxygenase; procollagen proline hydroxylase; procollagen prolyl hydroxylase; prolyl 4-hydroxylase; prolyl-glycyl-peptide, 2-oxoglutarate:oxygen oxidoreductase, 4-hydroxylating; procollagen-proline 4-dioxygenase (ambiguous)
Systematic name: procollagen-L-proline,2-oxoglutarate:oxygen oxidoreductase (4-hydroxylating)
Comments: Requires Fe²⁺ and ascorbate. The enzyme, which is located within the lumen of the endoplasmic reticulum, catalyses the 4-hydroxylation of prolines in -X-Pro-Gly- sequences. The 4-hydroxyproline residues are essential for the formation of the collagen triple helix. The enzyme forms a complex with protein disulfide isomerase and acts not only on procollagen but also on more than 15 other proteins that have collagen-like domains.
References: [1615, 1954, 1952, 266, 1752, 2120, 2678, 1953]

[EC 1.14.11.2 created 1972, modified 1981, modified 1983, modified 2017]

EC 1.14.11.3

- Accepted name:** pyrimidine-deoxynucleoside 2'-dioxygenase
Reaction: 2'-deoxyuridine + 2-oxoglutarate + O₂ = uridine + succinate + CO₂
Other name(s): deoxyuridine 2'-dioxygenase; deoxyuridine 2'-hydroxylase; pyrimidine deoxyribonucleoside 2'-hydroxylase; thymidine 2'-dioxygenase; thymidine 2'-hydroxylase; thymidine 2-oxoglutarate dioxygenase; thymidine dioxygenase
Systematic name: 2'-deoxyuridine,2-oxoglutarate:oxygen oxidoreductase (2'-hydroxylating)
Comments: Requires Fe(II) and ascorbate. Also acts on thymidine. *cf.* EC 1.14.11.10, pyrimidine-deoxynucleoside 1'-dioxygenase.
References: [192, 3691, 4134]

[EC 1.14.11.3 created 1972, modified 1976, modified 1989, modified 2002]

EC 1.14.11.4

- Accepted name:** procollagen-lysine 5-dioxygenase
Reaction: [procollagen]-L-lysine + 2-oxoglutarate + O₂ = [procollagen]-(2*S*,5*R*)-5-hydroxy-L-lysine + succinate + CO₂
Other name(s): lysine hydroxylase; lysine,2-oxoglutarate 5-dioxygenase; procollagen lysine dioxygenase; collagen lysine hydroxylase; lysine-2-oxoglutarate dioxygenase; lysyl hydroxylase; lysylprocollagen dioxygenase; procollagen lysyl hydroxylase; peptidyl-lysine, 2-oxoglutarate: oxygen oxidoreductase; peptidyllysine, 2-oxoglutarate:oxygen 5-oxidoreductase; procollagen lysine hydroxylase; procollagen-L-lysine,2-oxoglutarate:oxygen oxidoreductase (5-hydroxylating); L-lysine-[procollagen],2-oxoglutarate:oxygen oxidoreductase (5-hydroxylating)
Systematic name: [procollagen]-L-lysine,2-oxoglutarate:oxygen oxidoreductase (5-hydroxylating)
Comments: Requires Fe²⁺ and ascorbate.
References: [1428, 3177, 3074, 3075]

[EC 1.14.11.4 created 1972, modified 1983]

[1.14.11.5 Deleted entry. 5-hydroxymethyluracil,2-oxoglutarate dioxygenase. Now included with EC 1.14.11.6 thymine dioxygenase]

[EC 1.14.11.5 created 1972, deleted 1976]

EC 1.14.11.6

- Accepted name:** thymine dioxygenase
Reaction: thymine + 2-oxoglutarate + O₂ = 5-hydroxymethyluracil + succinate + CO₂
Other name(s): thymine 7-hydroxylase; 5-hydroxy-methyluracil dioxygenase; 5-hydroxymethyluracil oxygenase
Systematic name: thymine,2-oxoglutarate:oxygen oxidoreductase (7-hydroxylating)
Comments: Requires Fe²⁺ and ascorbate. Also acts on 5-hydroxymethyluracil to oxidize its -CH₂OH group first to -CHO and then to -COOH.
References: [191, 2275, 4134]

[EC 1.14.11.6 created 1972, modified 1976 (EC 1.14.11.5 created 1972, incorporated 1976)]

EC 1.14.11.7

- Accepted name:** procollagen-proline 3-dioxygenase
Reaction: [procollagen]-L-proline + 2-oxoglutarate + O₂ = [procollagen]-*trans*-3-hydroxy-L-proline + succinate + CO₂
Other name(s): proline,2-oxoglutarate 3-dioxygenase; prolyl 3-hydroxylase; procollagen proline 3-hydroxylase; prolyl-4-hydroxyprolyl-glycyl-peptide,2-oxoglutarate:oxygen oxidoreductase, 3-hydroxylating
Systematic name: [procollagen]-L-proline,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Requires Fe²⁺ and ascorbate. The enzyme forms a complex with protein disulfide isomerase, and is located in the endoplasmic reticulum. It modifies proline residues within the procollagen peptide of certain collagen types. The modification is essential for proper collagen triple helix formation.
References: [3194, 3195, 4068, 3884]

[EC 1.14.11.7 created 1981, modified 1983, modified 2017]

EC 1.14.11.8

- Accepted name:** trimethyllysine dioxygenase
Reaction: N⁶,N⁶,N⁶-trimethyl-L-lysine + 2-oxoglutarate + O₂ = (3*S*)-3-hydroxy-N⁶,N⁶,N⁶-trimethyl-L-lysine + succinate + CO₂
Other name(s): trimethyllysine α-ketoglutarate dioxygenase; TML-α-ketoglutarate dioxygenase; TML hydroxylase; 6-N,6-N,6-N-trimethyl-L-lysine,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Systematic name: N⁶,N⁶,N⁶-trimethyl-L-lysine,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Requires Fe²⁺ and ascorbate.
References: [1609, 3843, 2204, 3150]

[EC 1.14.11.8 created 1983]

EC 1.14.11.9

- Accepted name:** flavanone 3-dioxygenase
Reaction: a (2*S*)-flavan-4-one + 2-oxoglutarate + O₂ = a (2*R*,3*R*)-dihydroflavonol + succinate + CO₂
Other name(s): naringenin 3-hydroxylase; flavanone 3-hydroxylase; flavanone 3β-hydroxylase; flavanone synthase I; (2*S*)-flavanone 3-hydroxylase; naringenin,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating); F₃H; flavanone,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Systematic name: (2*S*)-flavan-4-one,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Requires Fe²⁺ and ascorbate. This plant enzyme catalyses an early step in the flavonoid biosynthesis pathway, leading to the production of flavanols and anthocyanins. Substrates include (2*S*)-naringenin, (2*S*)-eriodictyol, (2*S*)-dihydrotricetin and (2*S*)-pinocembrin. Some enzymes are bifunctional and also catalyse EC 1.14.20.6, flavonol synthase.
References: [1033, 552, 2976, 4172, 1745, 3474]

[EC 1.14.11.9 created 1983, modified 1989, modified 2004, modified 2016]

EC 1.14.11.10

Accepted name: pyrimidine-deoxynucleoside 1'-dioxygenase
Reaction: 2'-deoxyuridine + 2-oxoglutarate + O₂ = uracil + 2-deoxyribonolactone + succinate + CO₂
Other name(s): deoxyuridine-uridine 1'-dioxygenase
Systematic name: 2'-deoxyuridine,2-oxoglutarate:oxygen oxidoreductase (1'-hydroxylating)
Comments: Requires Fe(II) and ascorbate. *cf.* EC 1.14.11.3, pyrimidine-deoxynucleoside 2'-dioxygenase.
References: [3691]

[EC 1.14.11.10 created 1989, modified 2002]

EC 1.14.11.11

Accepted name: hyoscyamine (6*S*)-dioxygenase
Reaction: L-hyoscyamine + 2-oxoglutarate + O₂ = (6*S*)-hydroxyhyoscyamine + succinate + CO₂
Other name(s): hyoscyamine 6β-hydroxylase; hyoscyamine 6β-dioxygenase; hyoscyamine 6-hydroxylase
Systematic name: L-hyoscyamine,2-oxoglutarate:oxygen oxidoreductase [(6*S*)-hydroxylating]
Comments: Requires Fe²⁺ and ascorbate.
References: [1411]

[EC 1.14.11.11 created 1989]

EC 1.14.11.12

Accepted name: gibberellin-44 dioxygenase
Reaction: gibberellin 44 + 2-oxoglutarate + O₂ = gibberellin 19 + succinate + CO₂
Other name(s): oxygenase, gibberellin A44 oxidase; (gibberellin-44), 2-oxoglutarate:oxygen oxidoreductase
Systematic name: (gibberellin-44),2-oxoglutarate:oxygen oxidoreductase
Comments: Requires Fe²⁺.
References: [1206]

[EC 1.14.11.12 created 1990]

EC 1.14.11.13

Accepted name: gibberellin 2β-dioxygenase
Reaction: gibberellin 1 + 2-oxoglutarate + O₂ = 2β-hydroxygibberellin 1 + succinate + CO₂
Other name(s): gibberellin 2β-hydroxylase
Systematic name: (gibberellin-1),2-oxoglutarate:oxygen oxidoreductase (2β-hydroxylating)
Comments: Also acts on a number of other gibberellins.
References: [3567]

[EC 1.14.11.13 created 1990]

[1.14.11.14 *Transferred entry. 6β-hydroxyhyoscyamine epoxidase. Now EC 1.14.20.13, 6β-hydroxyhyoscyamine epoxidase*]

[EC 1.14.11.14 created 1992, deleted 2018]

EC 1.14.11.15

Accepted name: gibberellin 3β-dioxygenase
Reaction: gibberellin 20 + 2-oxoglutarate + O₂ = gibberellin 1 + succinate + CO₂
Other name(s): gibberellin 3β-hydroxylase; (gibberellin-20),2-oxoglutarate: oxygen oxidoreductase (3β-hydroxylating)
Systematic name: (gibberellin-20),2-oxoglutarate:oxygen oxidoreductase (3β-hydroxylating)
Comments: Requires Fe²⁺ and ascorbate.
References: [2105]

[EC 1.14.11.15 created 1992]

EC 1.14.11.16

Accepted name: peptide-aspartate β -dioxygenase
Reaction: peptide-L-aspartate + 2-oxoglutarate + O₂ = peptide-3-hydroxy-L-aspartate + succinate + CO₂
Other name(s): aspartate β -hydroxylase; aspartylpeptide β -dioxygenase
Systematic name: peptide-L-aspartate,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Requires Fe²⁺. Some vitamin K-dependent coagulation factors, as well as synthetic peptides based on the structure of the first epidermal growth factor domain of human coagulation factor IX or X, can act as acceptors.
References: [1293]

[EC 1.14.11.16 created 1992]

EC 1.14.11.17

Accepted name: taurine dioxygenase
Reaction: taurine + 2-oxoglutarate + O₂ = sulfite + aminoacetaldehyde + succinate + CO₂
Other name(s): 2-aminoethanesulfonate dioxygenase; α -ketoglutarate-dependent taurine dioxygenase
Systematic name: taurine, 2-oxoglutarate:oxygen oxidoreductase (sulfite-forming)
Comments: Requires Fe^{II}. The enzyme from *Escherichia coli* also acts on pentanesulfonate, 3-(*N*-morpholino)propanesulfonate and 2-(1,3-dioxoisindolin-2-yl)ethanesulfonate, but at lower rates.
References: [929]

[EC 1.14.11.17 created 2000]

EC 1.14.11.18

Accepted name: phytanoyl-CoA dioxygenase
Reaction: phytanoyl-CoA + 2-oxoglutarate + O₂ = 2-hydroxyphytanoyl-CoA + succinate + CO₂
Other name(s): phytanoyl-CoA hydroxylase
Systematic name: phytanoyl-CoA, 2-oxoglutarate:oxygen oxidoreductase (2-hydroxylating)
Comments: Part of the peroxisomal phytanic acid α -oxidation pathway. Requires Fe²⁺ and ascorbate.
References: [1718, 1719, 1720, 2534, 2533]

[EC 1.14.11.18 created 2000]

[1.14.11.19] *Transferred entry. anthocyanidin synthase. Now EC 1.14.20.4, anthocyanidin synthase*

[EC 1.14.11.19 created 2001, modified 2017, deleted 2018]

EC 1.14.11.20

Accepted name: deacetoxyvindoline 4-hydroxylase
Reaction: deacetoxyvindoline + 2-oxoglutarate + O₂ = deacetylvindoline + succinate + CO₂
Other name(s): desacetoxyvindoline 4-hydroxylase; desacetoxyvindoline-17-hydroxylase; D17H; desacetoxyvindoline,2-oxoglutarate:oxygen oxidoreductase (4 β -hydroxylating)
Systematic name: deacetoxyvindoline,2-oxoglutarate:oxygen oxidoreductase (4 β -hydroxylating)
Comments: Requires Fe²⁺ and ascorbate. Also acts on 3-hydroxy-16-methoxy-2,3-dihydrotabersonine and to a lesser extent on 16-methoxy-2,3-dihydrotabersonine.
References: [508, 509, 4023]

[EC 1.14.11.20 created 2002, modified 2005]

EC 1.14.11.21

Accepted name: clavamate synthase
Reaction: (1) deoxyamidinoproclavamate + 2-oxoglutarate + O₂ = amidinoproclavamate + succinate + CO₂
(2) proclavamate + 2-oxoglutarate + O₂ = dihydroclavamate + succinate + CO₂ + H₂O
(3) dihydroclavamate + 2-oxoglutarate + O₂ = clavamate + succinate + CO₂ + H₂O

Other name(s): clavamate synthase 2; clavamic acid synthase
Systematic name: deoxyamidinoproclavamate,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Contains nonheme iron. Catalyses three separate oxidative reactions in the pathway for the biosynthesis of the β -lactamase inhibitor clavulanate in *Streptomyces clavuligerus*. The first step (hydroxylation) is separated from the latter two (oxidative cyclization and desaturation) by the action of EC 3.5.3.22, proclavamate amidinohydrolase. The three reactions are all catalysed at the same nonheme iron site.
References: [3300, 4470, 4452, 4471, 3918]

[EC 1.14.11.21 created 2003]

[1.14.11.22 Transferred entry. flavone synthase. Now EC 1.14.20.5, flavone synthase]

[EC 1.14.11.22 created 2004, deleted 2018]

[1.14.11.23 Transferred entry. flavonol synthase. Now EC 1.14.20.6, flavonol synthase]

[EC 1.14.11.23 created 2004, deleted 2018]

EC 1.14.11.24

Accepted name: 2'-deoxymugineic-acid 2'-dioxygenase
Reaction: 2'-deoxymugineic acid + 2-oxoglutarate + O₂ = mugineic acid + succinate + CO₂
Other name(s): IDS3
Systematic name: 2'-deoxymugineic acid,2-oxoglutarate:oxygen oxidoreductase (2-hydroxylating)
Comments: Requires iron(II). It is also likely that this enzyme can catalyse the hydroxylation of 3-epihydroxy-2'-deoxymugineic acid to form 3-epihydroxymugineic acid.
References: [2709, 1983]

[EC 1.14.11.24 created 2005]

EC 1.14.11.25

Accepted name: mugineic-acid 3-dioxygenase
Reaction: (1) mugineic acid + 2-oxoglutarate + O₂ = 3-epihydroxymugineic acid + succinate + CO₂
(2) 2'-deoxymugineic acid + 2-oxoglutarate + O₂ = 3-epihydroxy-2'-deoxymugineic acid + succinate + CO₂
Other name(s): IDS2
Systematic name: mugineic acid,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Requires iron(II).
References: [2709, 2869]

[EC 1.14.11.25 created 2005]

EC 1.14.11.26

Accepted name: deacetoxycephalosporin-C hydroxylase
Reaction: deacetoxycephalosporin C + 2-oxoglutarate + O₂ = deacetylcephalosporin C + succinate + CO₂
Other name(s): deacetylcephalosporin C synthase; 3'-methylcephem hydroxylase; DACS; DAOC hydroxylase; deacetoxycephalosporin C hydroxylase
Systematic name: deacetoxycephalosporin-C,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Requires iron(II). The enzyme can also use 3-exomethylenecephalosporin C as a substrate to form deacetoxycephalosporin C, although more slowly [172]. In *Acremonium chrysogenum*, the enzyme forms part of a bifunctional protein along with EC 1.14.20.1, deacetoxycephalosporin-C synthase. It is a separate enzyme in *Streptomyces clavuligerus*.
References: [862, 172, 660, 1193, 2288, 4264, 2412]

[EC 1.14.11.26 created 2005]

EC 1.14.11.27

- Accepted name:** [histone-H3]-lysine-36 demethylase
- Reaction:** protein N^6,N^6 -dimethyl-L-lysine + 2 2-oxoglutarate + 2 O₂ = protein L-lysine + 2 succinate + 2 formaldehyde + 2 CO₂ (overall reaction)
(1a) protein N^6,N^6 -dimethyl-L-lysine + 2-oxoglutarate + O₂ = protein N^6 -methyl-L-lysine + succinate + formaldehyde + CO₂
(1b) protein N^6 -methyl-L-lysine + 2-oxoglutarate + O₂ = protein L-lysine + succinate + formaldehyde + CO₂
- Other name(s):** JHDM1A; JmjC domain-containing histone demethylase 1A; H3-K36-specific demethylase; histone-lysine (H3-K36) demethylase; histone demethylase; protein-6- $N,6-N$ -dimethyl-L-lysine,2-oxoglutarate:oxygen oxidoreductase
- Systematic name:** protein- N^6,N^6 -dimethyl-L-lysine,2-oxoglutarate:oxygen oxidoreductase
- Comments:** Requires iron(II). Of the seven potential methylation sites in histones H3 (K4, K9, K27, K36, K79) and H4 (K20, R3) from HeLa cells, the enzyme is specific for Lys-36. Lysine residues exist in three methylation states (mono-, di- and trimethylated). The enzyme preferentially demethylates the dimethyl form of Lys-36 (K36me₂), which is its natural substrate, to form the monomethyl and unmethylated forms of Lys-36. It can also demethylate the monomethyl- but not the trimethyl form of Lys-36.
- References:** [3941]

[EC 1.14.11.27 created 2006]

EC 1.14.11.28

- Accepted name:** proline 3-hydroxylase
- Reaction:** L-proline + 2-oxoglutarate + O₂ = *cis*-3-hydroxy-L-proline + succinate + CO₂
- Other name(s):** P-3-H
- Systematic name:** L-proline,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
- Comments:** Requires iron(II) for activity. Unlike the proline hydroxylases involved in collagen biosynthesis [EC 1.14.11.2 (procollagen-proline dioxygenase) and EC 1.14.11.7 (procollagen-proline 3-dioxygenase)], this enzyme does not require ascorbate for activity although it does increase the activity of the enzyme [2618]. The enzyme is specific for L-proline as D-proline, *trans*-4-hydroxy-L-proline, *cis*-4-hydroxy-L-proline and 3,4-dehydro-DL-proline are not substrates [2618].
- References:** [2617, 2618, 634]

[EC 1.14.11.28 created 2006]

EC 1.14.11.29

- Accepted name:** hypoxia-inducible factor-proline dioxygenase
- Reaction:** hypoxia-inducible factor-L-proline + 2-oxoglutarate + O₂ = hypoxia-inducible factor-*trans*-4-hydroxy-L-proline + succinate + CO₂
- Other name(s):** HIF hydroxylase
- Systematic name:** hypoxia-inducible factor-L-proline, 2-oxoglutarate:oxygen oxidoreductase (4-hydroxylating)
- Comments:** Contains iron, and requires ascorbate. Specifically hydroxylates a proline residue in HIF- α , the α subunit of the transcriptional regulator HIF (hypoxia-inducible factor), which targets HIF for proteasomal destruction. The requirement of oxygen for the hydroxylation reaction enables animals to respond to hypoxia.
- References:** [1701, 1688, 427, 960, 2841, 2491]

[EC 1.14.11.29 created 2010]

EC 1.14.11.30

- Accepted name:** hypoxia-inducible factor-asparagine dioxygenase
- Reaction:** hypoxia-inducible factor-L-asparagine + 2-oxoglutarate + O₂ = hypoxia-inducible factor-(3*S*)-3-hydroxy-L-asparagine + succinate + CO₂

Other name(s): HIF hydroxylase
Systematic name: hypoxia-inducible factor-L-asparagine, 2-oxoglutarate:oxygen oxidoreductase (4-hydroxylating)
Comments: Contains iron, and requires ascorbate. Catalyses hydroxylation of an asparagine in the C-terminal transcriptional activation domain of HIF- α , the α subunit of the transcriptional regulator HIF (hypoxia-inducible factor), which reduces its interaction with the transcriptional coactivator protein p300. The requirement of oxygen for the hydroxylation reaction enables animals to respond to hypoxia.
References: [2371, 1485, 744, 2124, 2011, 940]

[EC 1.14.11.30 created 2010]

EC 1.14.11.31

Accepted name: thebaine 6-*O*-demethylase
Reaction: thebaine + 2-oxoglutarate + O₂ = neopinone + formaldehyde + succinate + CO₂
Other name(s): T6ODM
Systematic name: thebaine,2-oxoglutarate:oxygen oxidoreductase (6-*O*-demethylating)
Comments: Requires Fe²⁺. Catalyses a step in morphine biosynthesis. The product neopinone spontaneously rearranges to the more stable codeinone. The enzyme also catalyses the 6-*O*-demethylation of oripavine to morphinone, with lower efficiency.
References: [1337]

[EC 1.14.11.31 created 2010]

EC 1.14.11.32

Accepted name: codeine 3-*O*-demethylase
Reaction: codeine + 2-oxoglutarate + O₂ = morphine + formaldehyde + succinate + CO₂
Other name(s): codeine *O*-demethylase; CODM
Systematic name: codeine,2-oxoglutarate:oxygen oxidoreductase (3-*O*-demethylating)
Comments: Requires Fe²⁺. Catalyses a step in morphine biosynthesis. The enzyme also catalyses the 3-*O*-demethylation of thebaine to oripavine, with lower efficiency.
References: [1337]

[EC 1.14.11.32 created 2010]

EC 1.14.11.33

Accepted name: DNA oxidative demethylase
Reaction: DNA-base-CH₃ + 2-oxoglutarate + O₂ = DNA-base + formaldehyde + succinate + CO₂
Other name(s): alkylated DNA repair protein; α -ketoglutarate-dependent dioxygenase ABH1; *alkB* (gene name)
Systematic name: methyl DNA-base, 2-oxoglutarate:oxygen oxidoreductase (formaldehyde-forming)
Comments: Contains iron; activity is slightly stimulated by ascorbate. Catalyses oxidative demethylation of the DNA base lesions *N*¹-methyladenine, *N*³-methylcytosine, *N*¹-methylguanine, and *N*³-methylthymine. It works better on single-stranded DNA (ssDNA) and is capable of repairing damaged bases in RNA.
References: [981, 4360, 4359]

[EC 1.14.11.33 created 2011]

[1.14.11.34 Transferred entry. 2-oxoglutarate/L-arginine monooxygenase/decarboxylase (succinate-forming). Now EC 1.14.20.7, 2-oxoglutarate/L-arginine monooxygenase/decarboxylase (succinate-forming)]

[EC 1.14.11.34 created 2011, deleted 2018]

EC 1.14.11.35

Accepted name: 1-deoxypentalenic acid 11 β -hydroxylase
Reaction: 1-deoxypentalenate + 2-oxoglutarate + O₂ = 1-deoxy-11 β -hydroxypentalenate + succinate + CO₂

Other name(s): *ptlH* (gene name); *sav2991* (gene name); *pntH* (gene name)
Systematic name: 1-deoxypentalenic acid,2-oxoglutarate:oxygen oxidoreductase
Comments: The enzyme requires Fe(II) and ascorbate. Isolated from the bacterium *Streptomyces avermitilis*. Part of the pathway for pentalenolactone biosynthesis.
References: [4389, 4391]

[EC 1.14.11.35 created 2012]

EC 1.14.11.36

Accepted name: pentalenolactone F synthase
Reaction: pentalenolactone D + 2 2-oxoglutarate + 2 O₂ = pentalenolactone F + 2 succinate + 2 CO₂ + H₂O (overall reaction)
(1a) pentalenolactone D + 2-oxoglutarate + O₂ = pentalenolactone E + succinate + CO₂ + H₂O
(1b) pentalenolactone E + 2-oxoglutarate + O₂ = pentalenolactone F + succinate + CO₂
Other name(s): *penD* (gene name); *pntD* (gene name); *ptlD* (gene name)
Systematic name: pentalenolactone-D,2-oxoglutarate:oxygen oxidoreductase
Comments: Requires Fe(II) and ascorbate. Isolated from the bacteria *Streptomyces exfoliatus*, *Streptomyces arenae* and *Streptomyces avermitilis*. Part of the pentalenolactone biosynthesis pathway.
References: [3443]

[EC 1.14.11.36 created 2012]

EC 1.14.11.37

Accepted name: kanamycin B dioxygenase
Reaction: kanamycin B + 2-oxoglutarate + O₂ = 2'-dehydrokanamycin A + succinate + NH₃ + CO₂
Other name(s): *kanJ* (gene name)
Systematic name: kanamycin-B,2-oxoglutarate:oxygen oxidoreductase (deaminating, 2'-hydroxylating)
Comments: Requires Fe²⁺ and ascorbate. Found in the bacterium *Streptomyces kanamyceticus* where it is involved in the conversion of the aminoglycoside antibiotic kanamycin B to kanamycin A.
References: [3704]

[EC 1.14.11.37 created 2013, modified 2013]

EC 1.14.11.38

Accepted name: verruculogen synthase
Reaction: fumitremorgin B + 2-oxoglutarate + 2 O₂ + reduced acceptor = verruculogen + succinate + CO₂ + H₂O + acceptor
Other name(s): *fmtF* (gene name); FmtOx1
Systematic name: fumitremorgin B,2-oxoglutarate:oxygen oxidoreductase (verruculogen-forming)
Comments: Requires Fe²⁺ and ascorbate. Found in the fungus *Aspergillus fumigatus*. Both atoms of a dioxygen molecule are incorporated into verruculogen [3630, 1839]. Involved in the biosynthetic pathways of several indole alkaloids such as fumitremorgin A.
References: [3630, 1839]

[EC 1.14.11.38 created 2013]

EC 1.14.11.39

Accepted name: L-asparagine hydroxylase
Reaction: L-asparagine + 2-oxoglutarate + O₂ = (2S,3S)-3-hydroxyasparagine + succinate + CO₂
Other name(s): L-asparagine 3-hydroxylase; AsnO
Systematic name: L-asparagine,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Requires Fe²⁺. The enzyme is only able to hydroxylate free L-asparagine. It is not active toward D-asparagine. The β-hydroxylated asparagine produced is incorporated at position 9 of the calcium-dependent antibiotic (CDA), an 11-residue non-ribosomally synthesized acidic lipopeptide lactone.

References: [3681]

[EC 1.14.11.39 created 2013]

EC 1.14.11.40

Accepted name: enduracididine β -hydroxylase
Reaction: L-enduracididine + 2-oxoglutarate + O₂ = (3*S*)-3-hydroxy-L-enduracididine + succinate + CO₂
Other name(s): MppO; L-enduracididine,2-oxoglutarate:O₂ oxidoreductase (3-hydroxylating)
Systematic name: L-enduracididine,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Fe²⁺-dependent enzyme. The enzyme is involved in biosynthesis of the nonproteinogenic amino acid β -hydroxyenduracididine, a component of the mannopeptimycins (cyclic glycopeptide antibiotic), produced by *Streptomyces hygroscopicus* NRRL 30439.
References: [1350, 2358]

[EC 1.14.11.40 created 2013]

EC 1.14.11.41

Accepted name: L-arginine hydroxylase
Reaction: L-arginine + 2-oxoglutarate + O₂ = (3*S*)-3-hydroxy-L-arginine + succinate + CO₂
Other name(s): VioC (ambiguous); L-arginine,2-oxoglutarate:O₂ oxidoreductase (3-hydroxylating)
Systematic name: L-arginine,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: Fe²⁺-dependent enzyme. The enzyme is involved in the biosynthesis of the cyclic pentapeptide antibiotic viomycin. It differs from EC 1.14.20.7, 2-oxoglutarate/L-arginine monooxygenase/decarboxylase (succinate-forming), because it does not form guanidine and (*S*)-1-pyrroline-5-carboxylate from 3-hydroxy-L-arginine.
References: [1781, 1472]

[EC 1.14.11.41 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
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: [2813, 1836]

[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
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 [4183, 2656].

References: [4183, 2656, 2657]

[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

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 [4183, 2656].

References: [4183, 2656, 2657]

[EC 1.14.11.44 created 2013]

EC 1.14.11.45

Accepted name: L-isoleucine 4-hydroxylase

Reaction: L-isoleucine + 2-oxoglutarate + O₂ = (4*S*)-4-hydroxy-L-isoleucine + succinate + CO₂

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

Systematic name: L-isoleucine,2-oxoglutarate:oxygen oxidoreductase (4-hydroxylating)

Comments: The enzyme, characterized from the bacterium *Bacillus thuringiensis*, can also catalyse the hydroxylation of L-leucine, L-norvaline, L-norleucine, and L-*allo*-isoleucine, as well as the sulfoxidation of L-methionine, L-ethionine, *S*-methyl-L-cysteine, *S*-ethyl-L-cysteine, and *S*-allyl-L-cysteine.

References: [1988, 1487, 1488]

[EC 1.14.11.45 created 2014]

EC 1.14.11.46

Accepted name: 2-aminoethylphosphonate dioxygenase

Reaction: (2-aminoethyl)phosphonate + 2-oxoglutarate + O₂ = (2-amino-1-hydroxyethyl)phosphonate + succinate + CO₂

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

Systematic name: (2-aminoethyl)phosphonate,2-oxoglutarate:oxygen oxidoreductase (1-hydroxylating)

Comments: Requires Fe²⁺ and ascorbate. The enzyme, characterized from an uncultured marine bacterium, is involved in a (2-aminoethyl)phosphonate degradation pathway.

References: [2493]

[EC 1.14.11.46 created 2014]

EC 1.14.11.47

Accepted name: 50S ribosomal protein L16 3-hydroxylase

Reaction: [50S ribosomal protein L16]-L-Arg⁸¹ + 2-oxoglutarate + O₂ = [50S ribosomal protein L16]-(3*R*)-3-hydroxy-L-Arg⁸¹ + succinate + CO₂

Other name(s): *ycfD* (gene name)
Systematic name: [50S ribosomal protein L16]-L-Arg⁸¹,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)
Comments: The enzyme, characterized from the bacterium *Escherichia coli*, hydroxylates an arginine residue on the 50S ribosomal protein L16, and is involved in regulation of bacterial ribosome assembly.
References: [1176, 4010]

[EC 1.14.11.47 created 2014]

EC 1.14.11.48

Accepted name: xanthine dioxygenase
Reaction: xanthine + 2-oxoglutarate + O₂ = urate + succinate + CO₂
Other name(s): XanA; α -ketoglutarate-dependent xanthine hydroxylase
Systematic name: xanthine,2-oxoglutarate:oxygen oxidoreductase
Comments: Requires Fe²⁺ and L-ascorbate. The enzyme, which was characterized from fungi, is specific for xanthine.
References: [703, 2601, 2230]

[EC 1.14.11.48 created 2015]

EC 1.14.11.49

Accepted name: uridine-5'-phosphate dioxygenase
Reaction: UMP + 2-oxoglutarate + O₂ = 5'-dehydrouridine + succinate + CO₂ + phosphate
Other name(s): *lipL* (gene name)
Systematic name: UMP,2-oxoglutarate:oxygen oxidoreductase
Comments: The enzyme catalyses a net dephosphorylation and oxidation of UMP to generate 5'-dehydrouridine, the first intermediate in the biosynthesis of the unusual aminoribosyl moiety found in several C⁷-furanosyl nucleosides such as A-90289s, caprazamycins, liposidomycins, muraymycins and FR-900453. Requires Fe²⁺.
References: [4343, 4345]

[EC 1.14.11.49 created 2015]

[1.14.11.50] *Transferred entry. (-)-deoxypodophyllotoxin synthase. Now EC 1.14.20.8, (-)-deoxypodophyllotoxin synthase*

[EC 1.14.11.50 created 2016, deleted 2018]

EC 1.14.11.51

Accepted name: DNA N⁶-methyladenine demethylase
Reaction: N⁶-methyladenine in DNA + 2-oxoglutarate + O₂ = adenine in DNA + formaldehyde + succinate + CO₂
Other name(s): ALKBH1
Systematic name: DNA-N⁶-methyladenosine,2-oxoglutarate:oxygen oxidoreductase (formaldehyde-forming)
Comments: Contains iron(II). Catalyses oxidative demethylation of DNA N⁶-methyladenine, a prevalent modification in LINE-1 transposons, which are specifically enriched on the human X chromosome.
References: [4263]

[EC 1.14.11.51 created 2016]

EC 1.14.11.52

Accepted name: validamycin A dioxygenase
Reaction: validamycin A + 2-oxoglutarate + O₂ = validamycin B + succinate + CO₂
Other name(s): *vldW* (gene name)
Systematic name: validamycin-A,2-oxoglutarate:oxygen oxidoreductase (6'-hydroxylating)

Comments: The enzyme was characterized from the bacterium *Streptomyces hygrosopicus* subsp. *limoneus*. Requires Fe²⁺.

References: [65]

[EC 1.14.11.52 created 2016]

EC 1.14.11.53

Accepted name: mRNA N⁶-methyladenine demethylase

Reaction: N⁶-methyladenine in mRNA + 2-oxoglutarate + O₂ = adenine in mRNA + formaldehyde + succinate + CO₂

Other name(s): ALKBH5; FTO

Systematic name: mRNA-N⁶-methyladenosine,2-oxoglutarate:oxygen oxidoreductase (formaldehyde-forming)

Comments: Contains iron(II). Catalyses oxidative demethylation of mRNA N⁶-methyladenine. The FTO enzyme from human can also demethylate N³-methylthymine from single stranded DNA and N³-methyluridine from single stranded RNA [1742, 1365] with low activity [1741].

References: [1742, 1365, 1741, 4467, 995, 4282, 39]

[EC 1.14.11.53 created 2016]

EC 1.14.11.54

Accepted name: mRNA N¹-methyladenine demethylase

Reaction: N¹-methyladenine in mRNA + 2-oxoglutarate + O₂ = adenine in mRNA + formaldehyde + succinate + CO₂

Other name(s): ALKBH3

Systematic name: mRNA-N¹-methyladenine,2-oxoglutarate:oxygen oxidoreductase (formaldehyde-forming)

Comments: Contains iron(II). Catalyses oxidative demethylation of mRNA N¹-methyladenine. The enzyme is also involved in alkylation repair in DNA [742].

References: [3739, 742, 2236]

[EC 1.14.11.54 created 2016]

EC 1.14.11.55

Accepted name: ectoine hydroxylase

Reaction: ectoine + 2-oxoglutarate + O₂ = 5-hydroxyectoine + succinate + CO₂

Other name(s): *ectD* (gene name); ectoine dioxygenase

Systematic name: ectoine,2-oxoglutarate:oxygen oxidoreductase (5-hydroxylating)

Comments: Requires Fe²⁺ and ascorbate. The enzyme, found in bacteria, is specific for ectoine.

References: [455, 454, 3174]

[EC 1.14.11.55 created 2017]

EC 1.14.11.56

Accepted name: L-proline *cis*-4-hydroxylase

Reaction: L-proline + 2-oxoglutarate + O₂ = *cis*-4-hydroxy-L-proline + succinate + CO₂

Systematic name: L-proline,2-oxoglutarate:oxygen oxidoreductase (*cis*-4-hydroxylating)

Comments: Requires Fe²⁺ and ascorbate. The enzyme, isolated from *Rhizobium* species, only produces *cis*-4-hydroxy-L-proline (*cf.* EC 1.14.11.57, L-proline *trans*-4-hydroxylase).

References: [1387]

[EC 1.14.11.56 created 2017]

EC 1.14.11.57

Accepted name: L-proline *trans*-4-hydroxylase
Reaction: L-proline + 2-oxoglutarate + O₂ = *trans*-4-hydroxy-L-proline + succinate + CO₂
Systematic name: L-proline,2-oxoglutarate:oxygen oxidoreductase (*trans*-4-hydroxylating)
Comments: Requires Fe²⁺ and ascorbate. The enzyme, isolated from multiple bacterial species, only produces *trans*-4-hydroxy-L-proline (*cf.* EC 1.14.11.56, L-proline *cis*-4-hydroxylase).
References: [2155, 3483]

[EC 1.14.11.57 created 2017]

EC 1.14.11.58

Accepted name: ornithine lipid ester-linked acyl 2-hydroxylase
Reaction: an ornithine lipid + 2-oxoglutarate + O₂ = a 2-hydroxyornithine lipid + succinate + CO₂
Other name(s): *olsC* (gene name)
Systematic name: ornithine lipid,2-oxoglutarate:oxygen oxidoreductase (ester-linked acyl 2-hydroxylase)
Comments: The enzyme, characterized from the bacterium *Rhizobium tropici*, catalyses the hydroxylation of C-2 of the fatty acyl group that is ester-linked to the 3-hydroxy position of the amide-linked fatty acid.
References: [3222, 4028]

[EC 1.14.11.58 created 2018]

EC 1.14.11.59

Accepted name: 2,4-dihydroxy-1,4-benzoxazin-3-one-glucoside dioxygenase
Reaction: (2*R*)-4-hydroxy-3-oxo-3,4-dihydro-2*H*-1,4-benzoxazin-2-yl β-D-glucopyranoside + 2-oxoglutarate + O₂ = (2*R*)-4,7-dihydroxy-3-oxo-3,4-dihydro-2*H*-1,4-benzoxazin-2-yl β-D-glucopyranoside + succinate + CO₂ + H₂O
Other name(s): BX6 (gene name); DIBOA-Glc dioxygenase
Systematic name: (2*R*)-4-hydroxy-3-oxo-3,4-dihydro-2*H*-1,4-benzoxazin-2-yl β-D-glucopyranoside:oxygen oxidoreductase (7-hydroxylating)
Comments: The enzyme is involved in the biosynthesis of protective and allelopathic benzoxazinoids in some plants, most commonly from the family of Poaceae (grasses).
References: [1768]

[EC 1.14.11.59 created 2012 as EC 1.14.20.2, transferred 2018 to EC 1.14.11.59]

EC 1.14.11.60

Accepted name: scopoletin 8-hydroxylase
Reaction: scopoletin + 2-oxoglutarate + O₂ = fraxetin + succinate + CO₂
Other name(s): S8H (gene name)
Systematic name: scopoletin,2-oxoglutarate:oxygen oxidoreductase (8-hydroxylating)
Comments: Requires iron(II) and ascorbate. A protein involved in biosynthesis of iron(III)-chelating coumarins in higher plants.
References: [3546, 3113]

[EC 1.14.11.60 created 2018]

EC 1.14.12 With NADH or NADPH as one donor, and incorporation of two atoms of oxygen into the other donor

EC 1.14.12.1

Accepted name: anthranilate 1,2-dioxygenase (deaminating, decarboxylating)
Reaction: anthranilate + NAD(P)H + 2 H⁺ + O₂ = catechol + CO₂ + NAD(P)⁺ + NH₃
Other name(s): anthranilate hydroxylase; anthranilic hydroxylase; anthranilic acid hydroxylase

Systematic name: anthranilate,NAD(P)H:oxygen oxidoreductase (1,2-hydroxylating, deaminating, decarboxylating)
Comments: Requires Fe²⁺.
References: [1982, 3814]

[EC 1.14.12.1 created 1972]

[1.14.12.2 *Transferred entry. now EC 1.14.13.35 anthranilate 3-monooxygenase (deaminating)*]

[EC 1.14.12.2 created 1972, deleted 1990]

EC 1.14.12.3

Accepted name: benzene 1,2-dioxygenase
Reaction: benzene + NADH + H⁺ + O₂ = *cis*-cyclohexa-3,5-diene-1,2-diol + NAD⁺
Other name(s): benzene hydroxylase; benzene dioxygenase
Systematic name: benzene,NADH:oxygen oxidoreductase (1,2-hydroxylating)
Comments: A system, containing a reductase which is an iron-sulfur flavoprotein (FAD), an iron-sulfur oxygenase and ferredoxin. Requires Fe²⁺.
References: [1200]

[EC 1.14.12.3 created 1972]

[1.14.12.4 *Transferred entry. 3-hydroxy-2-methylpyridinecarboxylate dioxygenase. Now EC 1.14.13.242, 3-hydroxy-2-methylpyridinecarboxylate monooxygenase*]

[EC 1.14.12.4 created 1972, deleted 2018]

[1.14.12.5 *Transferred entry. 5-pyridoxate dioxygenase. Now EC 1.14.13.241, 5-pyridoxate monooxygenase*]

[EC 1.14.12.5 created 1972, deleted 2018]

[1.14.12.6 *Transferred entry. 2-hydroxycyclohexanone 2-monooxygenase. Now EC 1.14.13.66, 2-hydroxycyclohexanone 2-monooxygenase*]

[EC 1.14.12.6 created 1978, deleted 1999]

EC 1.14.12.7

Accepted name: phthalate 4,5-dioxygenase
Reaction: phthalate + NADH + H⁺ + O₂ = *cis*-4,5-dihydroxycyclohexa-1(6),2-diene-1,2-dicarboxylate + NAD⁺
Other name(s): PDO ; phthalate dioxygenase
Systematic name: phthalate,NADH:oxygen oxidoreductase (4,5-hydroxylating)
Comments: A system, containing a reductase which is an iron-sulfur flavoprotein (FMN), an iron-sulfur oxygenase, and no independent ferredoxin. Requires Fe²⁺.
References: [212]

[EC 1.14.12.7 created 1990]

EC 1.14.12.8

Accepted name: 4-sulfobenzoate 3,4-dioxygenase
Reaction: 4-sulfobenzoate + NADH + H⁺ + O₂ = 3,4-dihydroxybenzoate + sulfite + NAD⁺
Other name(s): 4-sulfobenzoate dioxygenase; 4-sulfobenzoate 3,4-dioxygenase system
Systematic name: 4-sulfobenzoate,NADH:oxygen oxidoreductase (3,4-hydroxylating, sulfite-forming)
Comments: A system, containing a reductase which is an iron-sulfur flavoprotein (FMN), an iron-sulfur oxygenase, and no independent ferredoxin. Requires Fe²⁺.
References: [2289]

[EC 1.14.12.8 created 1992]

EC 1.14.12.9

- Accepted name:** 4-chlorophenylacetate 3,4-dioxygenase
Reaction: 4-chlorophenylacetate + NADH + H⁺ + O₂ = 3,4-dihydroxyphenylacetate + chloride + NAD⁺
Systematic name: 4-chlorophenylacetate,NADH:oxygen oxidoreductase (3,4-hydroxylating, dechlorinating)
Comments: A system, containing a reductase and an iron-sulfur oxygenase, and no independent ferredoxin. Requires Fe²⁺. Also acts on 4-bromophenyl acetate.
References: [2402]

[EC 1.14.12.9 created 1989 as EC 1.13.99.4, transferred 1992 to EC 1.14.12.9]

EC 1.14.12.10

- Accepted name:** benzoate 1,2-dioxygenase
Reaction: benzoate + NADH + H⁺ + O₂ = (1*R*,6*S*)-1,6-dihydroxycyclohexa-2,4-diene-1-carboxylate + NAD⁺
Other name(s): benzoate hydroxylase; benzoate hydroxylase; benzoic hydroxylase; benzoate dioxygenase; benzoate,NADH:oxygen oxidoreductase (1,2-hydroxylating, decarboxylating) [incorrect]
Systematic name: benzoate,NADH:oxygen oxidoreductase (1,2-hydroxylating)
Comments: A system, containing a reductase which is an iron-sulfur flavoprotein (FAD), and an iron-sulfur oxygenase. Requires Fe²⁺.
References: [4306, 4307, 4308]

[EC 1.14.12.10 created 1972 as EC 1.13.99.2, transferred 1992 to EC 1.14.12.10]

EC 1.14.12.11

- Accepted name:** toluene dioxygenase
Reaction: toluene + NADH + H⁺ + O₂ = (1*S*,2*R*)-3-methylcyclohexa-3,5-diene-1,2-diol + NAD⁺
Other name(s): toluene 2,3-dioxygenase
Systematic name: toluene,NADH:oxygen oxidoreductase (1,2-hydroxylating)
Comments: A system, containing a reductase which is an iron-sulfur flavoprotein (FAD), an iron-sulfur oxygenase, and a ferredoxin. Some other aromatic compounds, including ethylbenzene, 4-xylene and some halogenated toluenes, are converted into the corresponding *cis*-dihydrodiols.
References: [3168, 3702]

[EC 1.14.12.11 created 1992]

EC 1.14.12.12

- Accepted name:** naphthalene 1,2-dioxygenase
Reaction: naphthalene + NADH + H⁺ + O₂ = (1*R*,2*S*)-1,2-dihydronaphthalene-1,2-diol + NAD⁺
Other name(s): naphthalene dioxygenase; naphthalene oxygenase; NDO
Systematic name: naphthalene,NADH:oxygen oxidoreductase (1,2-hydroxylating)
Comments: This enzyme is a member of the ring-hydroxylating dioxygenase (RHD) family of bacterial enzymes that play a critical role in the degradation of aromatic compounds, such as polycyclic aromatic hydrocarbons [1779]. This enzyme comprises a multicomponent system, containing a reductase that is an iron-sulfur flavoprotein (FAD; EC 1.18.1.3, ferredoxin—NAD⁺ reductase), an iron-sulfur oxygenase, and ferredoxin. Requires Fe²⁺.
References: [958, 1729, 1854, 2937, 1779]

[EC 1.14.12.12 created 1992]

EC 1.14.12.13

- Accepted name:** 2-halobenzoate 1,2-dioxygenase
Reaction: a 2-halobenzoate + NADH + H⁺ + O₂ = catechol + a halide anion + NAD⁺ + CO₂
Other name(s): 2-chlorobenzoate 1,2-dioxygenase
Systematic name: 2-halobenzoate,NADH:oxygen oxidoreductase (1,2-hydroxylating, dehalogenating, decarboxylating)

Comments: A multicomponent enzyme system composed of a dioxygenase component and an electron transfer component. The latter contains FAD. The enzyme, characterized from the bacterium *Burkholderia cepacia* 2CBS, has a broad substrate specificity. Substrates include 2-fluorobenzoate, 2-chlorobenzoate, 2-bromobenzoate, and 2-iodobenzoate, which are processed in this order of preference.

References: [1006, 1007, 1328]

[EC 1.14.12.13 created 1992, modified 2012]

EC 1.14.12.14

Accepted name: 2-aminobenzenesulfonate 2,3-dioxygenase
Reaction: 2-aminobenzenesulfonate + NADH + H⁺ + O₂ = 2,3-dihydroxybenzenesulfonate + NH₃ + NAD⁺
Other name(s): 2-aminosulfobenzene 2,3-dioxygenase
Systematic name: 2-aminobenzenesulfonate,NADH:oxygen oxidoreductase (2,3-hydroxylating, ammonia-forming)
References: [1786, 1788]

[EC 1.14.12.14 created 1999]

EC 1.14.12.15

Accepted name: terephthalate 1,2-dioxygenase
Reaction: terephthalate + NADH + H⁺ + O₂ = (1R,6S)-dihydroxycyclohexa-2,4-diene-1,4-dicarboxylate + NAD⁺
Other name(s): benzene-1,4-dicarboxylate 1,2-dioxygenase; 1,4-dicarboxybenzoate 1,2-dioxygenase
Systematic name: benzene-1,4-dicarboxylate,NADH:oxygen oxidoreductase (1,2-hydroxylating)
Comments: Has been shown to contain a Rieske [2Fe-2S] cluster
References: [3368]

[EC 1.14.12.15 created 1999]

EC 1.14.12.16

Accepted name: 2-hydroxyquinoline 5,6-dioxygenase
Reaction: quinolin-2-ol + NADH + H⁺ + O₂ = 2,5,6-trihydroxy-5,6-dihydroquinoline + NAD⁺
Other name(s): 2-oxo-1,2-dihydroquinoline 5,6-dioxygenase; quinolin-2-ol 5,6-dioxygenase; quinolin-2(1H)-one 5,6-dioxygenase
Systematic name: quinolin-2-ol,NADH:oxygen oxidoreductase (5,6-hydroxylating)
Comments: 3-Methylquinolin-2-ol, quinolin-8-ol and quinolin-2,8-diol are also substrates. Quinolin-2-ols exist largely as their quinolin-2(1H)-one tautomers
References: [3345]

[EC 1.14.12.16 created 1999]

EC 1.14.12.17

Accepted name: nitric oxide dioxygenase
Reaction: 2 nitric oxide + 2 O₂ + NAD(P)H = 2 nitrate + NAD(P)⁺ + H⁺
Systematic name: nitric oxide,NAD(P)H:oxygen oxidoreductase
Comments: A flavohemoglobin (FAD). It has been proposed that FAD functions as the electron carrier from NADPH to the ferric heme prosthetic group.
References: [1155, 1156]

[EC 1.14.12.17 created 2000]

EC 1.14.12.18

Accepted name: biphenyl 2,3-dioxygenase
Reaction: biphenyl + NADH + H⁺ + O₂ = (1*S*,2*R*)-3-phenylcyclohexa-3,5-diene-1,2-diol + NAD⁺
Other name(s): biphenyl dioxygenase
Systematic name: biphenyl,NADH:oxygen oxidoreductase (2,3-hydroxylating)
Comments: Requires Fe²⁺. The enzyme from *Burkholderia fungorum* LB400 (previously *Pseudomonas* sp.) is part of a multicomponent system composed of an NADH:ferredoxin oxidoreductase (FAD cofactor), a [2Fe-2S] Rieske-type ferredoxin, and a terminal oxygenase that contains a [2Fe-2S] Rieske-type iron-sulfur cluster and a catalytic mononuclear nonheme iron centre. Chlorine-substituted biphenyls can also act as substrates. Similar to the three-component enzyme systems EC 1.14.12.3 (benzene 1,2-dioxygenase) and EC 1.14.12.11 (toluene dioxygenase).
References: [1333, 1334, 408]

[EC 1.14.12.18 created 2001]

EC 1.14.12.19

Accepted name: 3-phenylpropanoate dioxygenase
Reaction: (1) 3-phenylpropanoate + NADH + H⁺ + O₂ = 3-(*cis*-5,6-dihydroxycyclohexa-1,3-dien-1-yl)propanoate + NAD⁺
(2) (2*E*)-3-phenylprop-2-enoate + NADH + H⁺ + O₂ = (2*E*)-3-(2,3-dihydroxyphenyl)prop-2-enoate + NAD⁺
Other name(s): HcaA1A2CD; Hca dioxygenase; 3-phenylpropionate dioxygenase
Systematic name: 3-phenylpropanoate,NADH:oxygen oxidoreductase (2,3-hydroxylating)
Comments: This enzyme catalyses a step in the pathway of phenylpropanoid compounds degradation. It catalyses the insertion of both atoms of molecular oxygen into positions 2 and 3 of the phenyl ring of 3-phenylpropanoate or (2*E*)-3-phenylprop-2-enoate.
References: [813, 447]

[EC 1.14.12.19 created 2005, modified 2011]

[1.14.12.20 Transferred entry. pheophorbide a oxygenase. Now classified as EC 1.14.15.17, pheophorbide a oxygenase.]

[EC 1.14.12.20 created 2007, deleted 2016]

[1.14.12.21 Transferred entry. benzoyl-CoA 2,3-dioxygenase. Now EC 1.14.13.208, benzoyl-CoA 2,3-epoxidase]

[EC 1.14.12.21 created 2010, deleted 2015]

EC 1.14.12.22

Accepted name: carbazole 1,9a-dioxygenase
Reaction: 9*H*-carbazole + NAD(P)H + H⁺ + O₂ = 2'-aminobiphenyl-2,3-diol + NAD(P)⁺
Other name(s): CARDO
Systematic name: 9*H*-carbazole,NAD(P)H:oxygen oxidoreductase (2,3-hydroxylating)
Comments: This enzyme catalyses the first reaction in the pathway of carbazole degradation. The enzyme attacks at the 1 and 9a positions of carbazole, resulting in the formation of a highly unstable hemiaminal intermediate that undergoes a spontaneous cleavage and rearomatization, resulting in 2'-aminobiphenyl-2,3-diol. In most bacteria the enzyme is a complex composed of a terminal oxygenase, a ferredoxin, and a ferredoxin reductase. The terminal oxygenase component contains a nonheme iron centre and a Rieske [2Fe-2S] iron-sulfur cluster.
References: [2726, 1139]

[EC 1.14.12.22 created 2010]

EC 1.14.12.23

Accepted name: nitroarene dioxygenase
Reaction: nitrobenzene + NADH + O₂ = catechol + nitrite + NAD⁺

Other name(s): *cnbA* (gene name)
Systematic name: nitrobenzene,NADH:oxygen oxidoreductase (1,2-hydroxylating, nitrite-releasing)
Comments: This enzyme is a member of the naphthalene family of bacterial Rieske non-heme iron dioxygenases. It comprises a multicomponent system, containing a Rieske [2Fe-2S] ferredoxin, an NADH-dependent flavoprotein reductase (EC 1.18.1.3, ferredoxin—NAD⁺ reductase), and an $\alpha\beta\beta\beta$ oxygenase. The enzyme forms a *cis*-dihydroxylated product that spontaneously rearranges to form a catechol with accompanying release of nitrite. It can typically act on many different nitroaromatic compounds, including chlorinated species. Enzymes found in different strains may have different substrate preferences. Requires Fe²⁺.
References: [2936, 2205, 2277, 3536]

[EC 1.14.12.23 created 2015]

EC 1.14.12.24

Accepted name: 2,4-dinitrotoluene dioxygenase
Reaction: 2,4-dinitrotoluene + NADH + O₂ = 4-methyl-5-nitrocatechol + nitrite + NAD⁺
Other name(s): *dntA* (gene name)
Systematic name: 2,4-dinitrotoluene,NADH:oxygen oxidoreductase (4,5-hydroxylating, nitrite-releasing)
Comments: This enzyme, characterized from the bacterium *Burkholderia* sp. strain DNT, is a member of the naphthalene family of bacterial Rieske non-heme iron dioxygenases. It comprises a multicomponent system, containing a Rieske [2Fe-2S] ferredoxin, an NADH-dependent flavoprotein reductase (EC 1.18.1.3, ferredoxin—NAD⁺ reductase), and an $\alpha\beta\beta\beta$ oxygenase. The enzyme forms a *cis*-dihydroxylated product that spontaneously rearranges to form a catechol with accompanying release of nitrite. It does not act on nitrobenzene. *cf.* EC 1.14.12.23, nitroarene dioxygenase.
References: [3706]

[EC 1.14.12.24 created 2015]

EC 1.14.12.25

Accepted name: *p*-cumate 2,3-dioxygenase
Reaction: *p*-cumate + NADH + H⁺ + O₂ = (2*R*,3*S*)-2,3-dihydroxy-2,3-dihydro-*p*-cumate + NAD⁺
Systematic name: 4-isopropylbenzoate:oxygen 2,3-oxidoreductase
Comments: The enzyme, characterized from several *Pseudomonas* strains, is involved in the degradation of *p*-cymene and *p*-cumate. It comprises four components: a ferredoxin, a ferredoxin reductase, and two subunits of a catalytic component. The enzyme can also act on indole, transforming it to the water-insoluble blue dye indigo.
References: [776, 4209, 911, 909]

[EC 1.14.12.25 created 2016]

EC 1.14.12.26

Accepted name: chlorobenzene dioxygenase
Reaction: chlorobenzene + NADH + H⁺ + O₂ = (1*R*,2*R*)-3-chlorocyclohexa-3,5-diene-1,2-diol + NAD⁺
Other name(s): TecA
Systematic name: chlorobenzene,NADH:oxygen oxidoreductase (1,2-hydroxylating)
Comments: This bacterial enzyme is a class IIB dioxygenase, comprising three components - a heterodimeric terminal dioxygenase, a ferredoxin protein, and a ferredoxin reductase. The enzyme acts on a range of aromatic compounds, including mono-, di-, tri-, and tetra-chlorinated benzenes and toluenes.
References: [3604, 3578, 247, 248]

[EC 1.14.12.26 created 2018]

EC 1.14.13 With NADH or NADPH as one donor, and incorporation of one atom of oxygen into the other donor

EC 1.14.13.1

- Accepted name:** salicylate 1-monooxygenase
Reaction: salicylate + NADH + 2 H⁺ + O₂ = catechol + NAD⁺ + H₂O + CO₂
Other name(s): salicylate hydroxylase; salicylate 1-hydroxylase; salicylate monooxygenase; salicylate hydroxylase (decarboxylating)
Systematic name: salicylate,NADH:oxygen oxidoreductase (1-hydroxylating, decarboxylating)
Comments: A flavoprotein (FAD).
References: [3752, 3790, 3789, 4319]

[EC 1.14.13.1 created 1972]

EC 1.14.13.2

- Accepted name:** 4-hydroxybenzoate 3-monooxygenase
Reaction: 4-hydroxybenzoate + NADPH + H⁺ + O₂ = 3,4-dihydroxybenzoate + NADP⁺ + H₂O
Other name(s): *p*-hydroxybenzoate hydrolyase; *p*-hydroxybenzoate hydroxylase; 4-hydroxybenzoate 3-hydroxylase; 4-hydroxybenzoate monooxygenase; 4-hydroxybenzoic hydroxylase; *p*-hydroxybenzoate-3-hydroxylase; *p*-hydroxybenzoic acid hydrolase; *p*-hydroxybenzoic acid hydroxylase; *p*-hydroxybenzoic hydroxylase
Systematic name: 4-hydroxybenzoate,NADPH:oxygen oxidoreductase (3-hydroxylating)
Comments: A flavoprotein (FAD). Most enzymes from *Pseudomonas* are highly specific for NADPH (*cf.* EC 1.14.13.33 4-hydroxybenzoate 3-monooxygenase [NAD(P)H]).
References: [1581, 1587, 3594, 3592, 3593, 3429]

[EC 1.14.13.2 created 1972, modified 1999]

[1.14.13.3 *Transferred entry. 4-hydroxyphenylacetate 3-monooxygenase. Now EC 1.14.14.9, 4-hydroxyphenylacetate 3-monooxygenase.*]

[EC 1.14.13.3 created 1972, deleted 2011]

EC 1.14.13.4

- Accepted name:** melilotate 3-monooxygenase
Reaction: 3-(2-hydroxyphenyl)propanoate + NADH + H⁺ + O₂ = 3-(2,3-dihydroxyphenyl)propanoate + NAD⁺ + H₂O
Other name(s): 2-hydroxyphenylpropionate hydroxylase; melilotate hydroxylase; 2-hydroxyphenylpropionic hydroxylase; melilotic hydroxylase
Systematic name: 3-(2-hydroxyphenyl)propanoate,NADH:oxygen oxidoreductase (3-hydroxylating)
Comments: A flavoprotein (FAD).
References: [2213, 2214, 3678, 3677]

[EC 1.14.13.4 created 1972]

EC 1.14.13.5

- Accepted name:** imidazoleacetate 4-monooxygenase
Reaction: 4-imidazoleacetate + NADH + H⁺ + O₂ = 5-hydroxy-4-imidazoleacetate + NAD⁺ + H₂O
Other name(s): imidazoleacetic hydroxylase; imidazoleacetate hydroxylase; imidazoleacetic monooxygenase
Systematic name: 4-imidazoleacetate,NADH:oxygen oxidoreductase (5-hydroxylating)
Comments: A flavoprotein (FAD).
References: [2378]

[EC 1.14.13.5 created 1965 as EC 1.14.1.5, transferred 1972 to EC 1.14.13.5]

EC 1.14.13.6

Accepted name: orcinol 2-monooxygenase
Reaction: orcinol + NADH + H⁺ + O₂ = 2,3,5-trihydroxytoluene + NAD⁺ + H₂O
Other name(s): orcinol hydroxylase
Systematic name: orcinol,NADH:oxygen oxidoreductase (2-hydroxylating)
Comments: A flavoprotein (FAD).
References: [2909]

[EC 1.14.13.6 created 1972]

EC 1.14.13.7

Accepted name: phenol 2-monooxygenase (NADPH)
Reaction: phenol + NADPH + H⁺ + O₂ = catechol + NADP⁺ + H₂O
Other name(s): phenol hydroxylase; phenol *o*-hydroxylase
Systematic name: phenol,NADPH:oxygen oxidoreductase (2-hydroxylating)
Comments: A flavoprotein (FAD). The enzyme from the fungus *Trichosporon cutaneum* has a broad substrate specificity, and has been reported to catalyse the hydroxylation of a variety of substituted phenols, such as fluoro-, chloro-, amino- and methyl-phenols and also dihydroxybenzenes. *cf.* EC 1.14.14.20, phenol 2-monooxygenase (FADH₂).
References: [2699, 2767, 2768]

[EC 1.14.13.7 created 1972, modified 2011, modified 2016]

EC 1.14.13.8

Accepted name: flavin-containing monooxygenase
Reaction: *N,N*-dimethylaniline + NADPH + H⁺ + O₂ = *N,N*-dimethylaniline *N*-oxide + NADP⁺ + H₂O
Other name(s): dimethylaniline oxidase; dimethylaniline *N*-oxidase; FAD-containing monooxygenase; *N,N*-dimethylaniline monooxygenase; DMA oxidase; flavin mixed function oxidase; Ziegler's enzyme; mixed-function amine oxidase; FMO; FMO-I; FMO-II; FMO1; FMO2; FMO3; FMO4; FMO5; flavin monooxygenase; methylphenyltetrahydropyridine *N*-monooxygenase; 1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine:oxygen *N*-oxidoreductase; dimethylaniline monooxygenase (*N*-oxide-forming)
Systematic name: *N,N*-dimethylaniline,NADPH:oxygen oxidoreductase (*N*-oxide-forming)
Comments: A flavoprotein. A broad spectrum monooxygenase that accepts substrates as diverse as hydrazines, phosphines, boron-containing compounds, sulfides, selenides, iodide, as well as primary, secondary and tertiary amines [517, 518]. This enzyme is distinct from other monooxygenases in that the enzyme forms a relatively stable hydroperoxy flavin intermediate [518, 1771]. This microsomal enzyme generally converts nucleophilic heteroatom-containing chemicals and drugs into harmless, readily excreted metabolites. For example, *N*-oxygenation is largely responsible for the detoxification of the dopaminergic neurotoxin 1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine (MPTP) [591, 590]
References: [4486, 591, 517, 518, 1771, 590]

[EC 1.14.13.8 created 1972 (EC 1.13.12.11 created 1992, part-incorporated 2006), modified 2006]

EC 1.14.13.9

Accepted name: kynurenine 3-monooxygenase
Reaction: L-kynurenine + NADPH + H⁺ + O₂ = 3-hydroxy-L-kynurenine + NADP⁺ + H₂O
Other name(s): kynurenine 3-hydroxylase; kynurenine hydroxylase; L-kynurenine-3-hydroxylase
Systematic name: L-kynurenine,NADPH:oxygen oxidoreductase (3-hydroxylating)
Comments: A flavoprotein (FAD).
References: [758, 2861, 3287]

[EC 1.14.13.9 created 1961 as EC 1.99.1.5, transferred 1965 to EC 1.14.1.2, transferred 1972 to EC 1.14.13.9]

EC 1.14.13.10

Accepted name: 2,6-dihydroxypyridine 3-monooxygenase
Reaction: 2,6-dihydroxypyridine + NADH + H⁺ + O₂ = 2,3,6-trihydroxypyridine + NAD⁺ + H₂O
Other name(s): 2,6-dihydroxypyridine oxidase
Systematic name: 2,6-dihydroxypyridine,NADH:oxygen oxidoreductase (3-hydroxylating)
Comments: A flavoprotein.
References: [1547, 1548]

[EC 1.14.13.10 created 1976]

[1.14.13.11 *Transferred entry. trans-cinnamate 4-monooxygenase. Now EC 1.14.14.91, trans-cinnamate 4-monooxygenase*]

[EC 1.14.13.11 created 1976, deleted 2018]

[1.14.13.12 *Transferred entry. benzoate 4-monooxygenase. Now EC 1.14.14.92, benzoate 4-monooxygenase*]

[EC 1.14.13.12 created 1976, deleted 2018]

[1.14.13.13 *Transferred entry. calcidiol 1-monooxygenase. Now classified as EC 1.14.15.18, calcidiol 1-monooxygenase*]

[EC 1.14.13.13 created 1976, deleted 2016]

EC 1.14.13.14

Accepted name: *trans*-cinnamate 2-monooxygenase
Reaction: *trans*-cinnamate + NADPH + H⁺ + O₂ = 2-hydroxycinnamate + NADP⁺ + H₂O
Other name(s): cinnamic acid 2-hydroxylase; cinnamate 2-monooxygenase; cinnamic 2-hydroxylase; cinnamate 2-hydroxylase; *trans*-cinnamic acid 2-hydroxylase
Systematic name: *trans*-cinnamate,NADPH:oxygen oxidoreductase (2-hydroxylating)
References: [1189]

[EC 1.14.13.14 created 1976]

[1.14.13.15 *Transferred entry. cholestanetriol 26-monooxygenase. Now EC 1.14.15.15, cholestanetriol 26-monooxygenase.*]

[EC 1.14.13.15 created 1976, modified 2005, modified 2012, deleted 2016]

EC 1.14.13.16

Accepted name: cyclopentanone monooxygenase
Reaction: cyclopentanone + NADPH + H⁺ + O₂ = 5-valerolactone + NADP⁺ + H₂O
Other name(s): cyclopentanone oxygenase
Systematic name: cyclopentanone,NADPH:oxygen oxidoreductase (5-hydroxylating, lactonizing)
References: [1282, 1283]

[EC 1.14.13.16 created 1976]

[1.14.13.17 *Transferred entry. cholesterol 7 α -monooxygenase. Now EC 1.14.14.23, cholesterol 7 α -monooxygenase*]

[EC 1.14.13.17 created 1976, deleted 2016]

EC 1.14.13.18

Accepted name: 4-hydroxyphenylacetate 1-monooxygenase
Reaction: 4-hydroxyphenylacetate + NAD(P)H + H⁺ + O₂ = homogentisate + NAD(P)⁺ + H₂O
Other name(s): 4-hydroxyphenylacetate 1-hydroxylase; 4-hydroxyphenylacetic 1-hydroxylase; 4-HPA 1-hydroxylase
Systematic name: 4-hydroxyphenylacetate,NAD(P)H:oxygen oxidoreductase (1-hydroxylating)

Comments: A flavoprotein (FAD). Also acts on 4-hydroxyhydratropate (forming 2-methylhomogentisate) and on 4-hydroxyphenoxyacetate (forming hydroquinone and glycolate).

References: [1395]

[EC 1.14.13.18 created 1976]

EC 1.14.13.19

Accepted name: taxifolin 8-monoxygenase

Reaction: taxifolin + NAD(P)H + H⁺ + O₂ = 2,3-dihydrogossypetin + NAD(P)⁺ + H₂O

Other name(s): taxifolin hydroxylase

Systematic name: taxifolin,NAD(P)H:oxygen oxidoreductase (8-hydroxylating)

Comments: A flavoprotein, converting a flavanol into a flavanone. Also acts on fustin, but not on catechin, quercetin or mollisacidin.

References: [1728]

[EC 1.14.13.19 created 1976]

EC 1.14.13.20

Accepted name: 2,4-dichlorophenol 6-monoxygenase

Reaction: 2,4-dichlorophenol + NADPH + H⁺ + O₂ = 3,5-dichlorocatechol + NADP⁺ + H₂O

Other name(s): 2,4-dichlorophenol hydroxylase; 2,4-dichlorophenol monoxygenase

Systematic name: 2,4-dichlorophenol,NADPH:oxygen oxidoreductase (6-hydroxylating)

Comments: A flavoprotein (FAD). Also acts, more slowly, on 4-chlorophenol and 4-chloro-2-methylphenol; NADH can act instead of NADPH, but more slowly.

References: [226]

[EC 1.14.13.20 created 1983]

[1.14.13.21] *Transferred entry. flavonoid 3'-monoxygenase. Now EC 1.14.14.82, flavonoid 3'-monoxygenase.*

[EC 1.14.13.21 created 1983, deleted 2018]

EC 1.14.13.22

Accepted name: cyclohexanone monoxygenase

Reaction: cyclohexanone + NADPH + H⁺ + O₂ = hexano-6-lactone + NADP⁺ + H₂O

Other name(s): cyclohexanone 1,2-monoxygenase; cyclohexanone oxygenase; cyclohexanone:NADPH:oxygen oxidoreductase (6-hydroxylating, 1,2-lactonizing)

Systematic name: cyclohexanone,NADPH:oxygen oxidoreductase (lactone-forming)

Comments: A flavoprotein (FAD). In the catalytic mechanism of this enzyme, the nucleophilic species that attacks the carbonyl group is a peroxyflavin intermediate that is generated by reaction of the enzyme-bound flavin cofactor with NAD(P)H and oxygen [3477]. This enzyme is able to catalyse a wide range of oxidative reactions, including enantioselective Baeyer-Villiger reactions [3643], sulfoxidations [567], amine oxidations [2913] and epoxidations [646].

References: [856, 3477, 3643, 567, 2913, 646]

[EC 1.14.13.22 created 1984, modified 2004]

EC 1.14.13.23

Accepted name: 3-hydroxybenzoate 4-monoxygenase

Reaction: 3-hydroxybenzoate + NADPH + H⁺ + O₂ = 3,4-dihydroxybenzoate + NADP⁺ + H₂O

Other name(s): 3-hydroxybenzoate 4-hydroxylase

Systematic name: 3-hydroxybenzoate,NADPH:oxygen oxidoreductase (4-hydroxylating)

Comments: A flavoprotein (FAD). Acts also on a number of analogues of 3-hydroxybenzoate substituted in the 2, 4, 5 and 6 positions.

References: [2524, 3057]

[EC 1.14.13.23 created 1972 as EC 1.14.99.13, transferred 1984 to EC 1.14.13.23]

EC 1.14.13.24

Accepted name: 3-hydroxybenzoate 6-monooxygenase
Reaction: 3-hydroxybenzoate + NADH + H⁺ + O₂ = 2,5-dihydroxybenzoate + NAD⁺ + H₂O
Other name(s): 3-hydroxybenzoate 6-hydroxylase; *m*-hydroxybenzoate 6-hydroxylase; 3-hydroxybenzoic acid-6-hydroxylase
Systematic name: 3-hydroxybenzoate,NADH:oxygen oxidoreductase (6-hydroxylating)
Comments: A flavoprotein (FAD). Acts also on a number of analogues of 3-hydroxybenzoate substituted in the 2, 4, 5 and 6 positions; NADPH can act instead of NADH, but more slowly.
References: [1294]

[EC 1.14.13.24 created 1984]

EC 1.14.13.25

Accepted name: methane monooxygenase (soluble)
Reaction: methane + NAD(P)H + H⁺ + O₂ = methanol + NAD(P)⁺ + H₂O
Other name(s): methane hydroxylase
Systematic name: methane,NAD(P)H:oxygen oxidoreductase (hydroxylating)
Comments: The enzyme is soluble, in contrast to the particulate enzyme, EC 1.14.18.3. Broad specificity; many alkanes can be hydroxylated, and alkenes are converted into the corresponding epoxides; CO is oxidized to CO₂, ammonia is oxidized to hydroxylamine, and some aromatic compounds and cyclic alkanes can also be hydroxylated, but more slowly.
References: [640, 1618, 3652, 3908]

[EC 1.14.13.25 created 1984, modified 2011]

[1.14.13.26 *Transferred entry. phosphatidylcholine 12-monooxygenase. Now classified as EC 1.14.18.4, phosphatidylcholine 12-monooxygenase.*]

[EC 1.14.13.26 created 1984, deleted 2015]

EC 1.14.13.27

Accepted name: 4-aminobenzoate 1-monooxygenase
Reaction: 4-aminobenzoate + NAD(P)H + 2 H⁺ + O₂ = 4-hydroxyaniline + NAD(P)⁺ + H₂O + CO₂
Other name(s): 4-aminobenzoate hydroxylase; 4-aminobenzoate monooxygenase
Systematic name: 4-aminobenzoate,NAD(P)H:oxygen oxidoreductase (1-hydroxylating, decarboxylating)
Comments: A flavoprotein (FAD). Acts on anthranilate and 4-aminosalicylate but not on salicylate (*cf.* EC 1.14.13.1 salicylate 1-monooxygenase).
References: [3939]

[EC 1.14.13.27 created 1989]

[1.14.13.28 *Transferred entry. 3,9-dihydroxypterocarpan 6a-monooxygenase. Now EC 1.14.14.93, 3,9-dihydroxypterocarpan 6a-monooxygenase*]

[EC 1.14.13.28 created 1989, deleted 2018]

EC 1.14.13.29

Accepted name: 4-nitrophenol 2-monooxygenase
Reaction: 4-nitrophenol + NADH + H⁺ + O₂ = 4-nitrocatechol + NAD⁺ + H₂O
Other name(s): 4-nitrophenol hydroxylase; 4-nitrophenol-2-hydroxylase

Systematic name: 4-nitrophenol,NADH:oxygen oxidoreductase (2-hydroxylating)
Comments: A flavoprotein (FAD).
References: [2565]

[EC 1.14.13.29 created 1989]

[1.14.13.30 Transferred entry. leukotriene-B₄ 20-monoxygenase. Now EC 1.14.14.94, leukotriene-B₄ 20-monoxygenase]

[EC 1.14.13.30 created 1989, deleted 2018]

EC 1.14.13.31

Accepted name: 2-nitrophenol 2-monoxygenase
Reaction: 2-nitrophenol + 2 NADPH + 2 H⁺ + O₂ = catechol + nitrite + 2 NADP⁺ + H₂O
Other name(s): 2-nitrophenol oxygenase; nitrophenol oxygenase
Systematic name: 2-nitrophenol,NADPH:oxygen 2-oxidoreductase (2-hydroxylating, nitrite-forming)
Comments: Involved in the metabolism of nitro-aromatic compounds by a strain of *Pseudomonas putida*.
References: [4436]

[EC 1.14.13.31 created 1989]

EC 1.14.13.32

Accepted name: albendazole monoxygenase
Reaction: albendazole + NADPH + H⁺ + O₂ = albendazole S-oxide + NADP⁺ + H₂O
Other name(s): albendazole oxidase (misleading); albendazole sulfoxidase (ambiguous); FMO3 (gene name); albendazole monoxygenase (flavin-containing)
Systematic name: albendazole,NADPH:oxygen oxidoreductase (sulfoxide-forming)
Comments: A microsomal flavin-containing monoxygenase. A similar conversion is also carried out by some microsomal cytochrome P-450 enzymes [EC 1.14.14.73, albendazole monoxygenase (sulfoxide-forming)]. It is estimated that cytochrome P-450s are responsible for 70% of the activity.
References: [985, 2630, 3137]

[EC 1.14.13.32 created 1989, modified 2018]

EC 1.14.13.33

Accepted name: 4-hydroxybenzoate 3-monoxygenase [NAD(P)H]
Reaction: 4-hydroxybenzoate + NAD(P)H + H⁺ + O₂ = 3,4-dihydroxybenzoate + NAD(P)⁺ + H₂O
Other name(s): 4-hydroxybenzoate 3-monoxygenase (reduced nicotinamide adenine dinucleotide (phosphate)); 4-hydroxybenzoate-3-hydroxylase; 4-hydroxybenzoate 3-hydroxylase
Systematic name: 4-hydroxybenzoate,NAD(P)H:oxygen oxidoreductase (3-hydroxylating)
Comments: A flavoprotein (FAD). The enzyme from *Corynebacterium cyclohexanicum* is highly specific for 4-hydroxybenzoate, but uses NADH and NADPH at approximately equal rates (*cf.* EC 1.14.13.2 4-hydroxybenzoate 3-monoxygenase). It is less specific for NADPH than EC 1.14.13.2.
References: [1090, 3429]

[EC 1.14.13.33 created 1989, modified 1999]

EC 1.14.13.34

Accepted name: leukotriene-E₄ 20-monoxygenase
Reaction: (7E,9E,11Z,14Z)-(5S,6R)-6-(cystein-S-yl)-5-hydroxyicosa-7,9,11,14-tetraenoate + NADPH + H⁺ + O₂ = 20-hydroxyleukotriene E₄ + NADP⁺ + H₂O
Other name(s): leukotriene-E₄ ω-hydroxylase
Systematic name: (7E,9E,11Z,14Z)-(5S,6R)-6-(cystein-S-yl)-5-hydroxyicosa-7,9,11,14-tetraenoate,NADPH:oxygen oxidoreductase (20-hydroxylating)

Comments: Also acts on *N*-acetyl-leukotriene E₄, but more slowly. Not identical with EC 1.14.13.30 leukotriene-B₄ 20-monooxygenase.

References: [2896]

[EC 1.14.13.34 created 1989]

EC 1.14.13.35

Accepted name: anthranilate 3-monooxygenase (deaminating)

Reaction: anthranilate + NADPH + H⁺ + O₂ = 2,3-dihydroxybenzoate + NADP⁺ + NH₃

Other name(s): anthranilate hydroxylase; anthranilate 2,3-dioxygenase (deaminating); anthranilate hydroxylase (deaminating); anthranilic hydroxylase; anthranilate 2,3-hydroxylase (deaminating)

Systematic name: anthranilate,NADPH:oxygen oxidoreductase (3-hydroxylating, deaminating)

Comments: The enzyme from *Aspergillus niger* is an iron protein; that from the yeast *Trichosporon cutaneum* is a flavoprotein (FAD).

References: [3050, 3703]

[EC 1.14.13.35 created 1972 as EC 1.14.12.2, transferred 1990 to EC 1.14.13.35]

[1.14.13.36 Transferred entry. 5-*O*-(4-coumaroyl)-D-quinate 3'-monooxygenase. Now EC 1.14.14.96, 5-*O*-(4-coumaroyl)-D-quinate 3'-monooxygenase]

[EC 1.14.13.36 created 1990, deleted 2018]

[1.14.13.37 Transferred entry. methyltetrahydroprotoberberine 14-monooxygenase. Now EC 1.14.14.97, methyltetrahydroprotoberberine 14-monooxygenase]

[EC 1.14.13.37 created 1990, deleted 2018]

EC 1.14.13.38

Accepted name: anhydrotetracycline 6-monooxygenase

Reaction: anhydrotetracycline + NADPH + H⁺ + O₂ = 12-dehydrotetracycline + NADP⁺ + H₂O

Other name(s): ATC oxygenase; anhydrotetracycline oxygenase; *oxyS* (gene name); anhydrotetracycline monooxygenase

Systematic name: anhydrotetracycline,NADPH:oxygen oxidoreductase (6-hydroxylating)

Comments: The enzyme, characterized from the bacterium *Streptomyces rimosus*, participates in the biosynthesis of tetracycline antibiotics. It can also catalyse EC 1.14.13.234, 12-dehydrotetracycline 5-monooxygenase.

References: [244, 299, 4016, 4112]

[EC 1.14.13.38 created 1990, modified 2016]

EC 1.14.13.39

Accepted name: nitric-oxide synthase (NADPH)

Reaction: 2 L-arginine + 3 NADPH + 3 H⁺ + 4 O₂ = 2 L-citrulline + 2 nitric oxide + 3 NADP⁺ + 4 H₂O (overall reaction)

(1a) 2 L-arginine + 2 NADPH + 2 H⁺ + 2 O₂ = 2 *N*^ω-hydroxy-L-arginine + 2 NADP⁺ + 2 H₂O

(1b) 2 *N*^ω-hydroxy-L-arginine + NADPH + H⁺ + 2 O₂ = 2 L-citrulline + 2 nitric oxide + NADP⁺ + 2 H₂O

Other name(s): NOS (gene name); nitric oxide synthetase (ambiguous); endothelium-derived relaxation factor-forming enzyme; endothelium-derived relaxing factor synthase; NO synthase (ambiguous); NADPH-diaphorase (ambiguous)

Systematic name: L-arginine,NADPH:oxygen oxidoreductase (nitric-oxide-forming)

Comments: The enzyme consists of linked oxygenase and reductase domains. The eukaryotic enzyme binds FAD, FMN, heme (iron protoporphyrin IX) and tetrahydrobiopterin, and its two domains are linked via a regulatory calmodulin-binding domain. Upon calcium-induced calmodulin binding, the reductase and oxygenase domains form a complex, allowing electrons to flow from NADPH via FAD and FMN to the active center. The reductase domain of the enzyme from the bacterium *Sorangium cellulosum* utilizes a [2Fe-2S] cluster to transfer the electrons from NADPH to the active center. *cf.* EC 1.14.14.47, nitric-oxide synthase (flavodoxin).

References: [391, 3695, 3694, 28, 1032]

[EC 1.14.13.39 created 1992, modified 2012, modified 2017]

EC 1.14.13.40

Accepted name: anthraniloyl-CoA monooxygenase
Reaction: anthraniloyl-CoA + 2 NAD(P)H + 2 H⁺ + O₂ = 2-amino-5-oxocyclohex-1-enecarboxyl-CoA + H₂O + 2 NAD(P)⁺
Other name(s): anthraniloyl coenzyme A reductase; 2-aminobenzoyl-CoA monooxygenase/reductase
Systematic name: anthraniloyl-CoA,NAD(P)H:oxygen oxidoreductase (de-aromatizing)
Comments: A flavoprotein (FAD). The non-aromatic product is unstable and releases CO₂ and NH₃, forming 1,4-cyclohexanedione.
References: [441, 442, 2134]

[EC 1.14.13.40 created 1992]

[1.14.13.41 *Transferred entry. tyrosine N-monooxygenase. Now EC 1.14.14.36, tyrosine N-monooxygenase*]

[EC 1.14.13.41 created 1992, modified 2001, modified 2005, deleted 2016]

[1.14.13.42 *Deleted entry. hydroxyphenylacetone nitrile 2-monooxygenase. The activity is covered by EC 1.14.13.68, 4-hydroxyphenylacetaldehyde oxime monooxygenase, that performs the two consecutive reactions in the conversion of (Z)-4-hydroxyphenylacetaldehyde oxime to (S)-4-hydroxymandelonitrile*]

[EC 1.14.13.42 created 1992, deleted 2011]

EC 1.14.13.43

Accepted name: questin monooxygenase
Reaction: questin + NADPH + H⁺ + O₂ = demethylsulochrin + NADP⁺
Other name(s): questin oxygenase
Systematic name: questin,NADPH:oxygen oxidoreductase (hydroxylating, anthraquinone-ring-opening)
Comments: The enzyme cleaves the anthraquinone ring of questin to form a benzophenone. Involved in the biosynthesis of the seco-anthraquinone (+)-geodin.
References: [1089]

[EC 1.14.13.43 created 1992]

EC 1.14.13.44

Accepted name: 2-hydroxybiphenyl 3-monooxygenase
Reaction: 2-hydroxybiphenyl + NADH + H⁺ + O₂ = 2,3-dihydroxybiphenyl + NAD⁺ + H₂O
Systematic name: 2-hydroxybiphenyl,NADH:oxygen oxidoreductase (3-hydroxylating)
Comments: Also converts 2,2'-dihydroxybiphenyl into 2,2',3-trihydroxy-biphenyl.
References: [2002]

[EC 1.14.13.44 created 1992]

[1.14.13.45 *Transferred entry. CMP-N-acetylneuraminase monooxygenase. Now EC 1.14.18.2, CMP-N-acetylneuraminase monooxygenase*]

[EC 1.14.13.45 created 1992, deleted 2003]

EC 1.14.13.46

Accepted name: (-)-menthol monooxygenase
Reaction: (-)-menthol + NADPH + H⁺ + O₂ = *p*-menthane-3,8-diol + NADP⁺ + H₂O
Other name(s): *l*-menthol monooxygenase
Systematic name: (-)-menthol,NADPH:oxygen oxidoreductase (8-hydroxylating)
References: [2355]

[EC 1.14.13.46 created 1992]

[1.14.13.47 Transferred entry. (*S*)-limonene 3-monooxygenase. Now EC 1.14.14.99, (*S*)-limonene 3-monooxygenase]

[EC 1.14.13.47 created 1992, modified 2003, deleted 2018]

[1.14.13.48 Transferred entry. (*S*)-limonene 6-monooxygenase. Now classified as EC 1.14.14.51, (*S*)-limonene 6-monooxygenase]

[EC 1.14.13.48 created 1992, modified 2003, deleted 2017]

[1.14.13.49 Transferred entry. (*S*)-limonene 7-monooxygenase. Now classified as EC 1.14.14.52, (*S*)-limonene 7-monooxygenase]

[EC 1.14.13.49 created 1992, modified 2003, deleted 2017]

EC 1.14.13.50

Accepted name: pentachlorophenol monooxygenase
Reaction: (1) pentachlorophenol + NADPH + H⁺ + O₂ = 2,3,5,6-tetrachloro-1,4-benzoquinone + NADP⁺ + chloride + H₂O
(2) 2,3,5,6-tetrachlorophenol + NADPH + H⁺ + O₂ = 2,3,5,6-tetrachlorohydroquinone + NADP⁺ + H₂O
Other name(s): *pcpB* (gene name); pentachlorophenol dechlorinase; pentachlorophenol dehalogenase; pentachlorophenol 4-monooxygenase; PCP hydroxylase; pentachlorophenol hydroxylase; PCB 4-monooxygenase; PCB4MO
Systematic name: pentachlorophenol,NADPH:oxygen oxidoreductase (hydroxylating, dechlorinating)
Comments: A flavoprotein (FAD). The enzyme displaces a diverse range of substituents from the 4-position of polyhalogenated phenols but requires that a halogen substituent be present at the 2-position [4293]. If C-4 carries a halogen substituent, reaction 1 is catalysed; if C-4 is unsubstituted, reaction 2 is catalysed.
References: [3357, 4293, 4292, 2132, 2707, 571, 1523, 3251]

[EC 1.14.13.50 created 1992, modified 2005, modified 2017]

EC 1.14.13.51

Accepted name: 6-oxocineole dehydrogenase
Reaction: 6-oxocineole + NADPH + H⁺ + O₂ = 1,6,6-trimethyl-2,7-dioxabicyclo[3.2.2]nonan-3-one + NADP⁺ + H₂O
Other name(s): 6-oxocineole oxygenase
Systematic name: 6-oxocineole,NADPH:oxygen oxidoreductase
Comments: The product undergoes non-enzymic cleavage and subsequent ring closure to form the lactone 4,5-dihydro-5,5-dimethyl-4-(3-oxobutyl)furan-2(3*H*)-one.
References: [4217]

[EC 1.14.13.51 created 1992]

[1.14.13.52 Transferred entry. isoflavone 3'-hydroxylase. Now EC 1.14.14.88, isoflavone 3'-hydroxylase]

[EC 1.14.13.52 created 1992, deleted 2018]

[1.14.13.53 Transferred entry. 4'-methoxyisoflavone 2'-hydroxylase. Now EC 1.14.14.89, 4'-methoxyisoflavone 2'-hydroxylase]

[EC 1.14.13.53 created 1992, modified 2005, deleted 2018]

EC 1.14.13.54

- Accepted name:** ketosteroid monooxygenase
- Reaction:** a ketosteroid + NADPH + H⁺ + O₂ = a steroid ester/lactone + NADP⁺ + H₂O (general reaction)
(1) progesterone + NADPH + H⁺ + O₂ = testosterone acetate + NADP⁺ + H₂O
(2) androstenedione + NADPH + H⁺ + O₂ = testololactone + NADP⁺ + H₂O
(3) 17 α -hydroxyprogesterone + NADPH + H⁺ + O₂ = androstenedione + acetate + NADP⁺ + H₂O
- Other name(s):** steroid-ketone monooxygenase; progesterone, NADPH₂:oxygen oxidoreductase (20-hydroxylating, ester-producing); 17 α -hydroxyprogesterone, NADPH₂:oxygen oxidoreductase (20-hydroxylating, side-chain cleaving); androstenedione, NADPH₂:oxygen oxidoreductase (17-hydroxylating, lactonizing)
- Systematic name:** ketosteroid,NADPH:oxygen oxidoreductase (20-hydroxylating, ester-producing/20-hydroxylating, side-chain cleaving/17-hydroxylating, lactonizing)
- Comments:** A single FAD-containing enzyme catalyses three types of monooxygenase (Baeyer-Villiger oxidation) reaction. The oxidative esterification of a number of derivatives of progesterone to produce the corresponding 17 α -hydroxysteroid 17-acetate ester, such as testosterone acetate, is shown in Reaction (1). The oxidative lactonization of a number of derivatives of androstenedione to produce the 13,17-secoandrosten-17,13 α -lactone, such as testololactone, is shown in Reaction (2). The oxidative cleavage of the 17 β -side-chain of 17 α -hydroxyprogesterone to produce androstenedione and acetate is shown in Reaction (3). Reaction (1) is also catalysed by EC 1.14.99.4 (progesterone monooxygenase), and Reactions (2) and (3) correspond to that catalysed by EC 1.14.99.12 (androst-4-ene-3,17-dione monooxygenase). The possibility that a single enzyme is responsible for the reactions ascribed to EC 1.14.99.4 and EC 1.14.99.12 in other tissues cannot be excluded.
- References:** [1827, 1679, 1680]

[EC 1.14.13.54 created 1999]

[1.14.13.55 Transferred entry. protopine 6-monooxygenase. Now EC 1.14.14.98, protopine 6-monooxygenase]

[EC 1.14.13.55 created 1999, deleted 2018]

[1.14.13.56 Transferred entry. dihydrosanguinarine 10-monooxygenase. Now EC 1.14.14.100, dihydrosanguinarine 10-monooxygenase]

[EC 1.14.13.56 created 1999, deleted 2018]

[1.14.13.57 Transferred entry. dihydrochelirubine 12-monooxygenase. Now EC 1.14.14.101, dihydrochelirubine 12-monooxygenase]

[EC 1.14.13.57 created 1999, deleted 2018]

EC 1.14.13.58

- Accepted name:** benzoyl-CoA 3-monooxygenase
- Reaction:** benzoyl-CoA + NADPH + H⁺ + O₂ = 3-hydroxybenzoyl-CoA + NADP⁺ + H₂O
- Other name(s):** benzoyl-CoA 3-hydroxylase
- Systematic name:** benzoyl-CoA,NADPH:oxygen oxidoreductase (3-hydroxylating)
- Comments:** The enzyme from the denitrifying bacterium *Pseudomonas KB740* catalyses a flavin-requiring reaction (FAD or FMN). Benzoate is not a substrate.
- References:** [2787]

[EC 1.14.13.58 created 1999]

EC 1.14.13.59

- Accepted name:** L-lysine N⁶-monooxygenase (NADPH)
- Reaction:** L-lysine + NADPH + H⁺ + O₂ = N⁶-hydroxy-L-lysine + NADP⁺ + H₂O

Other name(s): lysine N^6 -hydroxylase; L-lysine 6-monooxygenase (NADPH) (ambiguous)
Systematic name: L-lysine,NADPH:oxygen oxidoreductase (6-hydroxylating)
Comments: A flavoprotein (FAD). The enzyme from strain EN 222 of *Escherichia coli* is highly specific for L-lysine; L-ornithine and L-homolysine are, for example, not substrates.
References: [3020, 2345, 3854, 766, 2406, 1229]

[EC 1.14.13.59 created 1999, modified 2001, modified 2012]

[1.14.13.60 Transferred entry. 27-hydroxycholesterol 7 α -monooxygenase. Now included with EC 1.14.13.100, 25-hydroxycholesterol 7 α -hydroxylase]

[EC 1.14.13.60 created 1999, deleted 2013]

EC 1.14.13.61

Accepted name: 2-hydroxyquinoline 8-monooxygenase
Reaction: quinolin-2-ol + NADH + H⁺ + O₂ = quinolin-2,8-diol + NAD⁺ + H₂O
Other name(s): 2-oxo-1,2-dihydroquinoline 8-monooxygenase
Systematic name: quinolin-2(1*H*)-one,NADH:oxygen oxidoreductase (8-oxygenating)
Comments: Requires iron. Quinolin-2-ol exists largely as the quinolin-2(1*H*)-one tautomer.
References: [3232]

[EC 1.14.13.61 created 1999]

EC 1.14.13.62

Accepted name: 4-hydroxyquinoline 3-monooxygenase
Reaction: quinolin-4-ol + NADH + H⁺ + O₂ = quinolin-3,4-diol + NAD⁺ + H₂O
Other name(s): quinolin-4(1*H*)-one 3-monooxygenase
Systematic name: quinolin-4(1*H*)-one,NADH:oxygen oxidoreductase (3-oxygenating)
Comments: Quinolin-4-ol exists largely as the quinolin-4(1*H*)-one tautomer.
References: [324]

[EC 1.14.13.62 created 1999]

EC 1.14.13.63

Accepted name: 3-hydroxyphenylacetate 6-hydroxylase
Reaction: 3-hydroxyphenylacetate + NAD(P)H + H⁺ + O₂ = 2,5-dihydroxyphenylacetate + NAD(P)⁺ + H₂O
Other name(s): 3-hydroxyphenylacetate 6-monooxygenase
Systematic name: 3-hydroxyphenylacetate,NAD(P)H:oxygen oxidoreductase (6-hydroxylating)
Comments: 3-hydroxyphenylacetate 6-hydroxylase from *Flavobacterium* sp. is highly specific for 3-hydroxyphenylacetate and uses NADH and NADPH as electron donors with similar efficiency.
References: [3992]

[EC 1.14.13.63 created 1999]

EC 1.14.13.64

Accepted name: 4-hydroxybenzoate 1-hydroxylase
Reaction: 4-hydroxybenzoate + NAD(P)H + 2 H⁺ + O₂ = hydroquinone + NAD(P)⁺ + H₂O + CO₂
Other name(s): 4-hydroxybenzoate 1-monooxygenase
Systematic name: 4-hydroxybenzoate,NAD(P)H:oxygen oxidoreductase (1-hydroxylating, decarboxylating)
Comments: Requires FAD. The enzyme from *Candida parapsilosis* is specific for 4-hydroxybenzoate derivatives and prefers NADH to NADPH as electron donor.
References: [3993]

[EC 1.14.13.64 created 1999]

[1.14.13.65 Deleted entry. 2-hydroxyquinoline 8-monooxygenase]

[EC 1.14.13.65 created 1999, deleted 2006]

EC 1.14.13.66

Accepted name: 2-hydroxycyclohexanone 2-monooxygenase
Reaction: 2-hydroxycyclohexan-1-one + NADPH + H⁺ + O₂ = 6-hydroxyhexan-6-olide + NADP⁺ + H₂O
Systematic name: 2-hydroxycyclohexan-1-one,NADPH:oxygen 2-oxidoreductase (1,2-lactonizing)
Comments: The product decomposes spontaneously to 6-oxohexanoic acid (adipic semialdehyde).
References: [752]

[EC 1.14.13.66 created 1978 as EC 1.14.12.6, transferred 1999 to EC 1.14.13.66]

[1.14.13.67 Transferred entry. quinine 3-monooxygenase. Now EC 1.14.14.55, quinine 3-monooxygenase]

[EC 1.14.13.67 created 2000, deleted 2017]

[1.14.13.68 Transferred entry. 4-hydroxyphenylacetaldehyde oxime monooxygenase. Now EC 1.14.14.37, 4-hydroxyphenylacetaldehyde oxime monooxygenase]

[EC 1.14.13.68 created 2000, modified 2005, deleted 2016]

EC 1.14.13.69

Accepted name: alkene monooxygenase
Reaction: propene + NADH + H⁺ + O₂ = 1,2-epoxypropane + NAD⁺ + H₂O
Other name(s): alkene epoxygenase; etnABCD (gene names); amoABCDE (gene names)
Systematic name: alkene,NADH:oxygen oxidoreductase
Comments: This bacterial binuclear non-heme iron enzyme is a multicomponent enzyme complex comprising an oxygenase, a reductase, and a Rieske-type ferredoxin. The enzyme from the bacterium *Xanthobacter* sp. strain Py2 contains an additional small protein of unknown function that is essential for activity. In general, the enzyme oxygenates C₂ to C₆ aliphatic alkenes, although enzymes from different organisms show different substrate range. With propene as substrate, the stereospecificity of the epoxypropane formed is 95% (R) and 5% (S).
References: [3553, 1143, 4473, 535, 534]

[EC 1.14.13.69 created 2001]

[1.14.13.70 Transferred entry. sterol 14 α -demethylase. Now EC 1.14.14.154, sterol 14 α -demethylase]

[EC 1.14.13.70 created 2001, modified 2013, deleted 2018]

[1.14.13.71 Transferred entry. N-methylcochlorine 3'-monooxygenase. Now EC 1.14.14.102, N-methylcochlorine 3'-monooxygenase]

[EC 1.14.13.71 created 2001, deleted 2018]

[1.14.13.72 Transferred entry. methylsterol monooxygenase. Now classified as EC 1.14.18.9, methylsterol monooxygenase]

[EC 1.14.13.72 created 1972 as EC 1.14.99.16, transferred 2002 to EC 1.14.13.72, deleted 2017]

[1.14.13.73 Transferred entry. tabersonine 16-hydroxylase. Now EC 1.14.14.103, tabersonine 16-hydroxylase]

[EC 1.14.13.73 created 2002, deleted 2018]

[1.14.13.74 Transferred entry. 7-deoxyloganin 7-hydroxylase. Now EC 1.14.14.85, 7-deoxyloganin 7-hydroxylase]

[EC 1.14.13.74 created 2002, deleted 2018]

[1.14.13.75 Transferred entry. vinorine hydroxylase. Now EC 1.14.14.104, vinorine hydroxylase]

[EC 1.14.13.75 created 2002, deleted 2018]

[1.14.13.76 Transferred entry. *taxane 10 β -hydroxylase*. Now EC 1.14.14.105, *taxane 10 β -hydroxylase*]

[EC 1.14.13.76 created 2002, deleted 2018]

[1.14.13.77 Transferred entry. *taxane 13 α -hydroxylase*. Now EC 1.14.14.106, *taxane 13 α -hydroxylase*]

[EC 1.14.13.77 created 2002, deleted 2018]

[1.14.13.78 Transferred entry. *ent-kaurene oxidase*. Now EC 1.14.14.86, *ent-kaurene monooxygenase*]

[EC 1.14.13.78 created 2002, deleted 2018]

[1.14.13.79 Transferred entry. *ent-kaurenoic acid oxidase*. Now EC 1.14.14.107, *ent-kaurenoic acid oxidase*]

[EC 1.14.13.79 created 2002, deleted 2018]

[1.14.13.80 Transferred entry. *(R)-limonene 6-monooxygenase*. Now classified as EC 1.14.14.53, *(R)-limonene 6-monooxygenase*]

[EC 1.14.13.80 created 2003, deleted 2017]

EC 1.14.13.81

Accepted name: magnesium-protoporphyrin IX monomethyl ester (oxidative) cyclase
Reaction: magnesium-protoporphyrin IX 13-monomethyl ester + 3 NADPH + 3 H⁺ + 3 O₂ = 3,8-divinyl protochlorophyllide *a* + 3 NADP⁺ + 5 H₂O (overall reaction)
(1a) magnesium-protoporphyrin IX 13-monomethyl ester + NADPH + H⁺ + O₂ = 13¹-hydroxy-magnesium-protoporphyrin IX 13-monomethyl ester + NADP⁺ + H₂O
(1b) 13¹-hydroxy-magnesium-protoporphyrin IX 13-monomethyl ester + NADPH + H⁺ + O₂ = 13¹-oxo-magnesium-protoporphyrin IX 13-monomethyl ester + NADP⁺ + 2 H₂O
(1c) 13¹-oxo-magnesium-protoporphyrin IX 13-monomethyl ester + NADPH + H⁺ + O₂ = 3,8-divinyl protochlorophyllide *a* + NADP⁺ + 2 H₂O
Other name(s): Mg-protoporphyrin IX monomethyl ester (oxidative) cyclase
Systematic name: magnesium-protoporphyrin-IX 13-monomethyl ester,NADPH:oxygen oxidoreductase (hydroxylating)
Comments: Requires Fe(II) for activity. The enzyme participates in the biosynthesis of chlorophyllide *a* in aerobic organisms. The same transformation is achieved in anaerobic organisms by EC 1.21.98.3, anaerobic magnesium-protoporphyrin IX monomethyl ester cyclase. Some facultative phototrophic bacteria, such as *Rubrivivax gelatinosus*, possess both enzymes.
References: [4085, 340, 3015, 3916]

[EC 1.14.13.81 created 2003, modified 2017]

EC 1.14.13.82

Accepted name: vanillate monooxygenase
Reaction: vanillate + O₂ + NADH + H⁺ = 3,4-dihydroxybenzoate + NAD⁺ + H₂O + formaldehyde
Other name(s): 4-hydroxy-3-methoxybenzoate demethylase; vanillate demethylase
Systematic name: vanillate:oxygen oxidoreductase (demethylating)
Comments: Forms part of the vanillin degradation pathway in *Arthrobacter sp.*
References: [429, 3062]

[EC 1.14.13.82 created 2000 as EC 1.2.3.12, transferred 2003 to EC 1.14.13.82]

EC 1.14.13.83

Accepted name: precorrin-3B synthase
Reaction: precorrin-3A + NADH + H⁺ + O₂ = precorrin-3B + NAD⁺ + H₂O
Other name(s): precorrin-3X synthase; CobG
Systematic name: precorrin-3A,NADH:oxygen oxidoreductase (20-hydroxylating)

Comments: An iron-sulfur protein. An oxygen atom from dioxygen is incorporated into the macrocycle at C-20. In the aerobic cobalamin biosynthesis pathway, four enzymes are involved in the conversion of precorrin-3A to precorrin-6A. The first of the four steps is carried out by EC 1.14.13.83, precorrin-3B synthase (CobG), yielding precorrin-3B as the product. This is followed by three methylation reactions, which introduce a methyl group at C-17 (CobJ; EC 2.1.1.131), C-11 (CobM; EC 2.1.1.133) and C-1 (CobF; EC 2.1.1.152) of the macrocycle, giving rise to precorrin-4, precorrin-5 and precorrin-6A, respectively.

References: [773, 3415, 4137]

[EC 1.14.13.83 created 2004]

EC 1.14.13.84

Accepted name: 4-hydroxyacetophenone monooxygenase
Reaction: (4-hydroxyphenyl)ethan-1-one + NADPH + H⁺ + O₂ = 4-hydroxyphenyl acetate + NADP⁺ + H₂O
Other name(s): HAPMO
Systematic name: (4-hydroxyphenyl)ethan-1-one,NADPH:oxygen oxidoreductase (ester-forming)
Comments: Contains FAD. The enzyme from *Pseudomonas fluorescens* ACB catalyses the conversion of a wide range of acetophenone derivatives. Highest activity occurs with compounds bearing an electron-donating substituent at the para position of the aromatic ring [1804]. In the absence of substrate, the enzyme can act as an NAD(P)H oxidase (EC 1.6.3.1).
References: [1804, 1805]

[EC 1.14.13.84 created 2004]

[1.14.13.85 *Transferred entry. glyceollin synthase. Now EC 1.14.14.135, glyceollin synthase*]

[EC 1.14.13.85 created 2004, deleted 2018]

[1.14.13.86 *Deleted entry. 2-hydroxyisoflavanone synthase. This enzyme was classified on the basis of an incorrect reaction. The activity is covered by EC 1.14.14.87, 2-hydroxyisoflavanone synthase*]

[EC 1.14.13.86 created 2004, deleted 2013]

[1.14.13.87 *Transferred entry. licodione synthase. Now EC 1.14.14.140, licodione synthase*]

[EC 1.14.13.87 created 2004, deleted 2018]

[1.14.13.88 *Transferred entry. flavanoid 3,5-hydroxylase. Now EC 1.14.14.81, flavanoid 3,5-hydroxylase*]

[EC 1.14.13.88 created 2004, deleted 2018]

[1.14.13.89 *Transferred entry. isoflavone 2-hydroxylase. Now EC 1.14.14.90, isoflavone 2-hydroxylase*]

[EC 1.14.13.89 created 2005, deleted 2018]

[1.14.13.90 *Transferred entry. zeaxanthin epoxidase. Now EC 1.14.15.21, zeaxanthin epoxidase*]

[EC 1.14.13.90 created 2005, deleted 2016]

[1.14.13.91 *Transferred entry. deoxysarpagine hydroxylase. Now EC 1.14.14.136, deoxysarpagine hydroxylase*]

[EC 1.14.13.91 created 2005, deleted 2018]

EC 1.14.13.92

Accepted name: phenylacetone monooxygenase
Reaction: phenylacetone + NADPH + H⁺ + O₂ = benzyl acetate + NADP⁺ + H₂O
Other name(s): PAMO
Systematic name: phenylacetone,NADPH:oxygen oxidoreductase
Comments: A flavoprotein (FAD). NADH cannot replace NADPH as coenzyme. In addition to phenylacetone, which is the best substrate found to date, this Baeyer-Villiger monooxygenase can oxidize other aromatic ketones [1-(4-hydroxyphenyl)propan-2-one, 1-(4-hydroxyphenyl)propan-2-one and 3-phenylbutan-2-one], some aliphatic ketones (e.g. dodecan-2-one) and sulfides (e.g. 1-methyl-4-(methylsulfanyl)benzene).
References: [2380, 1048]

[EC 1.14.13.92 created 2005]

[1.14.13.93 *Transferred entry. (+)-abscisic acid 8-hydroxylase. Now EC 1.14.14.137, (+)-abscisic acid 8-hydroxylase*]

[EC 1.14.13.93 created 2005, deleted 2018]

[1.14.13.94 *Transferred entry. lithocholate 6 β -hydroxylase. Now EC 1.14.14.138, lithocholate 6 β -hydroxylase*]

[EC 1.14.13.94 created 2005, deleted 2018]

[1.14.13.95 *Transferred entry. 7 α -hydroxycholest-4-en-3-one 12 α -hydroxylase. Now EC 1.14.18.8, 7 α -hydroxycholest-4-en-3-one 12 α -hydroxylase*]

[EC 1.14.13.95 created 2005, deleted 2015]

[1.14.13.96 *Transferred entry. 5 β -cholestane-3 α ,7 α -diol 12 α -hydroxylase. Now EC 1.14.14.139, 5 β -cholestane-3 α ,7 α -diol 12 α -hydroxylase*]

[EC 1.14.13.96 created 2005, deleted 2018]

[1.14.13.97 *Transferred entry. taurochenodeoxycholate 6 α -hydroxylase. Now EC 1.14.14.57, taurochenodeoxycholate 6 α -hydroxylase*]

[EC 1.14.13.97 created 2005, deleted 2018]

[1.14.13.98 *Transferred entry. cholesterol 24-hydroxylase. Now EC 1.14.14.25, cholesterol 24-hydroxylase*]

[EC 1.14.13.98 created 2005, deleted 2016]

[1.14.13.99 *Transferred entry. 24-hydroxycholesterol 7 α -hydroxylase. Now EC 1.14.14.26, 24-hydroxycholesterol 7 α -hydroxylase*]

[EC 1.14.13.99 created 2005, deleted 2016]

[1.14.13.100 *Transferred entry. 25/26-hydroxycholesterol 7 α -hydroxylase. Now classified as EC 1.14.14.29, 25/26-hydroxycholesterol 7 α -hydroxylase*]

[EC 1.14.13.100 created 2005, modified 2013 (EC 1.14.13.60 created 1999, incorporated 2013), deleted 2016]

EC 1.14.13.101

- Accepted name:** senecionine *N*-oxygenase
Reaction: senecionine + NADPH + H⁺ + O₂ = senecionine *N*-oxide + NADP⁺ + H₂O
Other name(s): senecionine monooxygenase (*N*-oxide-forming); SNO
Systematic name: senecionine,NADPH:oxygen oxidoreductase (*N*-oxide-forming)
Comments: A flavoprotein. NADH cannot replace NADPH. While pyrrolizidine alkaloids of the senecionine and monocrotaline types are generally good substrates (e.g. senecionine, retrorsine and monocrotaline), the enzyme does not use ester alkaloids lacking an hydroxy group at C-7 (e.g. supinine and phalaenopsine), 1,2-dihydro-alkaloids (e.g. sarracine) or unesterified necine bases (e.g. senkirikine) as substrates [2262]. *Senecionine N*-oxide is used by insects as a chemical defense: senecionine *N*-oxide is non-toxic, but it is bioactivated to a toxic form by the action of cytochrome *P*-450 oxidase when absorbed by insectivores.
References: [2262, 2743]

[EC 1.14.13.101 created 2006]

[1.14.13.102 *Transferred entry. psoralen synthase. Now EC 1.14.14.141, psoralen synthase*]

[EC 1.14.13.102 created 2007, deleted 2018]

[1.14.13.103 *Transferred entry. 8-dimethylallylnaringenin 2-hydroxylase. Now EC 1.14.14.142, 8-dimethylallylnaringenin 2-hydroxylase*]

[EC 1.14.13.103 created 2007, deleted 2018]

[1.14.13.104 Transferred entry. (+)-menthofuran synthase. Now EC 1.14.14.143, (+)-menthofuran synthase]

[EC 1.14.13.104 created 2008, deleted 2018]

EC 1.14.13.105

- Accepted name:** monocyclic monoterpene ketone monooxygenase
- Reaction:** (1) (–)-menthone + NADPH + H⁺ + O₂ = (4*R*,7*S*)-7-isopropyl-4-methyloxepan-2-one + NADP⁺ + H₂O
(2) dihydrocarvone + NADPH + H⁺ + O₂ = 4-isopropenyl-7-methyloxepan-2-one + NADP⁺ + H₂O
(3) (iso)-dihydrocarvone + NADPH + H⁺ + O₂ = 6-isopropenyl-3-methyloxepan-2-one + NADP⁺ + H₂O
(4a) 1-hydroxymenth-8-en-2-one + NADPH + H⁺ + O₂ = 7-hydroxy-4-isopropenyl-7-methyloxepan-2-one + NADP⁺ + H₂O
(4b) 7-hydroxy-4-isopropenyl-7-methyloxepan-2-one = 3-isopropenyl-6-oxoheptanoate (spontaneous)
- Other name(s):** 1-hydroxy-2-oxolimonene 1,2-monooxygenase; dihydrocarvone 1,2-monooxygenase; MMKMO
- Systematic name:** (–)-menthone,NADPH:oxygen oxidoreductase
- Comments:** A flavoprotein (FAD). This Baeyer-Villiger monooxygenase enzyme from the Gram-positive bacterium *Rhodococcus erythropolis* DCL14 has wide substrate specificity, catalysing the lactonization of a large number of monocyclic monoterpene ketones and substituted cyclohexanones [4176]. Both (1*R*,4*S*)- and (1*S*,4*R*)-1-hydroxymenth-8-en-2-one are metabolized, with the lactone product spontaneously rearranging to form 3-isopropenyl-6-oxoheptanoate [4000].
- References:** [4000, 4176, 3999]

[EC 1.14.13.105 created 2008]

EC 1.14.13.106

- Accepted name:** *epi*-isozizaene 5-monooxygenase
- Reaction:** (+)-*epi*-isozizaene + 2 NADPH + 2 H⁺ + 2 O₂ = albaflavenone + 2 NADP⁺ + 3 H₂O (overall reaction)
(1a) (+)-*epi*-isozizaene + NADPH + H⁺ + O₂ = (5*S*)-albaflavenol + NADP⁺ + H₂O
(1b) (5*S*)-albaflavenol + NADPH + H⁺ + O₂ = albaflavenone + NADP⁺ + 2 H₂O
(2a) (+)-*epi*-isozizaene + NADPH + H⁺ + O₂ = (5*R*)-albaflavenol + NADP⁺ + H₂O
(2b) (5*R*)-albaflavenol + NADPH + H⁺ + O₂ = albaflavenone + NADP⁺ + 2 H₂O
- Other name(s):** CYP170A1
- Systematic name:** (+)-*epi*-isozizaene,NADPH:oxygen oxidoreductase (5-hydroxylating)
- Comments:** This cytochrome-*P*-450 enzyme, from the soil-dwelling bacterium *Streptomyces coelicolor* A3(2), catalyses two sequential allylic oxidation reactions. The substrate *epi*-isozizaene, which is formed by the action of EC 4.2.3.37, *epi*-isozizaene synthase, is first oxidized to yield the epimeric intermediates (5*R*)-albaflavenol and (5*S*)-albaflavenol, which can be further oxidized to yield the sesquiterpenoid antibiotic albaflavenone.
- References:** [4457]

[EC 1.14.13.106 created 2008]

EC 1.14.13.107

- Accepted name:** limonene 1,2-monooxygenase
- Reaction:** (1) (*S*)-limonene + NAD(P)H + H⁺ + O₂ = 1,2-epoxymenth-8-ene + NAD(P)⁺ + H₂O
(2) (*R*)-limonene + NAD(P)H + H⁺ + O₂ = 1,2-epoxymenth-8-ene + NAD(P)⁺ + H₂O
- Systematic name:** limonene,NAD(P)H:oxygen oxidoreductase
- Comments:** A flavoprotein (FAD). Limonene is the most widespread terpene and is formed by more than 300 plants. *Rhodococcus erythropolis* DCL14, a Gram-positive bacterium, is able to grow on both (*S*)-limonene and (*R*)-limonene as the sole source of carbon and energy. NADPH can act instead of NADH, although more slowly. It has not been established if the product formed is optically pure or a mixture of two enantiomers.

References: [4000]

[EC 1.14.13.107 created 2009]

[1.14.13.108 Transferred entry. *abieta-7,13-diene hydroxylase*. Now EC 1.14.14.144, *abieta-7,13-diene hydroxylase*]

[EC 1.14.13.108 created 2009, modified 2012, deleted 2018]

[1.14.13.109 Transferred entry. *abieta-7,13-dien-18-ol hydroxylase*. Now EC 1.14.14.145, *abieta-7,13-dien-18-ol hydroxylase*]

[EC 1.14.13.109 created 2009, modified 2012, deleted 2018]

[1.14.13.110 Transferred entry. *geranylgeraniol 18-hydroxylase*. Now EC 1.14.14.146, *geranylgeraniol 18-hydroxylase*]

[EC 1.14.13.110 created 2009, deleted 2018]

EC 1.14.13.111

Accepted name: methanesulfonate monooxygenase (NADH)

Reaction: methanesulfonate + NADH + H⁺ + O₂ = formaldehyde + NAD⁺ + sulfite + H₂O

Other name(s): mesylate monooxygenase; mesylate, reduced-FMN: oxygen oxidoreductase; MsmABC; methanesulfonic acid monooxygenase; MSA monooxygenase; MSAMO

Systematic name: methanesulfonate, NADH: oxygen oxidoreductase

Comments: A flavoprotein. Methanesulfonate is the simplest of the sulfonates and is a substrate for the growth of certain methylotrophic microorganisms. Compared with EC 1.14.14.5, alkanesulfonate monooxygenase, this enzyme has a restricted substrate range that includes only the short-chain aliphatic sulfonates (methanesulfonate to butanesulfonate) and excludes all larger molecules, such as arylsulfonates [768]. The enzyme from the bacterium *Methylosulfonomonas methylovora* is a multicomponent system comprising a hydroxylase, a reductase (MsmD) and a ferredoxin (MsmC). The hydroxylase has both large (MsmA) and small (MsmB) subunits, with each large subunit containing a Rieske-type [2Fe-2S] cluster. cf. EC 1.14.14.34, methanesulfonate monooxygenase (FMNH₂).

References: [768, 1496]

[EC 1.14.13.111 created 2009 as EC 1.14.14.6, transferred 2010 to EC 1.14.13.111, modified 2016]

[1.14.13.112 Transferred entry. *3-epi-6-deoxocathasterone 23-monooxygenase*. Now EC 1.14.14.147, *3-epi-6-deoxocathasterone 23-monooxygenase*]

[EC 1.14.13.112 created 2010, deleted 2018]

EC 1.14.13.113

Accepted name: FAD-dependent urate hydroxylase

Reaction: urate + NADH + H⁺ + O₂ = 5-hydroxyisourate + NAD⁺ + H₂O

Other name(s): HpxO enzyme; FAD-dependent urate oxidase; urate hydroxylase

Systematic name: urate, NADH: oxygen oxidoreductase (5-hydroxyisourate forming)

Comments: A flavoprotein. The reaction is part of the purine catabolic pathway in the bacterium *Klebsiella pneumoniae*. The enzyme is different from EC 1.7.3.3, factor-independent urate hydroxylase, found in most plants, which produces hydrogen peroxide. The product of the enzyme is a substrate for EC 3.5.2.17, hydroxyisourate hydrolase.

References: [2871]

[EC 1.14.13.113 created 2010]

EC 1.14.13.114

Accepted name: 6-hydroxynicotinate 3-monooxygenase

Reaction: 6-hydroxynicotinate + NADH + H⁺ + O₂ = 2,5-dihydroxypyridine + NAD⁺ + H₂O + CO₂

Other name(s): NicC; 6HNA monooxygenase; HNA-3-monooxygenase

Systematic name: 6-hydroxynicotinate,NADH:oxygen oxidoreductase (3-hydroxylating, decarboxylating)
Comments: A flavoprotein (FAD) [2712]. The reaction is involved in the aerobic catabolism of nicotinic acid.
References: [2712, 1743]

[EC 1.14.13.114 created 2010]

[1.14.13.115 *Transferred entry. angelicin synthase. Now EC 1.14.14.148, angelicin synthase*]

[EC 1.14.13.115 created 2010, deleted 2018]

EC 1.14.13.116

Accepted name: geranylhydroquinone 3''-hydroxylase
Reaction: geranylhydroquinone + NADPH + H⁺ + O₂ = 3''-hydroxygeranylhydroquinone + NADP⁺ + H₂O
Other name(s): GHQ 3''-hydroxylase
Systematic name: geranylhydroquinone,NADPH:oxygen oxidoreductase (3''-hydroxylating)
Comments: Contains cytochrome *P*-450.
References: [4311]

[EC 1.14.13.116 created 2010]

[1.14.13.117 *Transferred entry. isoleucine N-monooxygenase, Now EC 1.14.14.39, isoleucine N-monooxygenase*]

[EC 1.14.13.117 created 2010, deleted 2017]

[1.14.13.118 *Transferred entry. valine N-monooxygenase. Now EC 1.14.14.38, valine N-monooxygenase*]

[EC 1.14.13.118 created 2010, deleted 2017]

[1.14.13.119 *Transferred entry. 5-epiaristolochene 1,3-dihydroxylase. Now EC 1.14.14.149, 5-epiaristolochene 1,3-dihydroxylase*]

[EC 1.14.13.119 created 2011, deleted 2018]

[1.14.13.120 *Transferred entry. costunolide synthase. Now EC 1.14.14.150, costunolide synthase*]

[EC 1.14.13.120 created 2011, deleted 2018]

[1.14.13.121 *Transferred entry. premnaspirodien oxygenase. Now EC 1.14.14.151, premnaspirodien oxygenase*]

[EC 1.14.13.121 created 2011, deleted 2018]

EC 1.14.13.122

Accepted name: chlorophyllide-*a* oxygenase
Reaction: chlorophyllide *a* + 2 O₂ + 2 NADPH + 2 H⁺ = chlorophyllide *b* + 3 H₂O + 2 NADP⁺ (overall reaction)
(1a) chlorophyllide *a* + O₂ + NADPH + H⁺ = 7¹-hydroxychlorophyllide *a* + H₂O + NADP⁺
(1b) 7¹-hydroxychlorophyllide *a* + O₂ + NADPH + H⁺ = chlorophyllide *b* + 2 H₂O + NADP⁺
Other name(s): chlorophyllide *a* oxygenase; chlorophyll-*b* synthase; CAO
Systematic name: chlorophyllide-*a*:oxygen 7¹-oxidoreductase
Comments: Chlorophyll *b* is required for the assembly of stable light-harvesting complexes (LHCs) in the chloroplast of green algae, cyanobacteria and plants [2903, 926]. Contains a mononuclear iron centre [926]. The enzyme catalyses two successive hydroxylations at the 7-methyl group of chlorophyllide *a*. The second step yields the aldehyde hydrate, which loses H₂O spontaneously to form chlorophyllide *b* [2903]. Chlorophyll *a* and protochlorophyllide *a* are not substrates [2903].
References: [965, 2903, 926, 3040]

[EC 1.14.13.122 created 2006 as EC 1.13.12.14, transferred 2011 to EC 1.14.13.122, modified 2011]

[1.14.13.123 *Transferred entry. germacrene A hydroxylase. Now EC 1.14.14.95, germacrene A hydroxylase*]

[EC 1.14.13.123 created 2011, deleted 2018]

[1.14.13.124 Transferred entry. phenylalanine *N*-monooxygenase, now classified as EC 1.14.14.40, phenylalanine *N*-monooxygenase]

[EC 1.14.13.124 created 2011, deleted 2017]

[1.14.13.125 Transferred entry. tryptophan *N*-monooxygenase. Now EC 1.14.14.156, tryptophan *N*-monooxygenase]

[EC 1.14.13.125 created 2011, deleted 2018]

[1.14.13.126 Transferred entry. vitamin D₃ 24-hydroxylase. Now EC 1.14.15.16, vitamin D₃ 24-hydroxylase]

[EC 1.14.13.126 created 2011, deleted 2016]

EC 1.14.13.127

Accepted name: 3-(3-hydroxyphenyl)propanoate hydroxylase
Reaction: (1) 3-(3-hydroxyphenyl)propanoate + NADH + H⁺ + O₂ = 3-(2,3-dihydroxyphenyl)propanoate + H₂O + NAD⁺
(2) (2*E*)-3-(3-hydroxyphenyl)prop-2-enoate + NADH + H⁺ + O₂ = (2*E*)-3-(2,3-dihydroxyphenyl)prop-2-enoate + H₂O + NAD⁺
Other name(s): *mhpA* (gene name)
Systematic name: 3-(3-hydroxyphenyl)propanoate,NADH:oxygen oxidoreductase (2-hydroxylating)
Comments: A flavoprotein (FAD). This enzyme participates in a meta-cleavage pathway employed by the bacterium *Escherichia coli* for the degradation of various phenylpropanoid compounds.
References: [447, 448, 1000, 813]

[EC 1.14.13.127 created 2011]

EC 1.14.13.128

Accepted name: 7-methylxanthine demethylase
Reaction: 7-methylxanthine + O₂ + NAD(P)H + H⁺ = xanthine + NAD(P)⁺ + H₂O + formaldehyde
Other name(s): *ndmC* (gene name)
Systematic name: 7-methylxanthine:oxygen oxidoreductase (demethylating)
Comments: A non-heme iron oxygenase. The enzyme from the bacterium *Pseudomonas putida* prefers NADH over NADPH. The enzyme is specific for 7-methylxanthine [3727]. Forms part of the caffeine degradation pathway.
References: [3728, 3727]

[EC 1.14.13.128 created 2011]

[1.14.13.129 Transferred entry. β-carotene 3-hydroxylase. Now EC 1.14.15.24, β-carotene 3-hydroxylase.]

[EC 1.14.13.129 created 2011, deleted 2017]

EC 1.14.13.130

Accepted name: pyrrole-2-carboxylate monooxygenase
Reaction: pyrrole-2-carboxylate + NADH + H⁺ + O₂ = 5-hydroxypyrrole-2-carboxylate + NAD⁺ + H₂O
Other name(s): pyrrole-2-carboxylate oxygenase
Systematic name: pyrrole-2-carboxylate,NADH:oxygen oxidoreductase (5-hydroxylating)
Comments: A flavoprotein (FAD). The enzyme initiates the degradation of pyrrole-2-carboxylate.
References: [1573, 236]

[EC 1.14.13.130 created 2011]

EC 1.14.13.131

Accepted name: dissimilatory dimethyl sulfide monooxygenase

Reaction: dimethyl sulfide + O₂ + NADH + H⁺ = methanethiol + formaldehyde + NAD⁺ + H₂O
Other name(s): *dmoAB* (gene names); dimethyl sulfide C-monooxygenase; dimethylsulfide monooxygenase (ambiguous); dimethyl sulfide monooxygenase (ambiguous)
Systematic name: dimethyl sulfide,NADH:oxygen oxidoreductase
Comments: The enzyme participates exclusively in sulfur dissimilation. It has lower activity with diethyl sulfide and other short-chain alkyl methyl sulfides. Its activity is stimulated by combined addition of FMN, and, after depletion of cations, of Mg²⁺ and Fe²⁺. The enzymes from bacteria of the *Hyphomicrobium* genus are a two component system that includes an FMN-dependent reductase subunit and a monooxygenase subunit.
References: [348, 328]

[EC 1.14.13.131 created 2011]

[1.14.13.132 Transferred entry. *squalene monooxygenase*. Now EC 1.14.14.17, *squalene monooxygenase*]

[EC 1.14.13.132 created 1961 as EC 1.99.1.13, transferred 1965 to EC 1.14.1.3, part transferred 1972 to EC 1.14.99.7, transferred 2011 to EC 1.14.13.132, deleted 2015]

[1.14.13.133 Transferred entry. *pentalenene oxygenase*. Now EC 1.14.15.32, *pentalenene oxygenase*]

[EC 1.14.13.133 created 2011, deleted 2018]

[1.14.13.134 Transferred entry. *β-amyrin 11-oxidase*. Now EC 1.14.14.152, *β-amyrin 11-oxidase*]

[EC 1.14.13.134 created 2011, deleted 2018]

EC 1.14.13.135

Accepted name: 1-hydroxy-2-naphthoate hydroxylase
Reaction: 1-hydroxy-2-naphthoate + NAD(P)H + H⁺ + O₂ = 1,2-dihydroxynaphthalene + NAD(P)⁺ + H₂O + CO₂
Other name(s): 1-hydroxy-2-naphthoic acid hydroxylase
Systematic name: 1-hydroxy-2-naphthoate,NAD(P)H:oxygen oxidoreductase (2-hydroxylating, decarboxylating)
Comments: The enzyme is involved in the catabolic pathway for the degradation of chrysene in some bacteria [2749].
References: [804, 2749]

[EC 1.14.13.135 created 2011]

[1.14.13.136 Transferred entry. *2-hydroxyisoflavanone synthase*. Now EC 1.14.14.87, *2-hydroxyisoflavanone synthase*]

[EC 1.14.13.136 created 2011, modified 2013, deleted 2018]

[1.14.13.137 Transferred entry. *indole-2-monooxygenase*. Now EC 1.14.14.153, *indole-2-monooxygenase*]

[EC 1.14.13.137 created 2012, deleted 2018]

[1.14.13.138 Transferred entry. *indolin-2-one monooxygenase*. Now EC 1.14.14.157, *indolin-2-one monooxygenase*]

[EC 1.14.13.138 created 2012, deleted 2018]

[1.14.13.139 Transferred entry. *3-hydroxyindolin-2-one monooxygenase*. Now EC 1.14.14.109, *3-hydroxyindolin-2-one monooxygenase*]

[EC 1.14.13.139 created 2012, deleted 2018]

[1.14.13.140 Transferred entry. *2-hydroxy-1,4-benzoxazin-3-one monooxygenase*. Now EC 1.14.14.110, *2-hydroxy-1,4-benzoxazin-3-one monooxygenase*.]

[EC 1.14.13.140 created 2012, deleted 2018]

[1.14.13.141 Transferred entry. *cholest-4-en-3-one 26-monooxygenase [(25S)-3-oxocholest-4-en-26-oate forming]*. Now EC 1.14.15.29, *cholest-4-en-3-one 26-monooxygenase [(25S)-3-oxocholest-4-en-26-oate forming]*..]

[EC 1.14.13.141 created 2012, modified 2016, deleted 2018]

[1.14.13.142 Transferred entry. 3-ketosteroid 9 α -monooxygenase. Now EC 1.14.15.30, 3-ketosteroid 9 α -monooxygenase]

[EC 1.14.13.142 created 2012, deleted 2018]

[1.14.13.143 Transferred entry. ent-isokaurene C2-hydroxylase. Now EC 1.14.14.76 ent-isokaurene C2/C3-hydroxylase]

[EC 1.14.13.143 created 2012, deleted 2018]

[1.14.13.144 Transferred entry. 9 β -pimara-7,15-diene oxidase. Now EC 1.14.14.111, 9 β -pimara-7,15-diene oxidase.]

[EC 1.14.13.144 created 2012, deleted 2018]

[1.14.13.145 Transferred entry. ent-cassa-12,15-diene 11-hydroxylase. Now EC 1.14.14.112, ent-cassa-12,15-diene 11-hydroxylase.]

[EC 1.14.13.145 created 2012, deleted 2018]

EC 1.14.13.146

Accepted name: taxoid 14 β -hydroxylase
Reaction: 10 β -hydroxytaxa-4(20),11-dien-5 α -yl acetate + O₂ + NADPH + H⁺ = 10 β ,14 β -dihydroxytaxa-4(20),11-dien-5 α -yl acetate + NADP⁺ + H₂O
Systematic name: 10 β -hydroxytaxa-4(20),11-dien-5 α -yl-acetate,NADPH:oxygen 14-oxidoreductase
Comments: Requires cytochrome P450. From the yew *Taxus cuspidata*. Also acts on taxa-4(20),11-dien-5 α -yl acetate.
References: [1731]

[EC 1.14.13.146 created 2012]

EC 1.14.13.147

Accepted name: taxoid 7 β -hydroxylase
Reaction: taxusin + O₂ + NADPH + H⁺ = 7 β -hydroxytaxusin + NADP⁺ + H₂O
Systematic name: taxusin,NADPH:oxygen 7-oxidoreductase
Comments: Requires cytochrome P-450. From the yew tree *Taxus cuspidata*. Does not act on earlier intermediates in taxol biosynthesis.
References: [556]

[EC 1.14.13.147 created 2012]

EC 1.14.13.148

Accepted name: trimethylamine monooxygenase
Reaction: *N,N,N*-trimethylamine + NADPH + H⁺ + O₂ = *N,N,N*-trimethylamine *N*-oxide + NADP⁺ + H₂O
Other name(s): flavin-containing monooxygenase 3; FMO3; tmm (gene name)
Systematic name: *N,N,N*-trimethylamine,NADPH:oxygen oxidoreductase (*N*-oxide-forming)
Comments: A flavoprotein. The bacterial enzyme enables bacteria to use trimethylamine as the sole source of carbon and energy [2139, 577]. The mammalian enzyme is involved in detoxification of trimethylamine. Mutations in the human enzyme cause the inheritable disease known as trimethylaminuria (fish odor syndrome) [849, 3924].
References: [2139, 849, 3924, 577]

[EC 1.14.13.148 created 2012]

EC 1.14.13.149

Accepted name: phenylacetyl-CoA 1,2-epoxidase
Reaction: phenylacetyl-CoA + NADPH + H⁺ + O₂ = 2-(1,2-epoxy-1,2-dihydrophenyl)acetyl-CoA + NADP⁺ + H₂O

Other name(s): ring 1,2-phenylacetyl-CoA epoxidase; phenylacetyl-CoA monooxygenase; PaaAC; PaaABC(D)E
Systematic name: phenylacetyl-CoA:oxygen oxidoreductase (1,2-epoxidizing)
Comments: Part of the aerobic pathway of phenylacetate catabolism in *Escherichia coli* and *Pseudomonas putida*.
References: [3853, 1288, 1287]

[EC 1.14.13.149 created 2012]

[1.14.13.150 Transferred entry. *α*-humulene 10-hydroxylase. Now EC 1.14.14.113, *α*-humulene 10-hydroxylase.]

[EC 1.14.13.150 created 2012, deleted 2018]

[1.14.13.151 Transferred entry. linalool 8-monooxygenase. Now EC 1.14.14.84, linalool 8-monooxygenase]

[EC 1.14.13.151 created 1989 as EC 1.14.99.28, transferred 2012 to EC 1.14.13.151, deleted 2018]

[1.14.13.152 Transferred entry. geraniol 8-hydroxylase. Now EC 1.14.14.83, geraniol 8-hydroxylase]

[EC 1.14.13.152 created 2012, deleted 2018]

EC 1.14.13.153

Accepted name: (+)-sabinene 3-hydroxylase
Reaction: (+)-sabinene + NADPH + H⁺ + O₂ = (+)-*cis*-sabinol + NADP⁺ + H₂O
Systematic name: (+)-sabinene,NADPH:oxygen oxidoreductase (3-hydroxylating)
Comments: Requires cytochrome *P*-450. The enzyme has been characterized from *Salvia officinalis* (sage).
References: [1815]

[EC 1.14.13.153 created 2012]

EC 1.14.13.154

Accepted name: erythromycin 12-hydroxylase
Reaction: erythromycin D + NADPH + H⁺ + O₂ = erythromycin C + NADP⁺ + H₂O
Other name(s): EryK
Systematic name: erythromycin-D,NADPH:oxygen oxidoreductase (12-hydroxylating)
Comments: The enzyme is responsible for the C-12 hydroxylation of the macrolactone ring, one of the last steps in erythromycin biosynthesis. It shows 1200-1900-fold preference for erythromycin D over the alternative substrate erythromycin B [2119].
References: [2119, 3329, 2600]

[EC 1.14.13.154 created 2012]

EC 1.14.13.155

Accepted name: *α*-pinene monooxygenase
Reaction: (–)-*α*-pinene + NADH + H⁺ + O₂ = *α*-pinene oxide + NAD⁺ + H₂O
Systematic name: (–)-*α*-pinene,NADH:oxygen oxidoreductase
Comments: Involved in the catabolism of *α*-pinene.
References: [645]

[EC 1.14.13.155 created 2012]

[1.14.13.156 Transferred entry. 1,8-cineole 2-endo-monooxygenase. Now EC 1.14.14.133, 1,8-cineole 2-endo-monooxygenase]

[EC 1.14.13.156 created 2012, deleted 2018]

[1.14.13.157 Transferred entry. 1,8-cineole 2-exo-monooxygenase. Now EC 1.14.14.56, 1,8-cineole 2-exo-monooxygenase]

[EC 1.14.13.157 created 2012, deleted 2017]

[1.14.13.158 Transferred entry. *amorpha-4,11-diene 12-monooxygenase*. Now EC 1.14.14.114, *amorpha-4,11-diene 12-monooxygenase*.]

[EC 1.14.13.158 created 2012, deleted 2018]

[1.14.13.159 Transferred entry. *vitamin D 25-hydroxylase*. Now EC 1.14.14.24, *vitamin D 25-hydroxylase*]

[EC 1.14.13.159 created 2012, deleted 2016]

EC 1.14.13.160

Accepted name: (2,2,3-trimethyl-5-oxocyclopent-3-enyl)acetyl-CoA 1,5-monooxygenase
Reaction: [(1*R*)-2,2,3-trimethyl-5-oxocyclopent-3-enyl]acetyl-CoA + O₂ + NADPH + H⁺ = [(2*R*)-3,3,4-trimethyl-6-oxo-3,6-dihydro-1*H*-pyran-2-yl]acetyl-CoA + NADP⁺ + H₂O
Other name(s): 2-oxo-Δ³-4,5,5-trimethylcyclopentenylacetyl-CoA monooxygenase; 2-oxo-Δ³-4,5,5-trimethylcyclopentenylacetyl-CoA 1,2-monooxygenase; OTEMO
Systematic name: [(1*R*)-2,2,3-trimethyl-5-oxocyclopent-3-enyl]acetyl-CoA,NADPH:oxygen oxidoreductase (1,5-lactonizing)
Comments: A FAD dependent enzyme isolated from *Pseudomonas putida*. Forms part of the catabolism pathway of camphor. It acts on the CoA ester in preference to the free acid.
References: [2918, 2194, 1792]

[EC 1.14.13.160 created 2012]

EC 1.14.13.161

Accepted name: (+)-camphor 6-*exo*-hydroxylase
Reaction: (+)-camphor + NADPH + H⁺ + O₂ = (+)-6-*exo*-hydroxycamphor + NADP⁺ + H₂O
Other name(s): (+)-camphor 6-hydroxylase
Systematic name: (+)-camphor,NADPH:oxygen oxidoreductase (6-*exo*-hydroxylating)
Comments: A cytochrome *P*-450 monooxygenase isolated from *Salvia officinalis* (sage). Involved in the catabolism of camphor in senescent tissue.
References: [1116, 1114]

[EC 1.14.13.161 created 2012]

[1.14.13.162 Transferred entry. *2,5-diketocamphane 1,2-monooxygenase*. Now EC 1.14.14.108, *2,5-diketocamphane 1,2-monooxygenase*]

[EC 1.14.13.162 created 1972 as EC 1.14.15.2, transferred 2012 to EC 1.14.13.162, deleted 2018]

EC 1.14.13.163

Accepted name: 6-hydroxy-3-succinoylpyridine 3-monooxygenase
Reaction: 4-(6-hydroxypyridin-3-yl)-4-oxobutanoate + 2 NADH + 2 H⁺ + O₂ = 2,5-dihydroxypyridine + succinate semialdehyde + 2 NAD⁺ + H₂O
Other name(s): 6-hydroxy-3-succinoylpyridine hydroxylase; *hspA* (gene name); *hspB* (gene name)
Systematic name: 4-(6-hydroxypyridin-3-yl)-4-oxobutanoate,NADH:oxygen oxidoreductase (3-hydroxylating, succinate semialdehyde releasing)
Comments: The enzyme catalyses a reaction in the nicotine degradation pathway of *Pseudomonas* species. One of the enzymes from the soil bacterium *Pseudomonas putida* S16 contains an FAD cofactor [3809].
References: [3808, 3809]

[EC 1.14.13.163 created 2012]

[1.14.13.164 Transferred entry. *carotenoid isomeroxygenase*. The enzyme was discovered at the public-review stage to have been misclassified and so was withdrawn. See EC 1.13.11.65, *carotenoid isomeroxygenase*]

[EC 1.14.13.164 created 2012, deleted 2012]

[1.14.13.165 Transferred entry. nitric-oxide synthase [NAD(P)H]. Now classified as EC 1.14.14.47, nitric-oxide synthase (flavodoxin)]

[EC 1.14.13.165 created 2012, deleted 2017]

EC 1.14.13.166

Accepted name: 4-nitrocatechol 4-monooxygenase
Reaction: 4-nitrocatechol + NAD(P)H + H⁺ + O₂ = 2-hydroxy-1,4-benzoquinone + nitrite + NAD(P)⁺ + H₂O
Systematic name: 4-nitrocatechol,NAD(P)H:oxygen 4-oxidoreductase (4-hydroxylating, nitrite-forming)
Comments: Contains FAD. The enzyme catalyses the oxidation of 4-nitrocatechol with the concomitant removal of the nitro group as nitrite. Forms a two-component system with a flavoprotein reductase [1791]. The enzymes from the bacteria *Lysinibacillus sphaericus* JS905 and *Rhodococcus* sp. strain PN1 were shown to also catalyse EC 1.14.13.29, 4-nitrophenol 2-monooxygenase [1791, 1943] while the enzyme from *Pseudomonas* sp. WBC-3 was shown to also catalyse EC 1.14.13.167, 4-nitrophenol 4-monooxygenase [4440].
References: [1791, 1943, 4440]

[EC 1.14.13.166 created 2012]

EC 1.14.13.167

Accepted name: 4-nitrophenol 4-monooxygenase
Reaction: 4-nitrophenol + NADPH + H⁺ + O₂ = 1,4-benzoquinone + nitrite + NADP⁺ + H₂O
Other name(s): *pnpA* (gene name); *pdcA* (gene name)
Systematic name: 4-nitrophenol,NAD(P)H:oxygen 4-oxidoreductase (4-hydroxylating, nitrite-forming)
Comments: Contains FAD. The enzyme catalyses the first step in a degradation pathway for 4-nitrophenol, the oxidation of 4-nitrophenol at position 4 with the concomitant removal of the nitro group as nitrite. The enzyme from the bacterium *Pseudomonas* sp. strain WBC-3 also catalyses EC 1.14.13.166, 4-nitrocatechol 4-monooxygenase.
References: [4440]

[EC 1.14.13.167 created 2012]

EC 1.14.13.168

Accepted name: indole-3-pyruvate monooxygenase
Reaction: (indol-3-yl)pyruvate + NADPH + H⁺ + O₂ = (indol-3-yl)acetate + NADP⁺ + H₂O + CO₂
Other name(s): YUC2 (gene name); *spi1* (gene name)
Systematic name: indole-3-pyruvate,NADPH:oxygen oxidoreductase (1-hydroxylating, decarboxylating)
Comments: This plant enzyme, along with EC 2.6.1.99 L-tryptophan—pyruvate aminotransferase, is responsible for the biosynthesis of the plant hormone indole-3-acetate from L-tryptophan.
References: [2428, 4465]

[EC 1.14.13.168 created 2012]

[1.14.13.169 Transferred entry. sphinganine C4-monooxygenase. Now EC 1.14.18.5, sphingolipid C4-monooxygenase]

[EC 1.14.13.169 created 2012, deleted 2015]

EC 1.14.13.170

Accepted name: pentalenolactone D synthase
Reaction: 1-deoxy-11-oxopentalenate + NADPH + H⁺ + O₂ = pentalenolactone D + NADP⁺ + H₂O
Other name(s): *penE* (gene name); *pntE* (gene name)
Systematic name: 1-deoxy-11-oxopentalenate,NADH:oxygen oxidoreductase (pentalenolactone-D forming)
Comments: A FAD-dependent oxygenase. Isolated from the bacteria *Streptomyces exfoliatus* and *Streptomyces arenae*. The ketone undergoes a biological Baeyer-Villiger reaction. Part of the pathway of pentalenolactone biosynthesis.
References: [3443]

[EC 1.14.13.170 created 2012]

EC 1.14.13.171

Accepted name: neopentalenolactone D synthase
Reaction: 1-deoxy-11-oxopentalenate + NADPH + H⁺ + O₂ = neopentalenolactone D + NADP⁺ + H₂O
Other name(s): *ptlE* (gene name)
Systematic name: 1-deoxy-11-oxopentalenate,NADH:oxygen oxidoreductase (neopentalenolactone-D forming)
Comments: A FAD-dependent oxygenase. Isolated from the bacterium *Streptomyces avermitilis*. The ketone undergoes a biological Baeyer-Villiger reaction.
References: [3443]

[EC 1.14.13.171 created 2012]

EC 1.14.13.172

Accepted name: salicylate 5-hydroxylase
Reaction: salicylate + NADH + H⁺ + O₂ = 2,5-dihydroxybenzoate + NAD⁺ + H₂O
Other name(s): *nagG* (gene name); *nagH* (gene name)
Systematic name: salicylate,NADH:oxygen oxidoreductase (5-hydroxylating)
Comments: This enzyme, which was characterized from the bacterium *Ralstonia* sp. U2, comprises a multi-component system, containing a reductase that is an iron-sulfur flavoprotein (FAD; EC 1.18.1.7, ferredoxin—NAD(P)⁺ reductase), an iron-sulfur oxygenase, and ferredoxin.
References: [1088]

[EC 1.14.13.172 created 2013]

[1.14.13.173 Transferred entry. 11-oxo-β-amyrin 30-oxidase. Now EC 1.14.14.115, 11-oxo-β-amyrin 30-oxidase.]

[EC 1.14.13.173 created 2013, deleted 2018]

[1.14.13.174 Transferred entry. averantin hydroxylase. Now EC 1.14.14.116, averantin hydroxylase]

[EC 1.14.13.174 created 2013, deleted 2018]

[1.14.13.175 Transferred entry. aflatoxin B synthase. Now EC 1.14.14.117, aflatoxin B synthase]

[EC 1.14.13.175 created 2013, deleted 2018]

[1.14.13.176 Transferred entry. tryprostatin B 6-hydroxylase. Now EC 1.14.14.118, tryprostatin B 6-hydroxylase]

[EC 1.14.13.176 created 2013, deleted 2018]

[1.14.13.177 Transferred entry. fumitremorgin C monooxygenase. Now EC 1.14.14.119, fumitremorgin C monooxygenase]

[EC 1.14.13.177 created 2013, deleted 2018]

EC 1.14.13.178

Accepted name: methylxanthine N¹-demethylase
Reaction: (1) caffeine + O₂ + NAD(P)H + H⁺ = theobromine + NAD(P)⁺ + H₂O + formaldehyde
(2) theophylline + O₂ + NAD(P)H + H⁺ = 3-methylxanthine + NAD(P)⁺ + H₂O + formaldehyde
(3) paraxanthine + O₂ + NAD(P)H + H⁺ = 7-methylxanthine + NAD(P)⁺ + H₂O + formaldehyde
Other name(s): *ndmA* (gene name)
Systematic name: caffeine:oxygen oxidoreductase (N¹-demethylating)
Comments: A non-heme iron oxygenase. The enzyme from the bacterium *Pseudomonas putida* shares an NAD(P)H-FMN reductase subunit with EC 1.14.13.179, methylxanthine N³-demethylase, and has a 5-fold higher activity with NADH than with NADPH [3727]. Also demethylate 1-methylxanthine with lower efficiency. Forms part of the degradation pathway of methylxanthines.
References: [3728, 3727]

[EC 1.14.13.178 created 2013]

EC 1.14.13.179

- Accepted name:** methylxanthine *N*³-demethylase
Reaction: (1) theobromine + O₂ + NAD(P)H + H⁺ = 7-methylxanthine + NAD(P)⁺ + H₂O + formaldehyde
(2) 3-methylxanthine + O₂ + NAD(P)H + H⁺ = xanthine + NAD(P)⁺ + H₂O + formaldehyde
Other name(s): *ndmB* (gene name)
Systematic name: theobromine:oxygen oxidoreductase (*N*³-demethylating)
Comments: A non-heme iron oxygenase. The enzyme from the bacterium *Pseudomonas putida* shares an NAD(P)H-FMN reductase subunit with EC 1.14.13.178, methylxanthine *N*¹-demethylase, and has higher activity with NADH than with NADPH [3728]. Also demethylates caffeine and theophylline with lower efficiency. Forms part of the degradation pathway of methylxanthines.
References: [3728, 3727]

[EC 1.14.13.179 created 2013]

EC 1.14.13.180

- Accepted name:** aklavinone 12-hydroxylase
Reaction: aklavinone + NADPH + H⁺ + O₂ = ε-rhodomyconone + NADP⁺ + H₂O
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: [1016, 2788]

[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
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: [4084, 817]

[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
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: [3361]

[EC 1.14.13.182 created 2013]

[1.14.13.183 Transferred entry. *dammarenediol 12-hydroxylase*. Now EC 1.14.14.120, *dammarenediol 12-hydroxylase*]

[EC 1.14.13.183 created 2013, deleted 2018]

[1.14.13.184 Transferred entry. *protopanaxadiol 6-hydroxylase*. Now EC 1.14.14.121, *protopanaxadiol 6-hydroxylase*]

[EC 1.14.13.184 created 2013, deleted 2018]

[1.14.13.185 Transferred entry. *pikromycin synthase*. Now EC 1.14.15.33, *pikromycin synthase*]

[EC 1.14.13.185 created 2014, deleted 2018]

[1.14.13.186 Transferred entry. *20-oxo-5-O-mycaminosyltylactone 23-monoxygenase*. Now EC 1.14.15.34, *20-oxo-5-O-mycaminosyltylactone 23-monoxygenase*]

[EC 1.14.13.186 created 2014, deleted 2018]

EC 1.14.13.187

Accepted name: L-evernosamine nitrososynthase

Reaction: dTDP-β-L-evernosamine + 2 NADPH + 2 H⁺ + 2 O₂ = dTDP-2,3,6-trideoxy-3-C-methyl-4-O-methyl-3-nitroso-β-L-*arabino*-hexopyranose + 2 NADP⁺ + 3 H₂O (overall reaction)
(1a) dTDP-β-L-evernosamine + NADPH + H⁺ + O₂ = dTDP-*N*-hydroxy-β-L-evernosamine + NADP⁺ + H₂O
(1b) dTDP-*N*-hydroxy-β-L-evernosamine + NADPH + H⁺ + O₂ = dTDP-2,3,6-trideoxy-3-C-methyl-4-O-methyl-3-nitroso-β-L-*arabino*-hexopyranose + NADP⁺ + 2 H₂O

Systematic name: dTDP-β-L-evernosamine,NADPH:oxygen oxidoreductase (*N*-hydroxylating)

Comments: Requires FAD. Isolated from the bacterium *Micromonospora carbonacea* var. *africana*. The nitroso group is probably spontaneously oxidized to a nitro group giving dTDP-β-L-evernitrose, which is involved in the biosynthesis of the antibiotic everninomycin. The reaction was studied using dTDP-β-L-4-*epi*-vancosamine (dTDP-4-*O*-desmethyl-β-L-evernitrosamine).

References: [1590, 4038]

[EC 1.14.13.187 created 2014]

[1.14.13.188 Transferred entry. *6-deoxyerythronolide B hydroxylase*. Now EC 1.14.15.35, *6-deoxyerythronolide B hydroxylase*]

[EC 1.14.13.188 created 2014, deleted 2018]

EC 1.14.13.189

Accepted name: 5-methyl-1-naphthoate 3-hydroxylase

Reaction: 5-methyl-1-naphthoate + NADPH + H⁺ + O₂ = 3-hydroxy-5-methyl-1-naphthoate + NADP⁺ + H₂O

Other name(s): AziB1

Systematic name: 5-methyl-1-naphthoate,NADPH:oxygen oxidoreductase (3-hydroxylating)

Comments: The enzyme from the bacterium *Streptomyces sahachiroi* is involved in the biosynthesis of 3-methoxy-5-methyl-1-naphthoate, a component of the antitumor antibiotic azinomycin B.

References: [831]

[EC 1.14.13.189 created 2014]

EC 1.14.13.190

Accepted name: ferruginol synthase

Reaction: abieta-8,11,13-triene + NADPH + H⁺ + O₂ = ferruginol + NADP⁺ + H₂O

Other name(s): miltiradiene oxidase (incorrect); CYP76AH1; miltiradiene,NADPH:oxygen oxidoreductase (ferruginol forming) (incorrect)

Systematic name: miltiradiene,NADPH:oxygen oxidoreductase (ferruginol-forming)

Comments: The enzyme is found in some members of the *Lamiaceae* (mint family). The enzyme from *Rosmarinus officinalis* (rosemary) is involved in biosynthesis of carnosic acid, while the enzyme from the Chinese medicinal herb *Salvia miltiorrhiza* is involved in the biosynthesis of the tanshinones, abietane-type norditerpenoid naphthoquinones that are the main lipophilic bioactive components found in the plant.

References: [1314, 4485, 375]

[EC 1.14.13.190 created 2014, modified 2015]

[1.14.13.191 Transferred entry. *ent-sandaracopimaradiene 3-hydroxylase*. Now EC 1.14.14.70, *ent-sandaracopimaradiene 3-hydroxylase*]

[EC 1.14.13.191 created 2014, deleted 2018]

[1.14.13.192 Transferred entry. *oryzalexin E synthase*. Now EC 1.14.14.122, *oryzalexin E synthase*]

[EC 1.14.13.192 created 2014, deleted 2018]

[1.14.13.193 Transferred entry. *oryzalexin D synthase*. Now EC 1.14.14.123, *oryzalexin D synthase*]

[EC 1.14.13.193 created 2014, deleted 2018]

[1.14.13.194 Transferred entry. *phyloquinone ω-hydroxylase*. Now EC 1.14.14.78, *phyloquinone ω-hydroxylase*]

[EC 1.14.13.194 created 2014, deleted 2018]

EC 1.14.13.195

Accepted name: L-ornithine *N*⁵-monooxygenase (NADPH)

Reaction: L-ornithine + NADPH + H⁺ + O₂ = *N*⁵-hydroxy-L-ornithine + NADP⁺ + H₂O

Other name(s): CchB; ornithine hydroxylase; EtcB; PvdA; Af-OMO; *dffA* (gene name)

Systematic name: L-ornithine,NADPH:oxygen oxidoreductase (*N*⁵-hydroxylating)

Comments: A flavoprotein (FAD). The enzyme is involved in biosynthesis of *N*⁵-hydroxy-L-ornithine, *N*⁵-formyl-*N*⁵-hydroxy-L-ornithine or *N*⁵-acetyl-*N*⁵-hydroxy-L-ornithine. These nonproteinogenic amino acids are building blocks of siderophores produced by some bacteria (e.g. *Streptomyces coelicolor*, *Saccharopolyspora erythraea* and *Pseudomonas aeruginosa*). The enzyme is specific for NADPH. *cf.* EC 1.14.13.196, L-ornithine *N*⁵-monooxygenase [NAD(P)H].

References: [1175, 2503, 3027, 3201]

[EC 1.14.13.195 created 2014]

EC 1.14.13.196

Accepted name: L-ornithine *N*⁵-monooxygenase [NAD(P)H]

Reaction: L-ornithine + NAD(P)H + H⁺ + O₂ = *N*⁵-hydroxy-L-ornithine + NAD(P)⁺ + H₂O

Other name(s): SidA (ambiguous)

Systematic name: L-ornithine,NAD(P)H:oxygen oxidoreductase (*N*⁵-hydroxylating)

Comments: A flavoprotein (FAD). The enzyme from the pathogenic fungus *Aspergillus fumigatus* catalyses a step in the biosynthesis of the siderophores triacetylfusarinine and desferri-ferricrocin, while the enzyme from the bacterium *Kutzneria* sp. 744 is involved in the biosynthesis of piperazate, a building block of the kutzneride family of antifungal antibiotics. Activity of the fungal enzyme is higher with NADPH, due to the fact that following the reduction of the flavin, NADP⁺ (but not NAD⁺) stabilizes the C4a-hydroperoxyflavin intermediate that oxidizes the substrate [3228]. *cf.* EC 1.14.13.195, L-ornithine *N*⁵-monooxygenase (NADPH).

References: [607, 1050, 3228, 2770]

[EC 1.14.13.196 created 2014]

[1.14.13.197 Transferred entry. dihydromonacolin L hydroxylase. Now EC 1.14.14.124, dihydromonacolin L hydroxylase]

[EC 1.14.13.197 created 2014, deleted 2018]

[1.14.13.198 Transferred entry. monacolin L hydroxylase. Now EC 1.14.14.125, monacolin L hydroxylase]

[EC 1.14.13.198 created 2014, deleted 2018]

[1.14.13.199 Transferred entry. docosahexaenoic acid ω -hydroxylase. Now EC 1.14.14.79, docosahexaenoic acid ω -hydroxylase]

[EC 1.14.13.199 created 2014, deleted 2018]

EC 1.14.13.200

Accepted name: tetracenomycin A2 monooxygenase-dioxygenase

Reaction: tetracenomycin A2 + 2 O₂ + 2 NAD(P)H + 2 H⁺ = tetracenomycin C + 2 NAD(P)⁺ + H₂O

Other name(s): TcmG; ElmG; tetracenomycin A2,NAD(P)H:O₂ oxidoreductase (tetracenomycin C forming)

Systematic name: tetracenomycin A2,NAD(P)H:oxygen oxidoreductase (tetracenomycin C forming)

Comments: Isolated from the bacterium *Streptomyces glaucescens*. The enzyme was also isolated from the bacterium *Streptomyces olivaceus*, where it acts on 8-demethyltetracenomycin A2 (tetracenomycin B2) as part of elloramycin biosynthesis. The reaction involves a monooxygenase reaction which is followed by a dioxygenase reaction giving a gem-diol and an epoxide. Water opens the epoxide giving two hydroxy groups. The gem-diol eliminates water to give a ketone which is then reduced to a hydroxy group.

References: [3473, 3100, 289]

[EC 1.14.13.200 created 2014]

[1.14.13.201 Transferred entry. β -amyrin 28-monooxygenase. Now EC 1.14.14.126, β -amyrin 28-monooxygenase]

[EC 1.14.13.201 created 2015, deleted 2018]

[1.14.13.202 Transferred entry. methyl farnesoate epoxidase. Now EC 1.14.14.127, methyl farnesoate epoxidase]

[EC 1.14.13.202 created 2015, deleted 2018]

[1.14.13.203 Transferred entry. farnesoate epoxidase. Now EC 1.14.14.128, farnesoate epoxidase]

[EC 1.14.13.203 created 2015, deleted 2018]

[1.14.13.204 Transferred entry. long-chain acyl-CoA ω -monooxygenase. Now EC 1.14.14.129, long-chain acyl-CoA ω -monooxygenase]

[EC 1.14.13.204 created 2015, deleted 2018]

[1.14.13.205 Transferred entry. long-chain fatty acid ω -monooxygenase. Now EC 1.14.14.80, long-chain fatty acid ω -monooxygenase]

[EC 1.14.13.205 created 2015, deleted 2018]

[1.14.13.206 Transferred entry. laurate 7-monooxygenase. Now EC 1.14.14.130, laurate 7-monooxygenase]

[EC 1.14.13.206 created 2015, deleted 2018]

[1.14.13.207 Transferred entry. ipsdienol synthase. Now EC 1.14.14.31, ipsdienol synthase]

[EC 1.14.13.207 created 2015, deleted 2016]

EC 1.14.13.208

Accepted name: benzoyl-CoA 2,3-epoxidase

Reaction: benzoyl-CoA + NADPH + H⁺ + O₂ = 2,3-epoxy-2,3-dihydrobenzoyl-CoA + NADP⁺ + H₂O

Other name(s): benzoyl-CoA dioxygenase/reductase (incorrect); BoxBA; BoxA/BoxB system; benzoyl-CoA 2,3-dioxygenase (incorrect)
Systematic name: benzoyl-CoA,NADPH:oxygen oxidoreductase (2,3-epoxydizing)
Comments: The enzyme is involved in aerobic benzoate metabolism in *Azoarcus evansii*. BoxB functions as the oxygenase part of benzoyl-CoA oxygenase in conjunction with BoxA, the reductase component, which upon binding of benzoyl-CoA, transfers two electrons to the ring in the course of monooxygenation. BoxA is a homodimeric 46 kDa iron-sulfur-flavoprotein (FAD), BoxB is a monomeric iron-protein [4416].
References: [4416, 1188, 2588, 3129]

[EC 1.14.13.208 created 2010 as EC 1.14.12.21, transferred 2015 to EC 1.14.13.208]

EC 1.14.13.209

Accepted name: salicyloyl-CoA 5-hydroxylase
Reaction: 2-hydroxybenzoyl-CoA + NADH + H⁺ + O₂ = gentisyl-CoA + NAD⁺ + H₂O
Other name(s): *sdgC* (gene name)
Systematic name: salicyloyl-CoA,NADH:oxygen oxidoreductase (5-hydroxylating)
Comments: The enzyme, characterized from the bacterium *Streptomyces* sp. WA46, participates in a pathway for salicylate degradation. *cf.* EC 1.14.13.172, salicylate 5-hydroxylase.
References: [1672]

[EC 1.14.13.209 created 2015]

EC 1.14.13.210

Accepted name: 4-methyl-5-nitrocatechol 5-monooxygenase
Reaction: 4-methyl-5-nitrocatechol + NAD(P)H + H⁺ + O₂ = 2-hydroxy-5-methylquinone + nitrite + NAD(P)⁺ + H₂O
Other name(s): *dntB* (gene name); 4-methyl-5-nitrocatechol oxygenase; MNC monooxygenase
Systematic name: 4-methyl-5-nitrocatechol,NAD(P)H:oxygen 5-oxidoreductase (5-hydroxylating, nitrite-forming)
Comments: Contains FAD. The enzyme, isolated from the bacterium *Burkholderia* sp. DNT, can use both NADH and NADPH, but prefers NADPH. It has a narrow substrate range, but can also act on 4-nitrocatechol.
References: [1343, 2207]

[EC 1.14.13.210 created 2016]

EC 1.14.13.211

Accepted name: rifampicin monooxygenase
Reaction: rifampicin + NAD(P)H + O₂ = 2'-N-hydroxyrifampicin + NAD(P)⁺ + H₂O
Other name(s): RIF-O
Systematic name: rifampicin:NAD(P)H:oxygen oxidoreductase (2'-N-hydroxyrifampicin-forming)
Comments: The enzyme has been found in the Corynebacteria *Rhodococcus equi* and *Nocardia farcinica*. It confers increased resistance to the antibiotic rifampicin by initiating its degradation.
References: [82, 1579]

[EC 1.14.13.211 created 2016]

EC 1.14.13.212

Accepted name: 1,3,7-trimethyluric acid 5-monooxygenase
Reaction: 1,3,7-trimethylurate + NADH + H⁺ + O₂ = 1,3,7-trimethyl-5-hydroxyisourate + NAD⁺ + H₂O
Other name(s): *tmuM* (gene name)
Systematic name: 1,3,7-trimethylurate,NADH:oxygen oxidoreductase (1,3,7-trimethyl-5-hydroxyisourate forming)

Comments: The enzyme, characterized from the bacterium *Pseudomonas* sp. CBB1, is part of the bacterial C-8 oxidation-based caffeine degradation pathway. The product decomposes spontaneously to a racemic mixture of 3,6,8-trimethylallantoin. The enzyme shows no activity with urate. *cf.* EC 1.14.13.113, FAD-dependent urate hydroxylase.

References: [2589, 3729]

[EC 1.14.13.212 created 2016]

[1.14.13.213 Transferred entry. *bursehernin 5-monoxygenase*. Now EC 1.14.14.131, *bursehernin 5-monoxygenase*]

[EC 1.14.13.213 created 2016, deleted 2018]

[1.14.13.214 Transferred entry. *(-)-4'-demethyl-deoxypodophyllotoxin 4-hydroxylase*. Now EC 1.14.14.132, *(-)-4'-demethyl-deoxypodophyllotoxin 4-hydroxylase*]

[EC 1.14.13.214 created 2016, deleted 2018]

EC 1.14.13.215

Accepted name: protoasukamycin 4-monoxygenase
Reaction: protoasukamycin + NADH + H⁺ + O₂ = 4-hydroxyprotoasukamycin + NAD⁺ + H₂O
Systematic name: protoasukamycin,NADH:oxygen oxidoreductase (4-hydroxylating)
Comments: The enzyme, characterized from the bacterium *Streptomyces nodosus* subsp. *asukaensis*, is involved in the biosynthesis of the antibiotic asukamycin. Requires a flavin cofactor, with no preference among FMN, FAD or riboflavin. When flavin concentration is low, activity is enhanced by the presence of the NADH-dependent flavin-reductase AsuE2.
References: [3258]

[EC 1.14.13.215 created 2016]

EC 1.14.13.216

Accepted name: asperlicin C monoxygenase
Reaction: asperlicin C + NAD(P)H + H⁺ + O₂ = asperlicin E + NAD(P)⁺ + H₂O
Other name(s): AspB
Systematic name: asperlicin C,NAD(P)H:oxygen oxidoreductase
Comments: The enzyme, characterized from the fungus *Aspergillus alliaceus*, contains an FAD cofactor. The enzyme inserts a hydroxyl group, leading to formation of a N-C bond that creates an additional cycle between the bicyclic indole and the tetracyclic core moieties, resulting in the heptacyclic asperlicin E.
References: [1442]

[EC 1.14.13.216 created 2016]

EC 1.14.13.217

Accepted name: protodeoxyviolaceinate monoxygenase
Reaction: protodeoxyviolaceinate + NAD(P)H + O₂ = protoviolaceinate + NAD(P)⁺ + H₂O
Other name(s): *vioD* (gene name); protoviolaceinate synthase
Systematic name: protodeoxyviolaceinate,NAD(P)H:O₂ oxidoreductase
Comments: The enzyme, characterized from the bacterium *Chromobacterium violaceum*, participates in the biosynthesis of the violet pigment violacein. The product, protoviolaceinate, can be acted upon by EC 1.14.13.224, violacein synthase, leading to violacein production. However, it is very labile, and in the presence of oxygen can undergo non-enzymic autooxidation to the shunt product proviolacein.
References: [180, 3515]

[EC 1.14.13.217 created 2016, modified 2016]

EC 1.14.13.218

Accepted name: 5-methylphenazine-1-carboxylate 1-monooxygenase
Reaction: 5-methylphenazine-1-carboxylate + NADH + O₂ = pyocyanin + NAD⁺ + CO₂ + H₂O
Other name(s): *phzS* (gene name)
Systematic name: 5-methylphenazine-1-carboxylate,NADH:oxygen oxidoreductase (1-hydroxylating, decarboxylating)
Comments: The enzyme, characterized from the bacterium *Pseudomonas aeruginosa*, is involved in the biosynthesis of pyocyanin, a toxin produced and secreted by the organism. It can also act on phenazine-1-carboxylate, converting it into phenazin-1-ol.
References: [2470, 2948, 1276]

[EC 1.14.13.218 created 2016]

EC 1.14.13.219

Accepted name: resorcinol 4-hydroxylase (NADPH)
Reaction: resorcinol + NADPH + H⁺ + O₂ = hydroxyquinol + NADP⁺ + H₂O
Systematic name: resorcinol,NADPH:oxygen oxidoreductase (4-hydroxylating)
Comments: The enzyme, characterized from the bacterium *Corynebacterium glutamicum*, is a single-component hydroxylase. The enzyme has no activity with NADH. *cf.* EC 1.14.13.220, resorcinol 4-hydroxylase (NADH), and EC 1.14.14.27, resorcinol 4-hydroxylase (FADH₂).
References: [1598]

[EC 1.14.13.219 created 2016]

EC 1.14.13.220

Accepted name: resorcinol 4-hydroxylase (NADH)
Reaction: resorcinol + NADH + H⁺ + O₂ = hydroxyquinol + NAD⁺ + H₂O
Other name(s): *tsdB* (gene name)
Systematic name: resorcinol,NADH:oxygen oxidoreductase (4-hydroxylating)
Comments: The enzyme, characterized from the bacterium *Rhodococcus jostii* RHA1, is a single-component hydroxylase. The enzyme has no activity with NADPH. *cf.* EC 1.14.13.219, resorcinol 4-hydroxylase (NADPH), and EC 1.14.14.27, resorcinol 4-hydroxylase (FADH₂).
References: [1823]

[EC 1.14.13.220 created 2016]

[1.14.13.221 Transferred entry. *cholest-4-en-3-one 26-monooxygenase [(25R)-3-oxocholest-4-en-26-oate forming]*. Now EC 1.14.15.28, *cholest-4-en-3-one 26-monooxygenase [(25R)-3-oxocholest-4-en-26-oate forming]*

[EC 1.14.13.221 created 2016, deleted 2018]

EC 1.14.13.222

Accepted name: aurachin C monooxygenase/isomerase
Reaction: aurachin C + NAD(P)H + H⁺ + O₂ = 4-hydroxy-2-methyl-3-oxo-4-[(2E,6E)-farnesyl]-3,4-dihydroquinoline 1-oxide + NAD(P)⁺ + H₂O (overall reaction)
(1a) aurachin C + NAD(P)H + H⁺ + O₂ = 2-hydroxy-1a-methyl-7a-[(2E,6E)-farnesyl]-1a,2-dihydrooxireno[2,3-*b*]quinolin-7(7aH)-one + NAD(P)⁺ + H₂O
(1b) 2-hydroxy-1a-methyl-7a-[(2E,6E)-farnesyl]-1a,2-dihydrooxireno[2,3-*b*]quinolin-7(7aH)-one = 4-hydroxy-2-methyl-3-oxo-4-[(2E,6E)-farnesyl]-3,4-dihydroquinoline 1-oxide
Other name(s): *auaG* (gene name); aurachin C monooxygenase
Systematic name: aurachin C:NAD(P)H:oxygen oxidoreductase (4-hydroxy-2-methyl-3-oxo-4-farnesyl-3,4-dihydroquinoline-1-oxide-forming)
Comments: The aurachin C monooxygenase from the bacterium *Stigmatella aurantiaca* accepts both NADH and NADPH as cofactor, but has a preference for NADH. It catalyses the initial steps in the conversion of aurachin C to aurachin B. The FAD-dependent monooxygenase catalyses the epoxidation of the C₂-C₃ double bond of aurachin C, which is followed by a semipinacol rearrangement, causing migration of the farnesyl group from C₃ to C₄.
References: [1846]

[EC 1.14.13.222 created 2016]

EC 1.14.13.223

- Accepted name:** 3-hydroxy-4-methylanthranilyl-[aryl-carrier protein] 5-monoxygenase
Reaction: 3-hydroxy-4-methylanthranilyl-[aryl-carrier protein] + NADH + H⁺ + O₂ = 3,5-dihydroxy-4-methylanthranilyl-[aryl-carrier protein] + NAD⁺ + H₂O
Other name(s): *sibG* (gene name)
Systematic name: 3-hydroxy-4-methylanthranilyl-[aryl-carrier protein],NADH:oxygen oxidoreductase (5-hydroxylating)
Comments: A flavoprotein (FAD). The enzyme, characterized from the bacterium *Streptosporangium sibiricum*, is involved in the biosynthesis of the antitumor antibiotic sibiromycin. The enzyme is not active with free 3-hydroxy-4-methylanthranilate.
References: [1203]

[EC 1.14.13.223 created 2016]

EC 1.14.13.224

- Accepted name:** violacein synthase
Reaction: (1) protoviolaceinate + NAD(P)H + O₂ = violaceinate + NAD(P)⁺ + H₂O
(2) protodeoxyviolaceinate + NAD(P)H + O₂ = deoxyviolaceinate + NAD(P)⁺ + H₂O
Other name(s): proviolaceinate monoxygenase; *vioC* (gene name)
Systematic name: protoviolaceinate,NAD(P)H:O₂ oxidoreductase
Comments: The enzyme, characterized from the bacterium *Chromobacterium violaceum*, participates in the biosynthesis of the violet pigment violacein. The products, violaceinate and deoxyviolaceinate, undergo non-enzymic autooxidation into violacein and deoxyviolacein, respectively.
References: [180, 3515]

[EC 1.14.13.224 created 2016]

EC 1.14.13.225

- Accepted name:** F-actin monoxygenase
Reaction: [F-actin]-L-methionine + NADPH + O₂ + H⁺ = [F-actin]-L-methionine-(*R*)-*S*-oxide + NADP⁺ + H₂O
Other name(s): MICAL (gene name)
Systematic name: [F-actin]-L-methionine,NADPH:O₂ *S*-oxidoreductase
Comments: The enzyme, characterized from the fruit fly *Drosophila melanogaster*, is a multi-domain oxidoreductase that acts as an F-actin disassembly factor. The enzyme selectively reduces two L-Met residues of F-actin, causing fragmentation of the filaments and preventing repolymerization [1613]. Free methionine is not a substrate [1611]. The reaction is stereospecific and generates the (*R*)-sulfoxide [1612]. In the absence of substrate, the enzyme can act as an NAD(P)H oxidase (EC 1.6.3.1) [4494, 4048].
References: [1613, 1611, 1612, 4494, 4048]

[EC 1.14.13.225 created 2016]

EC 1.14.13.226

- Accepted name:** acetone monoxygenase (methyl acetate-forming)
Reaction: acetone + NADPH + H⁺ + O₂ = methyl acetate + NADP⁺ + H₂O
Other name(s): *acmA* (gene name)
Systematic name: acetone,NADPH:oxygen oxidoreductase (methyl acetate-forming)
Comments: Contains FAD. The enzyme, characterized from the bacterium *Gordonia* sp. TY-5, is a Baeyer-Villiger type monoxygenase and participates in a propane utilization pathway.
References: [2042]

[EC 1.14.13.226 created 2016]

EC 1.14.13.227

Accepted name: propane 2-monooxygenase
Reaction: propane + NADH + H⁺ + O₂ = propan-2-ol + NAD⁺ + H₂O
Other name(s): prmABCD (gene names)
Systematic name: propane,NADH:oxygen oxidoreductase (2-hydroxylating)
Comments: The enzyme, characterized from several bacterial strains, is a multicomponent dinuclear iron monooxygenase that includes a hydroxylase, an NADH-dependent reductase, and a coupling protein. The enzyme has several additional activities, including acetone monooxygenase (acetol-forming) and phenol 4-monooxygenase.
References: [2041, 3464, 1125]

[EC 1.14.13.227 created 2016]

EC 1.14.13.228

Accepted name: jasmonic acid 12-hydroxylase
Reaction: (–)-jasmonate + NADPH + H⁺ + O₂ = *trans*-12-hydroxyjasmonate + NADP⁺ + H₂O
Other name(s): ABM (gene name)
Systematic name: jasmonate,NADPH:oxygen oxidoreductase (12-hydroxylating)
Comments: Although believed to occur in plants, the enzyme has so far been characterized only from the rice blast fungus, *Magnaporthe oryzae*. The fungus strategically deploys the enzyme to hydroxylate and inactivate endogenous jasmonate to evade the jasmonate-based innate immunity in rice plants.
References: [2962]

[EC 1.14.13.228 created 2016]

EC 1.14.13.229

Accepted name: *tert*-butyl alcohol monooxygenase
Reaction: *tert*-butyl alcohol + NADPH + H⁺ + O₂ = 2-methylpropane-1,2-diol + NADP⁺ + H₂O
Other name(s): *mdpJK* (gene names); *tert*-butanol monooxygenase
Systematic name: *tert*-butyl alcohol,NADPH:oxygen oxidoreductase
Comments: The enzyme, characterized from the bacterium *Aquicola tertiaricarbonis*, is a Rieske nonheme mononuclear iron oxygenase. It can also act, with lower efficiency, on propan-2-ol, converting it to propane-1,2-diol. Depending on the substrate, the enzyme also catalyses EC 1.14.19.48, *tert*-amyl alcohol desaturase.
References: [3347, 3406]

[EC 1.14.13.229 created 2016]

EC 1.14.13.230

Accepted name: butane monooxygenase (soluble)
Reaction: butane + NADH + H⁺ + O₂ = butan-1-ol + NAD⁺ + H₂O
Other name(s): sBMO; bmoBCDXYZ (gene names)
Systematic name: butane,NADH:oxygen oxidoreductase
Comments: The enzyme, characterized from the bacterium *Thauera butanivorans*, is similar to EC 1.14.13.25, methane monooxygenase (soluble), but has a very low activity with methane. It comprises three components - a carboxylate-bridged non-heme di-iron center-containing hydroxylase (made of three different subunits), a flavo-iron sulfur-containing NADH-oxidoreductase, and a small regulatory component protein. The enzyme can also act on other C₃-C₆ linear and branched aliphatic alkanes with lower activity.
References: [3552, 881, 864, 652]

[EC 1.14.13.230 created 2016]

EC 1.14.13.231

- Accepted name:** tetracycline 11a-monooxygenase
Reaction: tetracycline + NADPH + H⁺ + O₂ = 11a-hydroxytetracycline + NADP⁺ + H₂O
Other name(s): *tetX* (gene name)
Systematic name: tetracycline,NADPH:oxygen oxidoreductase (11a-hydroxylating)
Comments: A flavoprotein (FAD). This bacterial enzyme confers resistance to all clinically relevant tetracyclines when expressed under aerobic conditions. The hydroxylated products are very unstable and lead to intramolecular cyclization and non-enzymic breakdown to undefined products.
References: [4337, 2607, 4060]

[EC 1.14.13.231 created 2016]

EC 1.14.13.232

- Accepted name:** 6-methylpretetramide 4-monooxygenase
Reaction: 6-methylpretetramide + NADPH + H⁺ + O₂ = 4-hydroxy-6-methylpretetramide + NADP⁺ + H₂O
Systematic name: 6-methylpretetramide,NADPH:oxygen oxidoreductase (4-hydroxylating)
Comments: The enzyme, characterized from the bacterium *Streptomyces rimosus*, participates in the biosynthesis of tetracycline antibiotics. That bacterium possesses two enzymes that can catalyse the reaction - OxyE is the main isozyme, while OxyL has a lower activity. OxyL is bifunctional, and its main function is EC 1.14.13.233, 4-hydroxy-6-methylpretetramide 12a-monooxygenase. Contains FAD.
References: [4446, 4113]

[EC 1.14.13.232 created 2016]

EC 1.14.13.233

- Accepted name:** 4-hydroxy-6-methylpretetramide 12a-monooxygenase
Reaction: 4-hydroxy-6-methylpretetramide + NADPH + H⁺ + O₂ = 4-de(dimethylamino)-4-oxoanhydrotetracycline + NADP⁺ + H₂O
Other name(s): *oxyL* (gene name)
Systematic name: 4-hydroxy-6-methylpretetramide,NADPH:oxygen oxidoreductase (12a-hydroxylating)
Comments: Contains FAD. The enzyme, characterized from the bacterium *Streptomyces rimosus*, participates in the biosynthesis of tetracycline antibiotics. The enzyme is bifunctional, and can also catalyse EC 1.14.13.232, 6-methylpretetramide 4-monooxygenase.
References: [4446]

[EC 1.14.13.233 created 2016]

EC 1.14.13.234

- Accepted name:** 5a,11a-dehydrotetracycline 5-monooxygenase
Reaction: 5a,11a-dehydrotetracycline + NADPH + H⁺ + O₂ = 5a,11a-dehydroxytetracycline + NADP⁺ + H₂O
Other name(s): *oxyS* (gene name); 12-dehydrotetracycline 5-monooxygenase
Systematic name: 5a,11a-dehydrotetracycline,NADPH:oxygen oxidoreductase (5-hydroxylating)
Comments: The enzyme, characterized from the bacterium *Streptomyces rimosus*, is bifunctional, catalysing two successive monooxygenation reactions. It starts by catalysing the stereospecific hydroxylation of anhydrotetracycline at C-6 (EC 1.14.13.38). If the released product is captured by EC 1.3.98.4, 5a,11a-dehydrotetracycline dehydrogenase (OxyR), it is reduced to tetracycline. However, if the released product is recaptured by OxyS, it performs an additional hydroxylation at C-5, producing 5a,11a-dehydroxytetracycline, which, following the action of OxyR, becomes oxytetracycline.
References: [299, 2544, 4016, 4112]

[EC 1.14.13.234 created 2016]

EC 1.14.13.235

Accepted name: indole-3-acetate monooxygenase
Reaction: (indol-3-yl)acetate + NADH + H⁺ + O₂ = (2-hydroxy-1*H*-indol-3-yl)acetate + NAD⁺ + H₂O
Other name(s): *iacA* (gene name)
Systematic name: (indol-3-yl)acetate,NADH:oxygen oxidoreductase (2-hydroxylating)
Comments: The enzyme, characterized from *Pseudomonas putida* strains, catalyses the first step in a pathway for degradation of the plant hormone indole-3-acetate. When acting on indole, the enzyme forms indoxyl, which reacts spontaneously with oxygen to form the blue dye indigo.
References: [2210, 3418]

[EC 1.14.13.235 created 2017]

EC 1.14.13.236

Accepted name: toluene 4-monooxygenase
Reaction: toluene + NADH + H⁺ + O₂ = 4-methylphenol + NAD⁺ + H₂O
Other name(s): TMO
Systematic name: toluene,NADH:oxygen oxidoreductase (4-hydroxylating)
Comments: This bacterial enzyme belongs to a family of soluble diiron hydroxylases that includes toluene-, benzene-, xylene- and methane monooxygenases, phenol hydroxylases, and alkene epoxidases. The enzyme comprises a four-component complex that includes a hydroxylase, NADH-ferredoxin oxidoreductase, a Rieske-type [2Fe-2S] ferredoxin, and an effector protein.
References: [4193, 1475, 3410, 166, 1583]

[EC 1.14.13.236 created 2017]

EC 1.14.13.237

Accepted name: aliphatic glucosinolate *S*-oxygenase
Reaction: an ω-(methylsulfanyl)alkyl-glucosinolate + NADPH + H⁺ + O₂ = an ω-(methylsulfinyl)alkyl-glucosinolate + NADP⁺ + H₂O
Other name(s): ω-(methylthio)alkylglucosinolate *S*-oxygenase; GS-OX1 (gene name); ω-(methylthio)alkyl-glucosinolate,NADPH:oxygen *S*-oxidoreductase
Systematic name: ω-(methylsulfanyl)alkyl-glucosinolate,NADPH:oxygen *S*-oxidoreductase
Comments: The enzyme is a member of the flavin-dependent monooxygenase (FMO) family (*cf.* EC 1.14.13.8). The plant *Arabidopsis thaliana* contains five isoforms. GS-OX1 through GS-OX4 are able to catalyse the *S*-oxygenation independent of chain length, while GS-OX5 is specific for 8-(methylsulfanyl)octyl glucosinolate.
References: [1372, 2226]

[EC 1.14.13.237 created 2017]

EC 1.14.13.238

Accepted name: dimethylamine monooxygenase
Reaction: dimethylamine + NADPH + H⁺ + O₂ = methylamine + formaldehyde + NADP⁺ + H₂O
Other name(s): *dmmABC* (gene names)
Systematic name: dimethylamine,NADPH:oxygen oxidoreductase (formaldehyde-forming)
Comments: The enzyme, characterized from several bacterial species, is involved in a pathway for the degradation of methylated amines. It is composed of three subunits, one of which is a ferredoxin, and contains heme iron and an FMN cofactor.
References: [903, 901, 53, 2246]

[EC 1.14.13.238 created 2017]

EC 1.14.13.239

Accepted name: carnitine monooxygenase

Reaction: L-carnitine + NAD(P)H + H⁺ + O₂ = (3*R*)-3-hydroxy-4-oxobutanoate + trimethylamine + NAD(P)⁺ + H₂O

Other name(s): *cntAB* (gene names); *yeaWX* (gene names)

Systematic name: L-carnitine,NAD(P)H:oxygen oxidoreductase (trimethylamine-forming)

Comments: The bacterial enzyme is a complex consisting of a reductase and an oxygenase components. The reductase subunit contains a flavin and a plant-type ferredoxin [2Fe-2S] cluster, while the oxygenase subunit is a Rieske-type protein in which a [2Fe-2S] cluster is coordinated by two histidine and two cysteine residues.

References: [834, 4484, 1996]

[EC 1.14.13.239 created 2017]

EC 1.14.13.240

Accepted name: 2-polyprenylphenol 6-hydroxylase

Reaction: 2-(*all-trans*-polyprenyl)phenol + NADPH + H⁺ + O₂ = 3-(*all-trans*-polyprenyl)benzene-1,2-diol + NADP⁺ + H₂O

Other name(s): *ubiI* (gene name); *ubiM* (gene name)

Systematic name: 2-(*all-trans*-polyprenyl)phenol,NADPH:oxygen oxidoreductase (6-hydroxylating)

Comments: Contains FAD. The enzyme from the bacterium *Escherichia coli* (UbiI) catalyses the first hydroxylation during the aerobic biosynthesis of ubiquinone. The enzyme from the bacterium *Neisseria meningitidis* (UbiM) can also catalyse the two additional hydroxylations that occur in the pathway (*cf.* EC 1.14.99.60, 3-demethoxyubiquinol 3-hydroxylase).

References: [564, 2977]

[EC 1.14.13.240 created 2018]

EC 1.14.13.241

Accepted name: 5-pyridoxate monooxygenase

Reaction: 3-hydroxy-4-hydroxymethyl-2-methylpyridine-5-carboxylate + NADPH + H⁺ + O₂ = 2-(acetamidomethylene)-3-(hydroxymethyl)succinate + NADP⁺

Other name(s): 5-pyridoxate,NADPH:oxygen oxidoreductase (decyclizing); 5-pyridoxate oxidase (misleading); 5-pyridoxate dioxygenase (incorrect)

Systematic name: 5-pyridoxate,NADPH:oxygen oxidoreductase (ring-opening)

Comments: Contains FAD. The enzyme, characterized from the bacterium *Arthrobacter* sp. Cr-7, participates in the degradation of pyridoxine (vitamin B₆). Although the enzyme was initially thought to be a dioxygenase, oxygen-tracer experiments have suggested that it is a monooxygenase, incorporating only one oxygen atom from molecular oxygen into the product. The second oxygen atom originates from a water molecule, which is regenerated during the reaction and thus does not show up in the reaction equation.

References: [3591, 2761, 531]

[EC 1.14.13.241 created 2018 (EC 1.14.12.5 created 1972, incorporated 2018)]

EC 1.14.13.242

Accepted name: 3-hydroxy-2-methylpyridine-5-carboxylate monooxygenase

Reaction: 3-hydroxy-2-methylpyridine-5-carboxylate + NAD(P)H + H⁺ + O₂ = 2-(acetamidomethylidene)succinate + NAD(P)⁺

Other name(s): MHPCO; 3-hydroxy-2-methylpyridine-5-carboxylate,NAD(P)H:oxygen oxidoreductase (decyclizing); methylhydroxypyridinecarboxylate oxidase (misleading); 2-methyl-3-hydroxypyridine 5-carboxylic acid dioxygenase (incorrect); methylhydroxypyridine carboxylate dioxygenase (incorrect); 3-hydroxy-3-methylpyridinecarboxylate dioxygenase [incorrect]; 3-hydroxy-2-methylpyridinecarboxylate dioxygenase (incorrect)

Systematic name: 3-hydroxy-2-methylpyridine-5-carboxylate,NAD(P)H:oxygen oxidoreductase (ring-opening)

Comments: Contains FAD. The enzyme, characterized from the bacteria *Pseudomonas* sp. MA-1 and *Mesorhizobium loti*, participates in the degradation of pyridoxine (vitamin B₆). Although the enzyme was initially thought to be a dioxygenase, oxygen-tracer experiments have shown that it is a monooxygenase, incorporating only one oxygen atom from molecular oxygen. The second oxygen atom that is incorporated into the product originates from a water molecule, which is regenerated during the reaction and thus does not show up in the reaction equation.

References: [3591, 532, 2891, 4407, 2481, 3886, 3885]

[EC 1.14.13.242 created 2018 (EC 1.14.12.4 created 1972, incorporated 2018)]

EC 1.14.14 With reduced flavin or flavoprotein as one donor, and incorporation of one atom of oxygen into the other donor

EC 1.14.14.1

Accepted name: unspecific monooxygenase
Reaction: RH + [reduced NADPH—hemoprotein reductase] + O₂ = ROH + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): microsomal monooxygenase; xenobiotic monooxygenase; aryl-4-monooxygenase; aryl hydrocarbon hydroxylase; microsomal *P*-450; flavoprotein-linked monooxygenase; flavoprotein monooxygenase; substrate, reduced-flavoprotein:oxygen oxidoreductase (RH-hydroxylating or -epoxidizing)
Systematic name: substrate,NADPH—hemoprotein reductase:oxygen oxidoreductase (RH-hydroxylating or -epoxidizing)
Comments: A group of *P*-450 heme-thiolate proteins, acting on a wide range of substrates including many xenobiotics, steroids, fatty acids, vitamins and prostaglandins; reactions catalysed include hydroxylation, epoxidation, *N*-oxidation, sulfoxidation, *N*-, *S*- and *O*-dealkylations, desulfation, deamination, and reduction of azo, nitro and *N*-oxide groups. Together with EC 1.6.2.4, NADPH—hemoprotein reductase, it forms a system in which two reducing equivalents are supplied by NADPH. Some of the reactions attributed to EC 1.14.15.3, alkane 1-monooxygenase, belong here.
References: [351, 1099, 1425, 1644, 1756, 2086, 2129, 2130, 2199, 2306, 2563, 2564, 2731, 2754, 3719, 3857, 3868]

[EC 1.14.14.1 created 1961 as EC 1.99.1.1, transferred 1965 to EC 1.14.1.1, transferred 1972 to EC 1.14.14.1 (EC 1.14.14.2 created 1972, incorporated 1976, EC 1.14.99.8 created 1972, incorporated 1984), modified 2015]

[1.14.14.2 Deleted entry. benzopyrene 3-monooxygenase. Now included with EC 1.14.14.1 unspecific monooxygenase]

[EC 1.14.14.2 created 1972, deleted 1976]

EC 1.14.14.3

Accepted name: bacterial luciferase
Reaction: a long-chain aldehyde + FMNH₂ + O₂ = a long-chain fatty acid + FMN + H₂O + *hν*
Other name(s): aldehyde monooxygenase; luciferase; *Vibrio fischeri* luciferase; alkanal, reduced-FMN:oxygen oxidoreductase (1-hydroxylating, luminescing); alkanal, FMNH₂:oxygen oxidoreductase (1-hydroxylating, luminescing); alkanal monooxygenase (FMN); aldehyde, FMNH₂:oxygen oxidoreductase (1-hydroxylating, luminescing)
Systematic name: long-chain-aldehyde, FMNH₂:oxygen oxidoreductase (1-hydroxylating, luminescing)
Comments: The reaction sequence starts with the incorporation of a molecule of oxygen into reduced FMN bound to the enzyme, forming luciferase peroxyflavin. The peroxyflavin interacts with an aliphatic long-chain aldehyde, producing a highly fluorescent species believed to be luciferase hydroxyflavin. The enzyme is highly specific for reduced FMN and for long-chain aliphatic aldehydes with eight carbons or more. The highest efficiency is achieved with tetradecanal. *cf.* EC 1.13.12.18, dinoflagellate luciferase.
References: [1414, 1413, 1415, 2753, 3750, 2089]

[EC 1.14.14.3 created 1981, modified 2016]

[1.14.14.4 Deleted entry. choline monooxygenase. Identical to EC 1.14.15.7]

[EC 1.14.14.4 created 2000, deleted 2002]

EC 1.14.14.5

Accepted name: alkanesulfonate monooxygenase
Reaction: an alkanesulfonate + FMNH₂ + O₂ = an aldehyde + FMN + sulfite + H₂O
Other name(s): SsuD; sulfate starvation-induced protein 6; alkanesulfonate, reduced-FMN: oxygen oxidoreductase
Systematic name: alkanesulfonate, FMNH₂: oxygen oxidoreductase
Comments: The enzyme from *Escherichia coli* catalyses the desulfonation of a wide range of aliphatic sulfonates (unsubstituted C₁- to C₁₄-sulfonates as well as substituted C₂-sulfonates). Does not desulfonate taurine (2-aminoethanesulfonate) or aromatic sulfonates. Does not use FMN as a bound cofactor. Instead, it uses reduced FMN (i.e., FMNH₂) as a substrate. FMNH₂ is provided by SsuE, the associated FMN reductase (EC 1.5.1.38).
References: [930]

[EC 1.14.14.5 created 2002]

[1.14.14.6 Transferred entry. methanesulfonate monooxygenase. Now EC 1.14.13.111, methanesulfonate monooxygenase. Formerly thought to involve FMNH₂ but now shown to use NADH.]

[EC 1.14.14.6 created 2009, deleted 2010]

[1.14.14.7 Transferred entry. tryptophan 7-halogenase. As oxygen is completely reduced to H₂O and is not incorporated into the donor chloride, the enzyme has been transferred to EC 1.14.19.9, tryptophan 7-halogenase]

[EC 1.14.14.7 created 2009, deleted 2014]

EC 1.14.14.8

Accepted name: anthranilate 3-monooxygenase (FAD)
Reaction: anthranilate + FADH₂ + O₂ = 3-hydroxyanthranilate + FAD + H₂O
Other name(s): anthranilate 3-hydroxylase; anthranilate hydroxylase
Systematic name: anthranilate, FADH₂: oxygen oxidoreductase (3-hydroxylating)
Comments: This enzyme, isolated from the bacterium *Geobacillus thermodenitrificans*, participates in the pathway of tryptophan degradation. The enzyme is part of a system that also includes a bifunctional riboflavin kinase/FMN adenylyltransferase and an FAD reductase, which ensures ample supply of FAD to the monooxygenase.
References: [2285]

[EC 1.14.14.8 created 2010]

EC 1.14.14.9

Accepted name: 4-hydroxyphenylacetate 3-monooxygenase
Reaction: 4-hydroxyphenylacetate + FADH₂ + O₂ = 3,4-dihydroxyphenylacetate + FAD + H₂O
Other name(s): *p*-hydroxyphenylacetate 3-hydroxylase; 4-hydroxyphenylacetic acid-3-hydroxylase; *p*-hydroxyphenylacetate hydroxylase (FAD); 4 HPA 3-hydroxylase; *p*-hydroxyphenylacetate 3-hydroxylase (FAD); HpaB
Systematic name: 4-hydroxyphenylacetate, FADH₂: oxygen oxidoreductase (3-hydroxylating)
Comments: The enzyme from *Escherichia coli* attacks a broad spectrum of phenolic compounds. The enzyme uses FADH₂ as a substrate rather than a cofactor [4291]. FADH₂ is provided by EC 1.5.1.36, flavin reductase (NADH) [1141, 2302].
References: [12, 3064, 3063, 4291, 1141, 2302]

[EC 1.14.14.9 created 1972 as EC 1.14.13.3, transferred 2011 to EC 1.14.14.9]

EC 1.14.14.10

- Accepted name:** nitrilotriacetate monooxygenase
Reaction: nitrilotriacetate + FMNH₂ + H⁺ + O₂ = iminodiacetate + glyoxylate + FMN + H₂O
Systematic name: nitrilotriacetate,FMNH₂:oxygen oxidoreductase (glyoxylate-forming)
Comments: Requires Mg²⁺. The enzyme from *Aminobacter aminovorans* (previously *Chelatobacter heintzii*) is part of a two component system that also includes EC 1.5.1.42 (FMN reductase), which provides reduced flavin mononucleotide for this enzyme.
References: [3966, 1976, 4287]

[EC 1.14.14.10 created 2011]

EC 1.14.14.11

- Accepted name:** styrene monooxygenase
Reaction: styrene + FADH₂ + O₂ = (*S*)-2-phenyloxirane + FAD + H₂O
Other name(s): StyA; SMO; NSMOA
Systematic name: styrene,FADH₂:oxygen oxidoreductase
Comments: The enzyme catalyses the first step in the aerobic styrene degradation pathway. It forms a two-component system with a reductase (StyB) that utilizes NADH to reduce flavin-adenine dinucleotide, which is then transferred to the oxygenase.
References: [2912, 3897]

[EC 1.14.14.11 created 2011]

EC 1.14.14.12

- Accepted name:** 3-hydroxy-9,10-secoandrosta-1,3,5(10)-triene-9,17-dione monooxygenase
Reaction: 3-hydroxy-9,10-secoandrosta-1,3,5(10)-triene-9,17-dione + FMNH₂ + O₂ = 3,4-dihydroxy-9,10-secoandrosta-1,3,5(10)-triene-9,17-dione + FMN + H₂O
Other name(s): HsaA
Systematic name: 3-hydroxy-9,10-secoandrosta-1,3,5(10)-triene-9,17-dione,FMNH₂:oxygen oxidoreductase
Comments: This bacterial enzyme participates in the degradation of several steroids, including cholesterol and testosterone. It can use either FADH or FMNH₂ as flavin cofactor. The enzyme forms a two-component system with a reductase (HsaB) that utilizes NADH to reduce the flavin, which is then transferred to the oxygenase subunit.
References: [871]

[EC 1.14.14.12 created 2011]

EC 1.14.14.13

- Accepted name:** 4-(γ -L-glutamylamino)butanoyl-[BtrI acyl-carrier protein] monooxygenase
Reaction: 4-(γ -L-glutamylamino)butanoyl-[BtrI acyl-carrier protein] + FMNH₂ + O₂ = 4-(γ -L-glutamylamino)-(2*S*)-2-hydroxybutanoyl-[BtrI acyl-carrier protein] + FMN + H₂O
Other name(s): *btrO* (gene name)
Systematic name: 4-(γ -L-glutamylamino)butanoyl-[BtrI acyl-carrier protein],FMNH₂:oxygen oxidoreductase (2-hydroxylating)
Comments: Catalyses a step in the biosynthesis of the side chain of the aminoglycoside antibiotics of the butirosin family. FMNH₂ is used as a free cofactor. Forms a complex with a dedicated NAD(P)H:FMN oxidoreductase. The enzyme is not able to hydroxylate free substrates, activation by the acyl-carrier protein is mandatory. Octanoyl-*S*-[BtrI acyl-carrier protein] is also accepted.
References: [2238]

[EC 1.14.14.13 created 2012]

EC 1.14.14.14

Accepted name: aromatase

Reaction: (1) testosterone + 3 O₂ + 3 [reduced NADPH—hemoprotein reductase] = 17β-estradiol + formate + 4 H₂O + 3 [oxidized NADPH—hemoprotein reductase] (overall reaction)
 (1a) testosterone + O₂ + [reduced NADPH—hemoprotein reductase] = 19-hydroxytestosterone + H₂O + [oxidized NADPH—hemoprotein reductase]
 (1b) 19-hydroxytestosterone + O₂ + [reduced NADPH—hemoprotein reductase] = 19-oxotestosterone + 2 H₂O + [oxidized NADPH—hemoprotein reductase]
 (1c) 19-oxotestosterone + O₂ + [reduced NADPH—hemoprotein reductase] = 17β-estradiol + formate + H₂O + [oxidized NADPH—hemoprotein reductase]
 (2) androst-4-ene-3,17-dione + 3 O₂ + 3 [reduced NADPH—hemoprotein reductase] = estrone + formate + 4 H₂O + 3 [oxidized NADPH—hemoprotein reductase] (overall reaction)
 (2a) androst-4-ene-3,17-dione + O₂ + [reduced NADPH—hemoprotein reductase] = 19-hydroxyandrost-4-ene-3,17-dione + H₂O + [oxidized NADPH—hemoprotein reductase]
 (2b) 19-hydroxyandrost-4-ene-3,17-dione + O₂ + [reduced NADPH—hemoprotein reductase] = 19-oxo-androst-4-ene-3,17-dione + 2 H₂O + [oxidized NADPH—hemoprotein reductase]
 (2c) 19-oxoandrost-4-ene-3,17-dione + O₂ + [reduced NADPH—hemoprotein reductase] = estrone + formate + H₂O + [oxidized NADPH—hemoprotein reductase]

Other name(s): CYP19A1 (gene name); estrogen synthetase (incorrect)

Systematic name: testosteronol,NADPH—hemoprotein reductase:oxygen oxidoreductase (17β-estradiol-forming)

Comments: A cytochrome *P*-450. 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 17β-estradiol, respectively. The direct electron donor to the enzyme is EC 1.6.2.4, NADPH—hemoprotein reductase.

References: [3873, 1022, 1877, 1194]

[EC 1.14.14.14 created 2013]

EC 1.14.14.15

Accepted name: (3*S*)-3-amino-3-(3-chloro-4-hydroxyphenyl)propanoyl-[peptidyl-carrier protein SgcC2] monooxygenase

Reaction: (3*S*)-3-amino-3-(3-chloro-4-hydroxyphenyl)propanoyl-[peptidyl-carrier protein SgcC2] + FADH₂ + O₂ = (3*S*)-3-amino-3-(3-chloro-4,5-dihydroxyphenyl)propanoyl-[peptidyl-carrier protein SgcC2] + FAD + H₂O

Other name(s): SgcC

Systematic name: (3*S*)-3-amino-3-(3-chloro-4-hydroxyphenyl)propanoyl-[peptidyl-carrier protein SgcC2],FADH₂:oxygen oxidoreductase (5-hydroxylating)

Comments: The enzyme from the bacterium *Streptomyces globisporus* is involved in the biosynthesis of the (*S*)-3-chloro-5-hydroxy-β-tyrosine moiety prior to incorporation into the chromoprotein antitumor antibiotic C-1027.

References: [2257]

[EC 1.14.14.15 created 2014]

EC 1.14.14.16

Accepted name: steroid 21-monooxygenase

Reaction: a C₂₁ steroid + [reduced NADPH—hemoprotein reductase] + O₂ = a 21-hydroxy-C₂₁-steroid + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): steroid 21-hydroxylase; 21-hydroxylase; P450c21; CYP21A2 (gene name)

Systematic name: steroid,NADPH—hemoprotein reductase:oxygen oxidoreductase (21-hydroxylating)

Comments: A *P*-450 heme-thiolate protein responsible for the conversion of progesterone and 17α-hydroxyprogesterone to their respective 21-hydroxylated derivatives, 11-deoxycorticosterone and 11-deoxycortisol. Involved in the biosynthesis of the hormones aldosterone and cortisol. The electron donor is EC 1.6.2.4, NADPH—hemoprotein reductase.

References: [1437, 3019, 3267, 2018, 2416, 112]

[EC 1.14.14.16 created 1961 as EC 1.99.1.11, transferred 1965 to EC 1.14.1.8, transferred 1972 to EC 1.14.99.10, modified 2013, transferred 2015 to EC 1.14.14.16]

EC 1.14.14.17

Accepted name: squalene monooxygenase
Reaction: squalene + [reduced NADPH—hemoprotein reductase] + O₂ = (3*S*)-2,3-epoxy-2,3-dihydrosqualene + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): squalene epoxidase; squalene-2,3-epoxide cyclase; squalene 2,3-oxidocyclase; squalene hydroxylase; squalene oxydocyclase; squalene-2,3-epoxidase
Systematic name: squalene,NADPH—hemoprotein:oxygen oxidoreductase (2,3-epoxidizing)
Comments: A flavoprotein (FAD). This enzyme, together with EC 5.4.99.7, lanosterol synthase, was formerly known as squalene oxidocyclase. The electron donor is EC 1.6.2.4, NADPH—hemoprotein reductase [2890, 621].
References: [661, 3836, 4011, 4317, 2890, 3322, 621, 1446]

[EC 1.14.14.17 created 1961 as EC 1.99.1.13, transferred 1965 to EC 1.14.1.3, part transferred 1972 to EC 1.14.99.7, transferred 2011 to EC 1.14.13.132, transferred 2015 to EC 1.14.14.17]

EC 1.14.14.18

Accepted name: heme oxygenase (biliverdin-producing)
Reaction: protoheme + 3 [reduced NADPH—hemoprotein reductase] + 3 O₂ = biliverdin + Fe²⁺ + CO + 3 [oxidized NADPH—hemoprotein reductase] + 3 H₂O
Other name(s): ORP33 proteins; haem oxygenase (ambiguous); heme oxygenase (deacyclizing) (ambiguous); heme oxidase (ambiguous); haem oxidase (ambiguous); heme oxygenase (ambiguous); heme,hydrogen-donor:oxygen oxidoreductase (α -methene-oxidizing, hydroxylating)
Systematic name: protoheme,NADPH—hemoprotein reductase:oxygen oxidoreductase (α -methene-oxidizing, hydroxylating)
Comments: This mammalian enzyme participates in the degradation of heme. The terminal oxygen atoms that are incorporated into the carbonyl groups of pyrrole rings A and B of biliverdin are derived from two separate oxygen molecules [2810]. The third oxygen molecule provides the oxygen atom that converts the α -carbon to CO. The enzyme requires NAD(P)H and EC 1.6.2.4, NADPH—hemoprotein reductase. *cf.* EC 1.14.15.20, heme oxygenase (biliverdin-producing, ferredoxin).
References: [2375, 3738, 4380, 2810, 2111]

[EC 1.14.14.18 created 1972 as EC 1.14.99.3, modified 2006, transferred 2015 to EC 1.14.14.18, modified 2016]

EC 1.14.14.19

Accepted name: steroid 17 α -monooxygenase
Reaction: a C₂₁-steroid + [reduced NADPH—hemoprotein reductase] + O₂ = a 17 α -hydroxy-C₂₁-steroid + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): steroid 17 α -hydroxylase; cytochrome *P*-450 17 α ; cytochrome *P*-450 (*P*-450 17 α ,lyase); 17 α -hydroxylase-C17,20 lyase; CYP17; CYP17A1 (gene name)
Systematic name: steroid,NADPH—hemoprotein reductase:oxygen oxidoreductase (17 α -hydroxylating)
Comments: Requires NADPH and EC 1.6.2.4, NADPH—hemoprotein reductase. A microsomal hemeprotein that catalyses two independent reactions at the same active site - the 17 α -hydroxylation of pregnenolone and progesterone, which is part of glucocorticoid hormones biosynthesis, and the conversion of the 17 α -hydroxylated products via a 17,20-lyase reaction to form androstenedione and dehydroepiandrosterone, leading to sex hormone biosynthesis (EC 1.14.14.32, 17 α -hydroxyprogesterone deacetylase). The ratio of the 17 α -hydroxylase and 17,20-lyase activities is an important factor in determining the directions of steroid hormone biosynthesis towards biosynthesis of glucocorticoid or sex hormones.
References: [2326, 4377, 1205, 2014, 2970]

[EC 1.14.14.19 created 1961 as EC 1.99.1.9, transferred 1965 to EC 1.14.1.7, transferred 1972 to EC 1.14.99.9, modified 2013, transferred

EC 1.14.14.20

- Accepted name:** phenol 2-monooxygenase (FADH₂)
Reaction: phenol + FADH₂ + O₂ = catechol + FAD + H₂O
Other name(s): *pheA1* (gene name)
Systematic name: phenol,FADH₂:oxygen oxidoreductase (2-hydroxylating)
Comments: The enzyme catalyses the *ortho*-hydroxylation of simple phenols into the corresponding catechols. It accepts 4-methylphenol, 4-chlorophenol, and 4-fluorophenol [1937] as well as 4-nitrophenol, 3-nitrophenol, and resorcinol [3271]. The enzyme is part of a two-component system that also includes an NADH-dependent flavin reductase. It is strictly dependent on FADH₂ and does not accept FMNH₂ [1937, 3271]. *cf.* EC 1.14.13.7, phenol 2-monooxygenase (NADPH).
References: [1937, 3997, 3271]

[EC 1.14.14.20 created 2016]

EC 1.14.14.21

- Accepted name:** dibenzothiophene monooxygenase
Reaction: dibenzothiophene + 2 FMNH₂ + 2 O₂ = dibenzothiophene-5,5-dioxide + 2 FMN + 2 H₂O (overall reaction)
 (1a) dibenzothiophene + FMNH₂ + O₂ = dibenzothiophene-5-oxide + FMN + H₂O
 (1b) dibenzothiophene-5-oxide + FMNH₂ + O₂ = dibenzothiophene-5,5-dioxide + FMN + H₂O
Other name(s): *dszC* (gene name)
Systematic name: dibenzothiophene,FMNH₂:oxygen oxidoreductase
Comments: This bacterial enzyme catalyses the first two steps in the desulfurization pathway of dibenzothiophenes, the oxidation of dibenzothiophene into dibenzothiophene sulfone via dibenzothiophene-5-oxide. The enzyme forms a two-component system with a dedicated NADH-dependent FMN reductase (EC 1.5.1.42) encoded by the *dszD* gene, which also interacts with EC 1.14.14.22, dibenzothiophene sulfone monooxygenase.
References: [1266, 2284, 1306]

[EC 1.14.14.21 created 2016]

EC 1.14.14.22

- Accepted name:** dibenzothiophene sulfone monooxygenase
Reaction: dibenzothiophene-5,5-dioxide + 2 FMNH₂ + O₂ = 2'-hydroxybiphenyl-2-sulfinate + 2 FMN + H₂O
Other name(s): *dszA* (gene name)
Systematic name: dibenzothiophene-5,5-dioxide,FMNH₂:oxygen oxidoreductase
Comments: This bacterial enzyme catalyses a step in the desulfurization pathway of dibenzothiophenes. The enzyme forms a two-component system with a dedicated NADH-dependent FMN reductase (EC 1.5.1.42) encoded by the *dszD* gene, which also interacts with EC 1.14.14.21, dibenzothiophene monooxygenase.
References: [1266, 2852, 2023, 2851]

[EC 1.14.14.22 created 2016]

EC 1.14.14.23

- Accepted name:** cholesterol 7 α -monooxygenase
Reaction: cholesterol + [reduced NADPH—hemoprotein reductase] + O₂ = 7 α -hydroxycholesterol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): cholesterol 7 α -hydroxylase; CYP7A1 (gene name)
Systematic name: cholesterol,NADPH—hemoprotein reductase:oxygen oxidoreductase (7 α -hydroxylating)
Comments: A P-450 heme-thiolate liver protein that catalyses the first step in the biosynthesis of bile acids. The direct electron donor to the enzyme is EC 1.6.2.4, NADPH—hemoprotein reductase.

References: [2568, 373, 2843, 2778, 2777]

[EC 1.14.14.23 created 1976 as EC 1.14.13.17, transferred 2016 to EC 1.14.14.23]

EC 1.14.14.24

Accepted name: vitamin D 25-hydroxylase
Reaction: calcinol + O₂ + [reduced NADPH—hemoprotein reductase] = calcidiol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): vitamin D₂ 25-hydroxylase; vitamin D₃ 25-hydroxylase; CYP2R1
Systematic name: calcinol,NADPH—hemoprotein reductase:oxygen oxidoreductase (25-hydroxylating)
Comments: A microsomal enzyme isolated from human and mouse liver that bioactivates vitamin D₃. While multiple isoforms (CYP27A1, CYP2J2/3, CYP3A4, CYP2D25 and CYP2C11) are able to catalyse the reaction *in vitro*, only CYP2R1 is thought to catalyse the reaction in humans *in vivo* [4478]. The direct electron donor to the enzyme is EC 1.6.2.4, NADPH—hemoprotein reductase.
References: [581, 3514, 3690, 4478]

[EC 1.14.14.24 created 2012 as EC 1.14.13.159, transferred 2016 to EC 1.14.14.24]

EC 1.14.14.25

Accepted name: cholesterol 24-hydroxylase
Reaction: cholesterol + [reduced NADPH—hemoprotein reductase] + O₂ = (24S)-cholest-5-ene-3β,24-diol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): cholesterol 24-monooxygenase; CYP46; CYP46A1; cholesterol 24S-hydroxylase; cytochrome P450 46A1
Systematic name: cholesterol,NADPH—hemoprotein reductase:oxygen oxidoreductase (24-hydroxylating)
Comments: A P-450 heme-thiolate protein. The enzyme can also produce 25-hydroxycholesterol. In addition, it can further hydroxylate the product to 24,25-dihydroxycholesterol and 24,27-dihydroxycholesterol [333]. This reaction is the first step in the enzymic degradation of cholesterol in the brain as hydroxycholesterol can pass the blood—brain barrier whereas cholesterol cannot [2436]. The direct electron donor to the enzyme is EC 1.6.2.4, NADPH—hemoprotein reductase [2436].
References: [2318, 333, 2436, 2320, 3263]

[EC 1.14.14.25 created 2005 as EC 1.14.13.98, transferred 2016 to EC 1.14.14.25]

EC 1.14.14.26

Accepted name: 24-hydroxycholesterol 7α-hydroxylase
Reaction: (24S)-cholest-5-ene-3β,24-diol + [reduced NADPH—hemoprotein reductase] + O₂ = (24S)-cholest-5-ene-3β,7α,24-triol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): 24-hydroxycholesterol 7α-monooxygenase; CYP39A1; CYP39A1 oxysterol 7α-hydroxylase
Systematic name: (24S)-cholest-5-ene-3β,24-diol,NADPH—hemoprotein reductase:oxygen oxidoreductase (7α-hydroxylating)
Comments: A P-450 heme-thiolate protein that is found in liver microsomes and in ciliary non-pigmented epithelium [1631]. The enzyme is specific for (24S)-cholest-5-ene-3β,24-diol, which is formed mostly in the brain by EC 1.14.14.25, cholesterol 24-hydroxylase. The direct electron donor to the enzyme is EC 1.6.2.4, NADPH—hemoprotein reductase.
References: [2240, 1631, 3263]

[EC 1.14.14.26 created 2005 as EC 1.14.13.99, transferred 2016 to EC 1.14.14.26]

EC 1.14.14.27

Accepted name: resorcinol 4-hydroxylase (FADH₂)
Reaction: resorcinol + FADH₂ + O₂ = hydroxyquinol + FAD + H₂O
Other name(s): *graA* (gene name)

Systematic name: resorcinol,FADH₂:oxygen oxidoreductase (4-hydroxylating)
Comments: The enzyme, characterized from the bacterium *Rhizobium* sp. strain MTP-10005, uses FADH₂ as a substrate rather than a cofactor. FADH₂ is provided by a dedicated EC 1.5.1.36, flavin reductase (NADH). The enzyme participates in the degradation of γ -resorcyate and resorcinol. *cf.* EC 1.14.13.220, resorcinol 4-hydroxylase (NADH), and EC 1.14.13.219, resorcinol 4-hydroxylase (NADPH).
References: [2854, 4378]

[EC 1.14.14.27 created 2016]

EC 1.14.14.28

Accepted name: long-chain alkane monooxygenase
Reaction: a long-chain alkane + FMNH₂ + O₂ = a long-chain primary alcohol + FMN + H₂O
Systematic name: long-chain-alkane,FMNH₂:oxygen oxidoreductase
Comments: The enzyme, characterized from the bacterium *Geobacillus thermodenitrificans* NG80-2, is capable of converting alkanes ranging from C₁₅ to C₃₆ into their corresponding primary alcohols [996, 2228]. The FMNH₂ cofactor is provided by an FMN reductase [855].
References: [996, 2228, 855]

[EC 1.14.14.28 created 2016]

EC 1.14.14.29

Accepted name: 25/26-hydroxycholesterol 7 α -hydroxylase
Reaction: (1) cholest-5-ene-3 β ,25-diol + [reduced NADPH—hemoprotein reductase] + O₂ = cholest-5-ene-3 β ,7 α ,25-triol + [oxidized NADPH—hemoprotein reductase] + H₂O
(2) (25*R*)-cholest-5-ene-3 β ,26-diol + [reduced NADPH—hemoprotein reductase] + O₂ = (25*R*)-cholest-5-ene-3 β ,7 α ,26-triol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): 25-hydroxycholesterol 7 α -monooxygenase; CYP7B1; CYP7B1 oxysterol 7 α -hydroxylase; 27-hydroxycholesterol 7-monooxygenase; 27-hydroxycholesterol 7 α -hydroxylase; cholest-5-ene-3 β ,25-diol,NADPH:oxygen oxidoreductase (7 α -hydroxylating); 25-hydroxycholesterol 7 α -hydroxylase
Systematic name: cholest-5-ene-3 β ,25/26-diol,[NADPH—hemoprotein reductase]:oxygen oxidoreductase (7 α -hydroxylating)
Comments: A P-450 (heme-thiolate) protein. Unlike EC 1.14.14.26, 24-hydroxycholesterol 7 α -monooxygenase, which is specific for its oxysterol substrate, this enzyme can also metabolize the oxysterols 24,25-epoxycholesterol, 22-hydroxycholesterol and 24-hydroxycholesterol, but to a lesser extent [3903]. The direct electron donor to the enzyme is EC 1.6.2.4, NADPH—hemoprotein reductase.
References: [2074, 3903, 2240, 3167, 3263]

[EC 1.14.14.29 created 2005 as EC 1.14.13.100, modified 2013 (EC 1.14.13.60 created 1999, incorporated 2013), transferred 2016 to EC 1.14.14.29]

EC 1.14.14.30

Accepted name: isobutylamine *N*-monooxygenase
Reaction: (1) 2-methylpropan-1-amine + FADH₂ + O₂ = *N*-(2-methylpropyl)hydroxylamine + FAD + H₂O
(2) 2-methylpropan-1-amine + FMNH₂ + O₂ = *N*-(2-methylpropyl)hydroxylamine + FMN + H₂O
Other name(s): *vlmH* (gene name)
Systematic name: 2-methylpropan-1-amine,FADH₂:O₂ *N*-oxidoreductase
Comments: The enzyme, characterized from the bacterium *Streptomyces viridifaciens*, is part of a two component system that also includes a flavin reductase, which provides reduced flavin mononucleotide for this enzyme. The enzyme, which is involved in the biosynthesis of the azoxy antibiotic valanimycin, has a similar activity with either FMNH₂ or FADH₂. It exhibits broad specificity, and also accepts propan-1-amine, butan-1-amine, butan-2-amine and benzylamine.
References: [2945, 2946, 2944]

[EC 1.14.14.30 created 2016, modified 2017]

EC 1.14.14.31

- Accepted name:** ipsdienol synthase
Reaction: myrcene + [reduced NADPH—hemoprotein reductase] + O₂ = (*R*)-ipsdienol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): myrcene hydroxylase; CYP9T2; CYP9T3
Systematic name: myrcene,NADPH—hemoprotein reductase:O₂ oxidoreductase (hydroxylating)
Comments: A cytochrome *P*-450 heme-thiolate protein. Involved in the insect aggregation pheromone production. Isolated from the pine engraver beetle, *Ips pini*. A small amount of (*S*)-ipsdienol is also formed. *In vitro* it also hydroxylated (+)- and (–)- α -pinene, 3-carene, and (+)-limonene, but not α -phellandrene, (–)- β -pinene, γ -terpinene, or terpinolene.
References: [3307, 3581]

[EC 1.14.14.31 created 2015 as EC 1.14.13.207, transferred 2016 to EC 1.14.14.31]

EC 1.14.14.32

- Accepted name:** 17 α -hydroxyprogesterone deacetylase
Reaction: (1) 17 α -hydroxyprogesterone + [reduced NADPH—hemoprotein reductase] + O₂ = androstenedione + acetate + [oxidized NADPH—hemoprotein reductase] + H₂O
(2) 17 α -hydroxypregnenolone + [reduced NADPH—hemoprotein reductase] + O₂ = 3 β -hydroxyandrost-5-en-17-one + acetate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): C-17/C-20 lyase; 17 α -hydroxyprogesterone acetaldehyde-lyase; CYP17; CYP17A1 (gene name); 17 α -hydroxyprogesterone 17,20-lyase
Systematic name: 17 α -hydroxyprogesterone,NADPH—hemoprotein reductase:oxygen oxidoreductase (17 α -hydroxylating, acetate-releasing)
Comments: A microsomal cytochrome *P*-450 (heme-thiolate) protein that catalyses two independent reactions at the same active site - the 17-hydroxylation of pregnenolone and progesterone, which is part of glucocorticoid hormones biosynthesis (EC 1.14.14.19), and the conversion of the 17-hydroxylated products via a 17,20-lyase reaction to form androstenedione and 3 β -hydroxyandrost-5-en-17-one, leading to sex hormone biosynthesis. The activity of this reaction is dependent on the allosteric interaction of the enzyme with cytochrome *b*₅ without any transfer of electrons from the cytochrome [138, 3534]. The enzymes from different organisms differ in their substrate specificity. While the enzymes from pig, hamster, and rat accept both 17 α -hydroxyprogesterone and 17 α -hydroxypregnenolone, the enzymes from human, bovine, sheep, goat, and bison do not accept the former, and the enzyme from guinea pig does not accept the latter [1205].
References: [1205, 138, 2376, 3534, 293]

[EC 1.14.14.32 created 1976 as EC 4.1.2.30, transferred 2016 to EC 1.14.14.32]

EC 1.14.14.33

- Accepted name:** ethylenediaminetetraacetate monooxygenase
Reaction: ethylenediaminetetraacetate + 2 FMNH₂ + 2 O₂ = ethylenediamine-*N,N'*-diacetate + 2 glyoxylate + 2 FMN + 2 H₂O (overall reaction)
(1a) ethylenediaminetetraacetate + FMNH₂ + O₂ = ethylenediaminetriacetate + glyoxylate + FMN + H₂O
(1b) ethylenediaminetriacetate + FMNH₂ + O₂ = ethylenediamine-*N,N'*-diacetate + glyoxylate + FMN + H₂O
Systematic name: ethylenediaminetetraacetate,FMNH₂:O₂ oxidoreductase (glyoxylate-forming)
Comments: The enzyme is part of a two component system that also includes EC 1.5.1.42, FMN reductase (NADH), which provides reduced flavin mononucleotide for this enzyme. It acts on EDTA only when it is complexed with divalent cations such as Mg²⁺, Zn²⁺, Mn²⁺, Co²⁺, or Cu²⁺. While the enzyme has a substrate overlap with EC 1.14.14.10, nitrilotriacetate monooxygenase, it has a much wider substrate range, which includes nitrilotriacetate (NTA) and diethylenetriaminepentaacetate (DTPA) in addition to EDTA.

References: [4233, 2967, 336]

[EC 1.14.14.33 created 2016]

EC 1.14.14.34

Accepted name: methanesulfonate monooxygenase (FMNH₂)
Reaction: methanesulfonate + FMNH₂ + O₂ = formaldehyde + FMN + sulfite + H₂O
Other name(s): *msuD* (gene name); *ssuD* (gene name)
Systematic name: methanesulfonate,FMNH₂:oxygen oxidoreductase
Comments: The enzyme, characterized from *Pseudomonas* strains, allows the organisms to utilize methanesulfonate as their sulfur source. It acts in combination with a dedicated NADH-dependent FMN reductase (EC 1.5.1.42), which provides it with reduced FMN. *cf.* EC 1.14.13.111, methanesulfonate monooxygenase (NADH).
References: [1889, 948]

[EC 1.14.14.34 created 2016]

EC 1.14.14.35

Accepted name: dimethylsulfone monooxygenase
Reaction: dimethyl sulfone + FMNH₂ + O₂ = methanesulfinate + formaldehyde + FMN + H₂O
Other name(s): *sfnG* (gene name)
Systematic name: dimethyl sulfone,FMNH₂:oxygen oxidoreductase
Comments: The enzyme, characterized from *Pseudomonas* spp., is involved in a dimethyl sulfide degradation pathway. It is dependent on NAD(P)H-dependent FMN reductase (EC 1.5.1.38, EC 1.5.1.39, or EC 1.5.1.42), which provides it with reduced FMN. The product, methanesulfinate, is oxidized spontaneously to methanesulfonate in the presence of dioxygen and FMNH₂.
References: [947, 4203]

[EC 1.14.14.35 created 2016]

EC 1.14.14.36

Accepted name: tyrosine *N*-monooxygenase
Reaction: L-tyrosine + 2 O₂ + 2 [reduced NADPH—hemoprotein reductase] = (*E*)-[4-hydroxyphenylacetaldehyde oxime] + 2 [oxidized NADPH—hemoprotein reductase] + CO₂ + 3 H₂O (overall reaction)
(1a) L-tyrosine + O₂ + [reduced NADPH—hemoprotein reductase] = *N*-hydroxy-L-tyrosine + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) *N*-hydroxy-L-tyrosine + O₂ + [reduced NADPH—hemoprotein reductase] = *N,N*-dihydroxy-L-tyrosine + [oxidized NADPH—hemoprotein reductase] + H₂O
(1c) *N,N*-dihydroxy-L-tyrosine = (*E*)-[4-hydroxyphenylacetaldehyde oxime] + CO₂ + H₂O
Other name(s): tyrosine *N*-hydroxylase; CYP79A1
Systematic name: L-tyrosine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*N*-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme from *Sorghum* is involved in the biosynthesis of the cyanogenic glucoside dhurrin. In *Sinapis alba* (white mustard) the enzyme is involved in the biosynthesis of the glucosinolate sinalbin.
References: [1345, 3525, 259, 1801, 169, 2786, 460, 2060, 630]

[EC 1.14.14.36 created 1992 as EC 1.14.13.41, modified 2001, modified 2005, transferred 2016 to EC 1.14.14.36]

EC 1.14.14.37

Accepted name: 4-hydroxyphenylacetaldehyde oxime monooxygenase
Reaction: (*E*)-4-hydroxyphenylacetaldehyde oxime + [reduced NADPH—hemoprotein reductase] + O₂ = (*S*)-4-hydroxymandelonitrile + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)

(1a) (*E*)-4-hydroxyphenylacetaldehyde oxime = (*Z*)-4-hydroxyphenylacetaldehyde oxime
(1b) (*Z*)-4-hydroxyphenylacetaldehyde oxime = 4-hydroxyphenylacetonitrile + H₂O
(1c) 4-hydroxyphenylacetonitrile + [reduced NADPH—hemoprotein reductase] + O₂ = (*S*)-4-hydroxymandelonitrile + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): 4-hydroxybenzeneacetaldehyde oxime monooxygenase; cytochrome P450II-dependent monooxygenase; NADPH-cytochrome P450 reductase (CYP71E1); CYP71E1; 4-hydroxyphenylacetaldehyde oxime,NADPH:oxygen oxidoreductase
Systematic name: (*E*)-4-hydroxyphenylacetaldehyde oxime,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: This cytochrome *P*-450 (heme thiolate) enzyme is involved in the biosynthesis of the cyanogenic glucoside dhurrin in sorghum. It catalyses three different activities - isomerization of the (*E*) isomer to the (*Z*) isomer, dehydration, and C-hydroxylation.
References: [2344, 3494, 460, 2060, 630]

[EC 1.14.14.37 created 2000 as EC 1.14.13.68, modified 2005, transferred 2016 to EC 1.14.14.37]

EC 1.14.14.38

Accepted name: valine *N*-monooxygenase
Reaction: L-valine + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = (*E*)-2-methylpropanal oxime + 2 [oxidized NADPH—hemoprotein reductase] + CO₂ + 3 H₂O (overall reaction)
(1a) L-valine + [reduced NADPH—hemoprotein reductase] + O₂ = *N*-hydroxy-L-valine + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) *N*-hydroxy-L-valine + [reduced NADPH—hemoprotein reductase] + O₂ = *N,N*-dihydroxy-L-valine + [oxidized NADPH—hemoprotein reductase] + H₂O
(1c) *N,N*-dihydroxy-L-valine = (*E*)-2-methylpropanal oxime + CO₂ + H₂O
Other name(s): CYP79D1; CYP79D2
Systematic name: L-valine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*N*-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. This enzyme catalyses two successive *N*-hydroxylations of L-valine, the committed step in the biosynthesis of the cyanogenic glucoside linamarin in *Manihot esculenta* (cassava). The product of the two hydroxylations, *N,N*-dihydroxy-L-valine, is labile and undergoes dehydration and decarboxylation that produce the (*E*) isomer of the oxime. It is still not known whether the decarboxylation is spontaneous or catalysed by the enzyme. The enzyme can also accept L-isoleucine as substrate, with a lower activity. It is different from EC 1.14.14.39, isoleucine *N*-monooxygenase, which prefers L-isoleucine.
References: [80, 1040]

[EC 1.14.14.38 created 2010 as EC 1.14.13.118, transferred 2017 to EC 1.14.14.38]

EC 1.14.14.39

Accepted name: isoleucine *N*-monooxygenase
Reaction: L-isoleucine + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = (1*E*,2*S*)-2-methylbutanal oxime + 2 [oxidized NADPH—hemoprotein reductase] + CO₂ + 3 H₂O (overall reaction)
(1a) L-isoleucine + [reduced NADPH—hemoprotein reductase] + O₂ = *N*-hydroxy-L-isoleucine + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) *N*-hydroxy-L-isoleucine + [reduced NADPH—hemoprotein reductase] + O₂ = *N,N*-dihydroxy-L-isoleucine + [oxidized NADPH—hemoprotein reductase] + H₂O
(1c) *N,N*-dihydroxy-L-isoleucine = (1*E*,2*S*)-2-methylbutanal oxime + CO₂ + H₂O (spontaneous)
Other name(s): CYP79D3 (gene name); CYP79D4 (gene name)
Systematic name: L-isoleucine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*N*-hydroxylating)
Comments: This cytochrome *P*-450 (heme-thiolate) enzyme, found in plants, catalyses two successive *N*-hydroxylations of L-isoleucine, the committed step in the biosynthesis of the cyanogenic glucoside lotaustralin. The product of the two hydroxylations, *N,N*-dihydroxy-L-isoleucine, is labile and undergoes dehydration followed by decarboxylation, producing the oxime. It is still not known whether the decarboxylation is spontaneous or catalysed by the enzyme. The enzyme can also accept L-valine, but with a lower activity. *cf.* EC 1.14.14.38, valine *N*-monooxygenase.

References: [80, 1040]

[EC 1.14.14.39 created 2010 as EC 1.14.13.117, transferred 2017 to EC 1.14.14.39]

EC 1.14.14.40

Accepted name: phenylalanine *N*-monooxygenase
Reaction: L-phenylalanine + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = (*E*)-phenylacetaldoxime + 2 [oxidized NADPH—hemoprotein reductase] + CO₂ + 3 H₂O (overall reaction)
(1a) L-phenylalanine + [reduced NADPH—hemoprotein reductase] + O₂ = *N*-hydroxy-L-phenylalanine + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) *N*-hydroxy-L-phenylalanine + [reduced NADPH—hemoprotein reductase] + O₂ = *N,N*-dihydroxy-L-phenylalanine + [oxidized NADPH—hemoprotein reductase] + H₂O
(1c) *N,N*-dihydroxy-L-phenylalanine = (*E*)-phenylacetaldoxime + CO₂ + H₂O
Other name(s): phenylalanine *N*-hydroxylase; CYP79A2 (gene name); CYP79D16 (gene name)
Systematic name: L-phenylalanine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*N*-hydroxylating)
Comments: This cytochrome *P*-450 (heme-thiolate) enzyme, found in plants, catalyses two successive *N*-hydroxylations of L-phenylalanine, a committed step in the biosynthesis of benzylglucosinolate and the cyanogenic glucosides (*R*)-prunasin and (*R*)-amygdalin. The product of the two hydroxylations, *N,N*-dihydroxy-L-phenylalanine, is labile and undergoes dehydration followed by decarboxylation, producing an oxime. It is still not known whether the decarboxylation is spontaneous or catalysed by the enzyme.
References: [4234, 4310]

[EC 1.14.14.40 created 2011 as EC 1.14.13.124, transferred 2017 to EC 1.14.14.40]

EC 1.14.14.41

Accepted name: (*E*)-2-methylbutanal oxime monooxygenase
Reaction: (1) (*E*)-2-methylbutanal oxime + [reduced NADPH—hemoprotein reductase] + O₂ = 2-hydroxy-2-methylbutanenitrile + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(1a) (*E*)-2-methylbutanal oxime = (*Z*)-2-methylbutanal oxime
(1b) (*Z*)-2-methylbutanal oxime = 2-methylbutanenitrile + H₂O
(1c) 2-methylbutanenitrile + [reduced NADPH—hemoprotein reductase] + O₂ = 2-hydroxy-2-methylbutanenitrile + [oxidized NADPH—hemoprotein reductase] + H₂O
(2) (*E*)-2-methylpropanal oxime + [reduced NADPH—hemoprotein reductase] + O₂ = 2-hydroxy-2-methylpropanenitrile + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(2a) (*E*)-2-methylpropanal oxime = (*Z*)-2-methylpropanal oxime
(2b) (*Z*)-2-methylpropanal oxime = 2-methylpropanenitrile + H₂O
(2c) 2-methylpropanenitrile + [reduced NADPH—hemoprotein reductase] + O₂ = 2-hydroxy-2-methylpropanenitrile + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP71E7 (gene name)
Systematic name: (*E*)-2-methylbutanal oxime,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: This cytochrome *P*-450 (heme thiolate) enzyme is involved in the biosynthesis of the cyanogenic glucosides lotaustralin and linamarin. It catalyses three different activities - isomerization of its substrate, the (*E*) isomer, to the (*Z*) isomer, dehydration, and C-hydroxylation.
References: [1774]

[EC 1.14.14.41 created 2017]

EC 1.14.14.42

Accepted name: homomethionine *N*-monooxygenase
Reaction: an L-polyhomomethionine + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = an (*E*)- ω -(methylsulfanyl)alkanal oxime + 2 [oxidized NADPH—hemoprotein reductase] + CO₂ + 3 H₂O (overall reaction)

(1a) an L-polyhomomethionine + [reduced NADPH—hemoprotein reductase] + O₂ = an L-*N*-hydroxypolyhomomethionine + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) an L-*N*-hydroxypolyhomomethionine + [reduced NADPH—hemoprotein reductase] + O₂ = an L-*N,N*-dihydroxypolyhomomethionine + [oxidized NADPH—hemoprotein reductase] + H₂O

(1c) an L-*N,N*-dihydroxypolyhomomethionine = an (*E*)-ω-(methylsulfanyl)alkanal oxime + CO₂ + H₂O

Other name(s): CYP79F1 (gene name); CYP79F2 (gene name)
Systematic name: L-polyhomomethionine,[NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: This plant cytochrome *P*-450 (heme thiolate) enzyme is involved in methionine-derived aliphatic glucosinolates biosynthesis. It catalyses two successive *N*-hydroxylations, which are followed by dehydration and decarboxylation. CYP79F1 from *Arabidopsis thaliana* can metabolize mono-, di-, tri-, tetra-, penta-, and hexahomomethionine to their corresponding aldoximes, while CYP79F2 from the same plant can only metabolize penta- and hexahomomethionine.
References: [1373, 575]

[EC 1.14.14.42 created 2017]

EC 1.14.14.43

Accepted name: (methylsulfanyl)alkanaldoxime *N*-monooxygenase
Reaction: an (*E*)-ω-(methylsulfanyl)alkanal oxime + [reduced NADPH—hemoprotein reductase] + glutathione + O₂ = an *S*-[(1*E*)-1-(hydroxyimino)-ω-(methylsulfanyl)alkyl]-L-glutathione + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(1a) an (*E*)-ω-(methylsulfanyl)alkanal oxime + [reduced NADPH—hemoprotein reductase] + O₂ = a 1-(methylsulfanyl)-4-*aci*-nitroalkane + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) a 1-(methylsulfanyl)-4-*aci*-nitroalkane + glutathione = an *S*-[(1*E*)-1-(hydroxyimino)-ω-(methylsulfanyl)alkyl]-L-glutathione + H₂O
Other name(s): CYP83A1 (gene name); (methylthio)alkanaldoxime *N*-monooxygenase; (*E*)-ω-(methylthio)alkanaldoxime,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*N*-hydroxylating)
Systematic name: (*E*)-ω-(methylsulfanyl)alkanaldoxime,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*N*-hydroxylating)
Comments: This cytochrome *P*-450 (heme thiolate) enzyme is involved in the biosynthesis of glucosinolates in plants. The enzyme catalyses an *N*-hydroxylation of the *E* isomer of ω-(methylsulfanyl)alkanal oximes, forming an *aci*-nitro intermediate that reacts non-enzymically with glutathione to produce an *N*-alkyl-thiohydroximate adduct, the committed precursor of glucosinolates. In the absence of a thiol compound, the enzyme is suicidal, probably due to interaction of the reactive *aci*-nitro intermediate with active site residues.
References: [170, 2745, 630]

[EC 1.14.14.43 created 2017]

EC 1.14.14.44

Accepted name: phenylacetaldehyde oxime monooxygenase
Reaction: (*E*)-phenylacetaldehyde oxime + [reduced NADPH—hemoprotein reductase] + O₂ = (*R*)-mandelonitrile + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(1a) (*E*)-phenylacetaldehyde oxime = (*Z*)-phenylacetaldehyde oxime
(1b) (*Z*)-phenylacetaldehyde oxime = phenylacetone + H₂O
(1c) phenylacetone + [reduced NADPH—hemoprotein reductase] + O₂ = (*R*)-mandelonitrile + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP71AN24 (gene name)
Systematic name: (*E*)-phenylacetaldehyde oxime,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: This cytochrome *P*-450 (heme-thiolate) enzyme is involved in the biosynthesis of the cyanogenic glucosides (*R*)-prunasin and (*R*)-amygdalin. It catalyses three different activities - isomerization of the (*E*) isomer to the (*Z*) isomer, dehydration, and C-hydroxylation.
References: [4310]

[EC 1.14.14.44 created 2017]

EC 1.14.14.45

- Accepted name:** aromatic aldoxime *N*-monooxygenase
- Reaction:** (1) (*E*)-indol-3-ylacetaldehyde oxime + [reduced NADPH—hemoprotein reductase] + glutathione + O₂ = *S*-[(*E*)-*N*-hydroxy(indol-3-yl)acetimidoyl]-L-glutathione + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(1a) (*E*)-indol-3-ylacetaldehyde oxime + [reduced NADPH—hemoprotein reductase] + O₂ = 1-(1*H*-indol-3-yl)-2-*aci*-nitroethane + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) 1-(1*H*-indol-3-yl)-2-*aci*-nitroethane + glutathione = *S*-[(*E*)-*N*-hydroxy(indol-3-yl)acetimidoyl]-L-glutathione + H₂O (spontaneous)
(2) (*E*)-phenylacetaldehyde oxime + [reduced NADPH—hemoprotein reductase] + glutathione + O₂ = *S*-[(*Z*)-*N*-hydroxy(phenyl)acetimidoyl]-L-glutathione + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(2a) (*E*)-phenylacetaldehyde oxime + [reduced NADPH—hemoprotein reductase] + O₂ = 1-*aci*-nitro-2-phenylethane + [oxidized NADPH—hemoprotein reductase] + H₂O
(2b) 1-*aci*-nitro-2-phenylethane + glutathione = *S*-[(*Z*)-*N*-hydroxy(phenyl)acetimidoyl]-L-glutathione + H₂O (spontaneous)
- Other name(s):** CYP83B1 (gene name)
- Systematic name:** (*E*)-indol-3-ylacetaldoxime,[reduced NADPH—hemoprotein reductase],glutathione:oxygen oxidoreductase (oxime-hydroxylating)
- Comments:** This cytochrome *P*-450 (heme thiolate) enzyme is involved in the biosynthesis of glucosinolates in plants. The enzyme catalyses the *N*-hydroxylation of aromatic aldoximes derived from L-tryptophan, L-phenylalanine, and L-tyrosine, forming an *aci*-nitro intermediate that reacts non-enzymically with glutathione to produce an *N*-alkyl-thiohydroximate adduct, the committed precursor of glucosinolates. In the absence of glutathione, the enzyme is suicidal, probably due to interaction of the reactive *aci*-nitro compound with catalytic residues in the active site.
- References:** [170, 2745, 1191]

[EC 1.14.14.45 created 2017]

EC 1.14.14.46

- Accepted name:** pimeloyl-[acyl-carrier protein] synthase
- Reaction:** a long-chain acyl-[acyl-carrier protein] + 2 reduced flavodoxin + 3 O₂ = pimeloyl-[acyl-carrier protein] + an *n*-alkanal + 2 oxidized flavodoxin + 3 H₂O (overall reaction)
(1a) a long-chain acyl-[acyl-carrier protein] + reduced flavodoxin + O₂ = a (*7S*)-7-hydroxy-long-chain-acyl-[acyl-carrier protein] + oxidized flavodoxin + H₂O
(1b) a (*7S*)-7-hydroxy-long-chain-acyl-[acyl-carrier protein] + reduced flavodoxin + O₂ = a (*7R,8R*)-7,8-dihydroxy-long-chain-acyl-[acyl-carrier protein] + oxidized flavodoxin + H₂O
(1c) a (*7R,8R*)-7,8-dihydroxy-long-chain-acyl-[acyl-carrier protein] + reduced flavodoxin + O₂ = a 7-oxoheptanoyl-[acyl-carrier protein] + an *n*-alkanal + oxidized flavodoxin + 2 H₂O
(1d) a 7-oxoheptanoyl-[acyl-carrier protein] + oxidized flavodoxin + H₂O = a pimeloyl-[acyl-carrier protein] + reduced flavodoxin + H⁺
- Other name(s):** *bioI* (gene name); P450BioI; CYP107H1
- Systematic name:** acyl-[acyl-carrier protein],reduced-flavodoxin:oxygen oxidoreductase (pimeloyl-[acyl-carrier protein] forming)
- Comments:** A cytochrome *P*-450 (heme-thiolate) protein. The enzyme catalyses an oxidative C-C bond cleavage of long-chain acyl-[acyl-carrier protein]s of various lengths to generate pimeloyl-[acyl-carrier protein], an intermediate in the biosynthesis of biotin. The preferred substrate of the enzyme from the bacterium *Bacillus subtilis* is palmitoyl-[acyl-carrier protein] which then gives heptanal as the alkanal. The mechanism is similar to EC 1.14.15.6, cholesterol monooxygenase (side-chain-cleaving), followed by a hydroxylation step, which may occur spontaneously [702].
- References:** [3661, 702, 701, 699]

[EC 1.14.14.46 created 2013 as EC 1.14.15.12, transferred 2017 to EC 1.14.14.46]

EC 1.14.14.47

- Accepted name:** nitric-oxide synthase (flavodoxin)
Reaction: $2 \text{ L-arginine} + 3 \text{ reduced flavodoxin} + 4 \text{ O}_2 = 2 \text{ L-citrulline} + 2 \text{ nitric oxide} + 3 \text{ oxidized flavodoxin} + 4 \text{ H}_2\text{O}$ (overall reaction)
(1a) $2 \text{ L-arginine} + 2 \text{ reduced flavodoxin} + 2 \text{ O}_2 = 2 \text{ N}^{\omega}\text{-hydroxy-L-arginine} + 2 \text{ oxidized flavodoxin} + 2 \text{ H}_2\text{O}$
(1b) $2 \text{ N}^{\omega}\text{-hydroxy-L-arginine} + \text{reduced flavodoxin} + 2 \text{ O}_2 = 2 \text{ L-citrulline} + 2 \text{ nitric oxide} + \text{oxidized flavodoxin} + 2 \text{ H}_2\text{O}$
- Other name(s):** nitric oxide synthetase (ambiguous); NO synthase (ambiguous)
Systematic name: L-arginine, reduced-flavodoxin:oxygen oxidoreductase (nitric-oxide-forming)
Comments: Binds heme (iron protoporphyrin IX) and tetrahydrobiopterin. The enzyme, found in bacteria and archaea, consist of only an oxygenase domain and functions together with bacterial ferredoxins or flavodoxins. The orthologous enzymes from plants and animals also contain a reductase domain and use only NADPH as the electron donor (*cf.* EC 1.14.13.39).
References: [2934, 17, 4128, 28, 1539]

[EC 1.14.14.47 created 2012 as EC 1.14.13.165, transferred 2017 to EC 1.14.14.47]

EC 1.14.14.48

- Accepted name:** jasmonoyl-L-amino acid 12-hydroxylase
Reaction: a jasmonoyl-L-amino acid + [reduced NADPH—hemoprotein reductase] + $\text{O}_2 =$ a 12-hydroxyjasmonoyl-L-amino acid + [oxidized NADPH—hemoprotein reductase] + H_2O
- Other name(s):** CYP94B1 (gene name); CYP94B3 (gene name)
Systematic name: jasmonoyl-L-amino acid,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (12-hydroxylating)
Comments: A cytochrome P450 (heme thiolate) enzyme found in plants. The enzyme acts on jasmonoyl-L-amino acid conjugates, catalysing the hydroxylation of the C-12 position of jasmonic acid. While the best studied substrate is (+)-7-*epi*-jasmonoyl-L-isoleucine, the enzyme was shown to be active with jasmonoyl-L-valine and jasmonoyl-L-phenylalanine, and is likely to be active with other jasmonoyl-amino acid conjugates.
References: [2026, 1946, 1466, 1945, 2027, 4206]

[EC 1.14.14.48 created 2017]

EC 1.14.14.49

- Accepted name:** 12-hydroxyjasmonoyl-L-amino acid 12-hydroxylase
Reaction: a 12-hydroxyjasmonoyl-L-amino acid + 2 [reduced NADPH—hemoprotein reductase] + 2 $\text{O}_2 =$ a 12-hydroxy-12-oxojasmonoyl-L-amino acid + 2 [oxidized NADPH—hemoprotein reductase] + 3 H_2O (overall reaction)
(1a) a 12-hydroxyjasmonoyl-L-amino acid + [reduced NADPH—hemoprotein reductase] + $\text{O}_2 =$ a 12-oxojasmonoyl-L-amino acid + [oxidized NADPH—hemoprotein reductase] + 2 H_2O
(1b) a 12-oxojasmonoyl-L-amino acid + [reduced NADPH—hemoprotein reductase] + $\text{O}_2 =$ a 12-hydroxy-12-oxojasmonoyl-L-amino acid + [oxidized NADPH—hemoprotein reductase] + H_2O
- Other name(s):** CYP94C1 (gene name)
Systematic name: 12-hydroxyjasmonoyl-L-amino acid,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (12-hydroxylating)
Comments: A cytochrome P450 (heme thiolate) enzyme found in plants. The enzyme acts on jasmonoyl-L-amino acid conjugates that have been hydroxylated at the C-12 position of jasmonic acid by EC 1.14.14.48, jasmonoyl-L-amino acid 12-hydroxylase, further oxidizing that position to a carboxylate via an aldehyde intermediate. While the best studied substrate is (+)-7-*epi*-jasmonoyl-L-isoleucine, the enzyme was shown to be active with jasmonoyl-L-phenylalanine, and is likely to be active with other jasmonoyl-amino acid conjugates.
References: [1466, 4206, 421]

[EC 1.14.14.49 created 2017]

EC 1.14.14.50

- Accepted name:** tabersonine 3-oxygenase
- Reaction:** (1) 16-methoxytabersonine + [reduced NADPH—hemoprotein reductase] + O₂ = (3*R*)-3-hydroxy-16-methoxy-1,2-didehydro-2,3-dihydrotabersonine + [oxidized NADPH—hemoprotein reductase] + H₂O
(2) tabersonine + [reduced NADPH—hemoprotein reductase] + O₂ = (3*R*)-3-hydroxy-1,2-didehydro-2,3-dihydrotabersonine + [oxidized NADPH—hemoprotein reductase] + H₂O
- Other name(s):** T3O; CYP71D1V2
- Systematic name:** 16-methoxytabersonine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3-hydroxylating)
- Comments:** This cytochrome *P*-450 (heme thiolate) enzyme acts on 16-methoxytabersonine, leading to biosynthesis of vindoline in the plant *Catharanthus roseus* (Madagascar periwinkle). It can also act on tabersonine, resulting in the production of small amounts of vindorosine. The products are unstable and, in the absence of EC 1.1.99.41, 3-hydroxy-1,2-didehydro-2,3-dihydrotabersonine reductase, will convert into 3-epoxylated compounds.
- References:** [3085]

[EC 1.14.14.50 created 2017]

EC 1.14.14.51

- Accepted name:** (*S*)-limonene 6-monooxygenase
- Reaction:** (*S*)-limonene + [reduced NADPH—hemoprotein reductase] + O₂ = (–)-*trans*-carveol + [oxidized NADPH—hemoprotein reductase] + H₂O
- Other name(s):** (–)-limonene 6-hydroxylase; (–)-limonene 6-monooxygenase; (–)-limonene,NADPH:oxygen oxidoreductase (6-hydroxylating)
- Systematic name:** (*S*)-limonene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (6-hydroxylating)
- Comments:** A cytochrome *P*-450 (heme thiolate) enzyme. The enzyme participates in the biosynthesis of (–)-carvone, which is responsible for the aroma of spearmint.
- References:** [1816]

[EC 1.14.14.51 created 1992 as EC 1.14.13.48, modified 2003, transferred 2017 to EC 1.14.14.51]

EC 1.14.14.52

- Accepted name:** (*S*)-limonene 7-monooxygenase
- Reaction:** (*S*)-limonene + [reduced NADPH—hemoprotein reductase] + O₂ = (–)-perillyl alcohol + [oxidized NADPH—hemoprotein reductase] + H₂O
- Other name(s):** (–)-limonene 7-monooxygenase; (–)-limonene hydroxylase; (–)-limonene monooxygenase; (–)-limonene,NADPH:oxygen oxidoreductase (7-hydroxylating)
- Systematic name:** (*S*)-limonene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (7-hydroxylating)
- Comments:** A cytochrome *P*-450 (heme thiolate) enzyme. The enzyme, characterized from the plant *Perilla frutescens*, participates in the biosynthesis of perillyl aldehyde, the major constituent of the essential oil that accumulates in the glandular trichomes of this plant. Some forms of the enzyme also catalyse the oxidation of (–)-perillyl alcohol to (–)-perillyl aldehyde.
- References:** [1816, 2469, 1102]

[EC 1.14.14.52 created 1992 as EC 1.14.13.49, modified 2003, transferred 2017 to EC 1.14.14.52]

EC 1.14.14.53

- Accepted name:** (*R*)-limonene 6-monooxygenase
- Reaction:** (*R*)-limonene + [reduced NADPH—hemoprotein reductase] + O₂ = (+)-*trans*-carveol + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): (+)-limonene-6-hydroxylase; (+)-limonene 6-monooxygenase
Systematic name: (*R*)-limonene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (6-hydroxylating)
Comments: The reaction is stereospecific with over 95% yield of (+)-*trans*-carveol from (*R*)-limonene. (*S*)-Limonene, the substrate for EC 1.14.14.51, (*S*)-limonene 6-monooxygenase, is not a substrate. Forms part of the carvone biosynthesis pathway in *Carum carvi* (caraway) seeds.
References: [368, 369]

[EC 1.14.14.53 created 2003 as EC 1.14.13.80, transferred 2017 to EC 1.14.14.53]

EC 1.14.14.54

Accepted name: phenylacetate 2-hydroxylase
Reaction: phenylacetate + [reduced NADPH—hemoprotein reductase] + O₂ = (2-hydroxyphenyl)acetate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP504; *phaA* (gene name)
Systematic name: phenylacetate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (2-hydroxylating)
Comments: This cytochrome *P*-450 (heme-thiolate) enzyme, found in *Aspergillus nidulans*, is involved in the degradation of phenylacetate.
References: [2552, 3213]

[EC 1.14.14.54 created 2017]

EC 1.14.14.55

Accepted name: quinine 3-monooxygenase
Reaction: quinine + [reduced NADPH—hemoprotein reductase] + O₂ = 3-hydroxyquinine + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP3A4 (gene name)
Systematic name: quinine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein.
References: [3164, 4437, 4463, 4464]

[EC 1.14.14.55 created 2000 as EC 1.14.13.67, transferred 2017 to EC 1.14.14.55]

EC 1.14.14.56

Accepted name: 1,8-cineole 2-*exo*-monooxygenase
Reaction: 1,8-cineole + [reduced NADPH—hemoprotein reductase] + O₂ = 2-*exo*-hydroxy-1,8-cineole + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP3A4
Systematic name: 1,8-cineole,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (2-*exo*-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The mammalian enzyme, expressed in liver microsomes, performs a variety of oxidation reactions of structurally unrelated compounds, including steroids, fatty acids, and xenobiotics. *cf.* EC 1.14.14.55, quinine 3-monooxygenase, EC 1.14.14.57, taurochenodeoxycholate 6-hydroxylase and EC 1.14.14.73, albendazole monooxygenase (sulfoxide-forming).
References: [2577, 2576, 2578]

[EC 1.14.14.56 created 2012 as EC 1.14.13.157, transferred 2017 to EC 1.14.14.56, modified 2018]

EC 1.14.14.57

Accepted name: taurochenodeoxycholate 6 α -hydroxylase
Reaction: (1) taurochenodeoxycholate + [reduced NADPH—hemoprotein reductase] + O₂ = taurohyocholate + [oxidized NADPH—hemoprotein reductase] + H₂O
(2) lithocholate + [reduced NADPH—hemoprotein reductase] + O₂ = hyodeoxycholate + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP3A4; CYP4A21; taurochenodeoxycholate 6 α -monooxygenase
Systematic name: taurochenodeoxycholate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (6 α -hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Requires cytochrome *b*₅ for maximal activity. Acts on taurochenodeoxycholate, taurodeoxycholate and less readily on lithocholate and chenodeoxycholate. In adult pig (*Sus scrofa*), hyocholic acid replaces cholic acid as a primary bile acid [2322].
References: [115, 114, 2053, 2321, 2322, 3263]

[EC 1.14.14.57 created 2005 as EC 1.14.13.97, transferred 2018 to EC 1.14.14.57]

EC 1.14.14.58

Accepted name: trimethyltridecatetraene synthase
Reaction: (6*E*,10*E*)-geranylinalool + [reduced NADPH—hemoprotein reductase] + O₂ = (3*E*,7*E*)-4,8,12-trimethyltrideca-1,3,7,11-tetraene + [oxidized NADPH—hemoprotein reductase] + but-3-en-2-one + 2 H₂O
Other name(s): CYP82G1; CYP92C5; CYP92C6; DMNT/TMTT homoterpene synthase
Systematic name: (6*E*,10*E*)-geranylinalool,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plants *Arabidopsis thaliana* (thale cress) and *Zea mays* (maize). It forms this C₁₆ homoterpene in response to herbivore attack. *In vitro* some variants of the enzyme also convert (3*S*,6*E*)-nerolidol to (3*E*)-4,8-dimethylnona-1,3,7-triene (see EC 1.14.14.59, dimethylnonatriene synthase).
References: [2174, 3182]

[EC 1.14.14.58 created 2018]

EC 1.14.14.59

Accepted name: dimethylnonatriene synthase
Reaction: (3*S*,6*E*)-nerolidol + [reduced NADPH—hemoprotein reductase] + O₂ = (3*E*)-4,8-dimethylnona-1,3,7-triene + [oxidized NADPH—hemoprotein reductase] + but-3-en-2-one + 2 H₂O
Other name(s): CYP82G1; CYP92C5; DMNT/TMTT homoterpene synthase
Systematic name: (3*S*,6*E*)-nerolidol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plants *Arabidopsis thaliana* (thale cress) and *Zea mays* (maize). It forms this C₁₁ homoterpene in response to herbivore attack. *In vitro* the enzyme also converts (6*E*,10*E*)-geranylinalool to (3*E*,7*E*)-4,8,12-trimethyltrideca-1,3,7,11-tetraene (see EC 1.14.14.58, trimethyltridecatetraene synthase).
References: [2174, 3182]

[EC 1.14.14.59 created 2018]

EC 1.14.14.60

Accepted name: ferruginol monooxygenase
Reaction: ferruginol + [reduced NADPH—hemoprotein reductase] + O₂ = 11-hydroxyferruginol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP76AH24; CYP76AH3
Systematic name: ferruginol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (11-hydroxyferruginol forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plants *Salvia pomifera* (apple sage) and *Salvia miltiorrhiza* (danshen). 11-Hydroxyferruginol is a precursor of carnosic acid, a potent antioxidant.
References: [1629, 3355, 1313]

[EC 1.14.14.60 created 2018]

EC 1.14.14.61

Accepted name: carnosic acid synthase
Reaction: 11-hydroxyferruginol + 3 [reduced NADPH—hemoprotein reductase] + 3 O₂ = carnosic acid + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O
Other name(s): CYP76AK6; CYP76AK7; CYP76AK8
Systematic name: 11-hydroxyferruginol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plants *Salvia pomifera* (apple sage), *S. miltiorrhiza* (red sage), *S. fruticosa* (Greek sage) and *Rosmarinus officinalis* (Rosemary).
References: [1629, 3355]

[EC 1.14.14.61 created 2018]

EC 1.14.14.62

Accepted name: salviol synthase
Reaction: ferruginol + [reduced NADPH—hemoprotein reductase] + O₂ = salviol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP71BE52
Systematic name: ferruginol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (salviol forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Salvia pomifera* (apple sage).
References: [1629]

[EC 1.14.14.62 created 2018]

EC 1.14.14.63

Accepted name: β-amyrin 16β-monooxygenase
Reaction: β-amyrin + [reduced NADPH—hemoprotein reductase] + O₂ = maniladiol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP716A141
Systematic name: β-amyrin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (maniladiol forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Platycodon grandiflorus* (balloon flower). The enzyme is also able to oxidize oleanolic acid to cochalic acid.
References: [3799]

[EC 1.14.14.63 created 2018]

EC 1.14.14.64

Accepted name: β-amyrin 6β-monooxygenase
Reaction: β-amyrin + [reduced NADPH—hemoprotein reductase] + O₂ = daturadiol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP716E26
Systematic name: β-amyrin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (daturadiol forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Solanum lycopersicum* (tomato).
References: [4351]

[EC 1.14.14.64 created 2018]

EC 1.14.14.65

Accepted name: sugiol synthase
Reaction: ferruginol + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = sugiol + 2 [oxidized NADPH—hemoprotein reductase] + 3 H₂O
Other name(s): CYP76AH3
Systematic name: ferruginol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (sugiol forming)

Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Salvia miltiorrhiza* (danshen). The enzyme also oxidizes 11-hydroxyferruginol to 11-hydroxysugiol. It also oxidizes at C-12 of ferruginol (EC 1.14.14.60 ferruginol monooxygenase).

References: [1313]

[EC 1.14.14.65 created 2018]

EC 1.14.14.66

Accepted name: marmesin synthase

Reaction: demethylsuberosin + [reduced NADPH—hemoprotein reductase] + O₂ = (+)-marmesin + [oxidized NADPH—hemoprotein reductase] + H₂O

Systematic name: demethylsuberosin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase

Comments: A *P*-450 monooxygenase involved in psoralen biosynthesis, see EC 1.14.13.102, psoralen synthase.

References: [1356]

[EC 1.14.14.66 created 2018]

EC 1.14.14.67

Accepted name: 11-hydroxysugiol 20-monooxygenase

Reaction: 11-hydroxysugiol + [reduced NADPH—hemoprotein reductase] + O₂ = 11,20-dihydroxysugiol + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP76AK1

Systematic name: 11-hydroxysugiol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (11,20-dihydroxysugiol forming)

Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Salvia miltiorrhiza* (danshen). The enzyme also oxidizes 11-hydroxyferruginol to 11,20-dihydroxyferruginol.

References: [1313]

[EC 1.14.14.67 created 2018]

EC 1.14.14.68

Accepted name: *syn*-pimaradiene 3-monooxygenase

Reaction: 9β-pimara-7,15-diene + [reduced NADPH—hemoprotein reductase] + O₂ = 9β-pimara-7,15-diene-3β-ol + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP701A8

Systematic name: 9β-pimara7,15-diene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (9β-pimara-7,15-diene-3β-ol forming)

Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from rice, *Oryza sativa*.

References: [1947]

[EC 1.14.14.68 created 2018]

EC 1.14.14.69

Accepted name: *ent*-cassadiene hydroxylase

Reaction: *ent*-cassa-12,15-diene + 3 [reduced NADPH—hemoprotein reductase] + 3 O₂ = *ent*-3β-hydroxycassa-12,15-dien-2-one + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)

(1a) *ent*-cassa-12,15-diene + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-cassa-12,15-dien-2β-ol + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) *ent*-cassa-12,15-dien-2β-ol + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-cassa-12,15-dien-2-one + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1b') *ent*-cassa-12,15-dien-2β-ol + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-cassa-12,15-diene-2β,3β-diol + [oxidized NADPH—hemoprotein reductase] + H₂O

(1c) *ent*-cassa-12,15-dien-2-one + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-3β-hydroxycassa-12,15-dien-2-one + [oxidized NADPH—hemoprotein reductase] + H₂O

(1c') *ent*-cassa-12,15-diene-2 β ,3 β -diol + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-3 β -hydroxycassa-12,15-dien-2-one + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

- Other name(s):** CYP71Z7
Systematic name: *ent*-cassa-12,15-diene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*ent*-3 β -hydroxycassa-12,15-dien-2-one forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Oryza sativa* (rice) that is involved in phytocassanes biosynthesis. Depending on the order of activities, the enzyme may form either *ent*-cassa-12,15-dien-2-one or *ent*-cassa-12,15-diene-2 β ,3 β -diol as an intermediate.
References: [1947]

[EC 1.14.14.69 created 2018]

EC 1.14.14.70

- Accepted name:** *ent*-sandaracopimaradiene 3-hydroxylase
Reaction: *ent*-sandaracopimaradiene + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-sandaracopimaradien-3 β -ol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP701A; OsKOL4
Systematic name: *ent*-sandaracopimaradiene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*ent*-sandaracopimaradien-3 β -ol forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from *Oryza sativa* (rice). Participates in the pathway for the biosynthesis of oryzalexins, a group of related phytoalexins produced by rice. Can also use 9 β -pimara-7,15-diene as substrate (*cf.* EC 1.14.14.68, *syn*-pimaradiene 3-monooxygenase).
References: [4116, 4266]

[EC 1.14.14.70 created 2014 as EC 1.14.13.191, transferred 2018 to EC 1.14.14.70]

EC 1.14.14.71

- Accepted name:** cucurbitadienol 11-hydroxylase
Reaction: cucurbitadienol + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = 11-oxocucurbitadienol + 2 [oxidized NADPH—hemoprotein reductase] + 3 H₂O (overall reaction)
(1a) cucurbitadienol + [reduced NADPH—hemoprotein reductase] + O₂ = 11-hydroxycucurbitadienol + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) 11-hydroxycucurbitadienol + [reduced NADPH—hemoprotein reductase] + O₂ = 11-oxocucurbitadienol + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): CYP87D18
Systematic name: cucurbitadienol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (11-oxocucurbitadienol forming)
Comments: Isolated from the plant *Siraitia grosvenorii* (monk fruit).
References: [4439]

[EC 1.14.14.71 created 2018]

EC 1.14.14.72

- Accepted name:** drimenol monooxygenase
Reaction: drimenol + [reduced NADPH—hemoprotein reductase] + O₂ = drimendiol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): PhDOX1
Systematic name: drimenol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (drimendiol forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Persicaria hydropiper* (water pepper).
References: [1478]

[EC 1.14.14.72 created 2018]

EC 1.14.14.73

- Accepted name:** albendazole monooxygenase (sulfoxide-forming)
- Reaction:** (1) albendazole + [reduced NADPH—hemoprotein reductase] + O₂ = albendazole *S*-oxide + [oxidized NADPH—hemoprotein reductase] + H₂O
(2) fenbendazole + [reduced NADPH—hemoprotein reductase] + O₂ = fenbendazole *S*-oxide + [oxidized NADPH—hemoprotein reductase] + H₂O
- Other name(s):** albendazole sulfoxidase (ambiguous); albendazole hydroxylase (ambiguous); CYP3A4 (gene name); CYP2J2 (gene name); CYP1A2 (gene name)
- Systematic name:** albendazole,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (sulfoxide-forming)
- Comments:** This is one of the activities carried out by some microsomal cytochrome *P*-450 monooxygenases. A similar conversion is also carried out by a different microsomal enzyme (EC 1.14.13.32, albendazole monooxygenase (flavin-containing)), but it is estimated that cytochrome *P*-450s are responsible for 70% of the activity.
- References:** [2630, 3137, 135, 2164, 4267]

[EC 1.14.14.73 created 2018]

EC 1.14.14.74

- Accepted name:** albendazole monooxygenase (hydroxylating)
- Reaction:** albendazole + [reduced NADPH—hemoprotein reductase] + O₂ = hydroxyalbendazole + [oxidized NADPH—hemoprotein reductase] + H₂O
- Other name(s):** CYP2J2 (gene name)
- Systematic name:** albendazole,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (hydroxylating)
- Comments:** CYP2J2 is a microsomal cytochrome *P*-450 monooxygenase that catalyses the hydroxylation of the terminal carbon of the propylsulfanyl chain in albendazole, a broad-spectrum anthelmintic used against gastrointestinal nematodes and the larval stages of cestodes. *cf.* EC 1.14.14.73, albendazole monooxygenase (sulfoxide-forming).
- References:** [4267]

[EC 1.14.14.74 created 2018]

EC 1.14.14.75

- Accepted name:** fenbendazole monooxygenase (4'-hydroxylating)
- Reaction:** fenbendazole + [reduced NADPH—hemoprotein reductase] + O₂ = 4'-hydroxyfenbendazole + [oxidized NADPH—hemoprotein reductase] + H₂O
- Other name(s):** CYP2C19 (gene name)
- Systematic name:** fenbendazole,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (4'-hydroxylating)
- Comments:** CYP2C19 is microsomal cytochrome *P*-450 monooxygenase that catalyses the hydroxylation of the benzene ring of fenbendazole, a broad-spectrum anthelmintic used against gastrointestinal nematodes and the larval stages of cestodes. This activity is also carried out by CYP2J2. *cf.* EC 1.14.14.74, albendazole monooxygenase (hydroxylating). CYP2C19 does not act on albendazole.
- References:** [4267]

[EC 1.14.14.75 created 2018]

EC 1.14.14.76

- Accepted name:** *ent*-isokaurene C2/C3-hydroxylase
- Reaction:** *ent*-isokaurene + 2 O₂ + 2 [reduced NADPH—hemoprotein reductase] = *ent*-isokaurene-2β,3β-diol + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(1a) *ent*-isokaurene + O₂ + [reduced NADPH—hemoprotein reductase] = *ent*-isokauren-2β-ol + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) *ent*-isokauren-2β-ol + O₂ + [reduced NADPH—hemoprotein reductase] = *ent*-isokaurene-2β,3β-diol + [oxidized NADPH—hemoprotein reductase] + H₂O
- Other name(s):** CYP71Z6; *ent*-isokaurene C2-hydroxylase

Systematic name: *ent*-isokaurene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*ent*-isokaurene-2 β ,3 β -diol forming)
Comments: This cytochrome *P*-450 (heme thiolate) enzyme has been characterized from the plant *Oryza sativa* (rice). It may be involved in production of oryzadione.
References: [4265, 1947]

[EC 1.14.14.76 created 2012 as EC 1.14.13.143, transferred 2018 to EC 1.14.14.76]

EC 1.14.14.77

Accepted name: phenylacetonitrile α -monooxygenase
Reaction: phenylacetonitrile + [reduced NADPH—hemoprotein reductase] + O₂ = (*R*)-mandelonitrile + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP3201B1 (gene name)
Systematic name: phenylacetonitrile,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase [(*R*)-mandelonitrile-forming]
Comments: The enzyme has been characterized from the cyanogenic millipede *Chamberlinius hualienensis*. Unlike plant enzymes that can catalyse this reaction (EC 1.14.14.44, phenylacetaldehyde oxime monooxygenase), this enzyme cannot act on phenylacetaldehyde oximes. It can accept (4-hydroxyphenyl)acetonitrile, (2-methylphenyl)acetonitrile, and (3-methylphenyl)acetonitrile as substrates at a lower rate.
References: [4309]

[EC 1.14.14.77 created 2018]

EC 1.14.14.78

Accepted name: phyloquinone ω -hydroxylase
Reaction: phyloquinone + [reduced NADPH—hemoprotein reductase] + O₂ = ω -hydroxyphyloquinone + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): vitamin K₁ ω -hydroxylase; CYP4F2; CYP4F11
Systematic name: phyloquinone,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (ω -hydroxyphyloquinone forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Isolated from human tissue. The enzyme will also act on menaquinone-4. Prolonged action of CYP4F2, but not CYP4F11, on the ω hydroxyl group oxidizes it to the corresponding carboxylic acid. CYP4F2 also oxidizes leukotriene B₄; see EC 1.14.13.30, leukotriene-B₄ 20-monooxygenase [1744].
References: [1744, 3811, 922]

[EC 1.14.14.78 created 2014 as EC 1.14.13.194, transferred 2018 to EC 1.14.14.78]

EC 1.14.14.79

Accepted name: docosahexaenoic acid ω -hydroxylase
Reaction: docosahexaenoate + [reduced NADPH—hemoprotein reductase] + O₂ = 22-hydroxydocosahexaenoate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP4F3B; CYP4V2; docosahexaenoate,NADPH:O₂ oxidoreductase (22-hydroxydocosahexaenoate forming)
Systematic name: docosahexaenoate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (22-hydroxydocosahexaenoate forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from human eye tissue. Defects in the enzyme are associated with Bietti crystalline corneoretinal dystrophy. The enzyme also produces some 21-hydroxydocosahexaenoate. Acts in a similar way on icosapentaenoic acid.
References: [2714]

[EC 1.14.14.79 created 2014 as EC 1.14.13.199, transferred 2018 to EC 1.14.14.79]

EC 1.14.14.80

- Accepted name:** long-chain fatty acid ω -monooxygenase
Reaction: a long-chain fatty acid + [reduced NADPH—hemoprotein reductase] + O₂ = an ω -hydroxy-long-chain fatty acid + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP704B1 (gene name); CYP52M1 (gene name); CYP4A (gene name); CYP86A (gene name)
Systematic name: long-chain fatty acid,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (ω -hydroxylating)
Comments: A cytochrome *P*-450 (heme thiolate) enzyme. The plant enzyme CYP704B1, which is involved in the synthesis of sporopollenin, a complex polymer found at the outer layer of spores and pollen, acts on palmitate (18:0), stearate (18:0) and oleate (18:1). The plant enzyme CYP86A1 also acts on laurate (12:0). The enzyme from the yeast *Starmerella bombicola* (CYP52M1) acts on C₁₆ to C₂₀ saturated and unsaturated fatty acids and can also hydroxylate the (ω -1) position. The mammalian enzyme CYP4A acts on laurate (12:0), myristate (14:0), palmitate (16:0), oleate (18:1), and arachidonate (20:4).
References: [261, 1525, 846, 1593]

[EC 1.14.14.80 created 2015 as EC 1.14.13.205, transferred 2018 to EC 1.14.14.80]

EC 1.14.14.81

- Accepted name:** flavanoid 3',5'-hydroxylase
Reaction: a flavanone + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = a 3',5'-dihydroxyflavanone + 2 [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(1a) a flavanone + [reduced NADPH—hemoprotein reductase] + O₂ = a 3'-hydroxyflavanone + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) a 3'-hydroxyflavanone + [reduced NADPH—hemoprotein reductase] + O₂ = a 3',5'-dihydroxyflavanone + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): flavanoid 3',5'-hydroxylase
Systematic name: flavanone,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3',5'-dihydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. The 3',5'-dihydroxyflavanone is formed via the 3'-hydroxyflavanone. In *Petunia hybrida* the enzyme acts on naringenin, eriodictyol, dihydroquercetin (taxifolin) and dihydrokaempferol (aromadendrin). The enzyme catalyses the hydroxylation of 5,7,4'-trihydroxyflavanone (naringenin) at either the 3' position to form eriodictyol or at both the 3' and 5' positions to form 5,7,3',4',5'-pentahydroxyflavanone (dihydrotricetin). The enzyme also catalyses the hydroxylation of 3,5,7,3',4'-pentahydroxyflavanone (taxifolin) at the 5' position, forming ampelopsin.
References: [2506, 3495, 769]

[EC 1.14.14.81 created 2004 as EC 1.14.13.88, transferred 2018 to EC 1.14.14.81]

EC 1.14.14.82

- Accepted name:** flavonoid 3'-monooxygenase
Reaction: a flavonoid + [reduced NADPH—hemoprotein reductase] + O₂ = a 3'-hydroxyflavonoid + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP75B1 (gene name); flavonoid 3'-hydroxylase; flavonoid 3-hydroxylase (incorrect); NADPH:flavonoid-3'-hydroxylase (incorrect); flavonoid 3-monooxygenase (incorrect)
Systematic name: flavonoid,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3'-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. Acts on a number of flavonoids, including the flavanone naringenin and the flavone apigenin. Does not act on 4-coumarate or 4-coumaroyl-CoA.
References: [1033, 425, 3388]

[EC 1.14.14.82 created 1983 as EC 1.14.13.21, transferred 2018 to EC 1.14.14.82]

EC 1.14.14.83

Accepted name: geraniol 8-hydroxylase
Reaction: geraniol + [reduced NADPH—hemoprotein reductase] + O₂ = (6*E*)-8-hydroxygeraniol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP76B6 (gene name); G10H (gene name)
Systematic name: geraniol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (8-hydroxylating)
Comments: A cytochrome *P*-450 (heme thiolate) protein found in plants. Also hydroxylates nerol and citronellol, *cf.* EC 1.14.14.84, linalool 8-monooxygenase. The recommended numbering of geraniol gives 8-hydroxygeraniol as the product rather than 10-hydroxygeraniol as used by references 1-3. See prenol nomenclature Pr-1. The cloned enzyme also catalysed, but less efficiently, the 3'-hydroxylation of naringenin (*cf.* EC 1.14.14.82, flavonoid 3'-monooxygenase) [3743].
References: [644, 4107, 3743]

[EC 1.14.14.83 created 2012 as EC 1.14.13.152, transferred 2018 to EC 1.14.14.83]

EC 1.14.14.84

Accepted name: linalool 8-monooxygenase
Reaction: linalool + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = (6*E*)-8-oxolinalool + 2 [oxidized NADPH—hemoprotein reductase] + 3 H₂O (overall reaction)
(1a) linalool + [reduced NADPH—hemoprotein reductase] + O₂ = (6*E*)-8-hydroxylinalool + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) (6*E*)-8-hydroxylinalool + [reduced NADPH—hemoprotein reductase] + O₂ = (6*E*)-8-oxolinalool + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): *P*-450lin; CYP111
Systematic name: linalool,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (8-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. The secondary electron donor is a specific [2Fe-2S] ferredoxin from the same bacterial strain.
References: [3968, 3230]

[EC 1.14.14.84 created 1989 as EC 1.14.99.28, transferred 2012 to EC 1.14.13.151, transferred 2018 to EC 1.14.14.84]

EC 1.14.14.85

Accepted name: 7-deoxyloganate 7-hydroxylase
Reaction: 7-deoxyloganate + [reduced NADPH—hemoprotein reductase] + O₂ = loganate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP72A224 (gene name); 7-deoxyloganin 7-hydroxylase (incorrect); 7-deoxyloganin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (7α-hydroxylating) (incorrect)
Systematic name: 7-deoxyloganate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (7α-hydroxylating)
Comments: The enzyme, characterized from the plant *Catharanthus roseus*, is a cytochrome *P*-450 (heme-thiolate) enzyme. It catalyses a reaction in the pathway leading to biosynthesis of monoterpene indole alkaloids.
References: [1829, 2531]

[EC 1.14.14.85 created 2002 as EC 1.14.13.74, transferred 2018 to EC 1.14.14.85, modified 2018]

EC 1.14.14.86

Accepted name: *ent*-kaurene monooxygenase
Reaction: *ent*-kaur-16-ene + 3 [reduced NADPH—hemoprotein reductase] + 3 O₂ = *ent*-kaur-16-en-19-oate + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)
(1a) *ent*-kaur-16-ene + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-kaur-16-en-19-ol + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) *ent*-kaur-16-en-19-ol + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-kaur-16-en-19-al + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1c) *ent*-kaur-16-en-19-al + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-kaur-16-en-19-oate + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): *ent*-kaurene oxidase (misleading)
Systematic name: *ent*-kaur-16-ene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (hydroxylating)
Comments: A cytochrome *P*-450 (heme thiolate) protein found in plants. Catalyses three successive oxidations of the 4-methyl group of *ent*-kaurene giving kaurenoic acid.
References: [131, 116, 1471]

[EC 1.14.14.86 created 2002 as EC 1.14.13.78, transferred 2018 to EC 1.14.14.86]

EC 1.14.14.87

Accepted name: 2-hydroxyisoflavanone synthase
Reaction: (1) liquiritigenin + O₂ + [reduced NADPH—hemoprotein reductase] = 2,4',7-trihydroxyisoflavanone + H₂O + [oxidized NADPH—hemoprotein reductase]
(2) (2*S*)-naringenin + O₂ + [reduced NADPH—hemoprotein reductase] = 2,4',5,7-tetrahydroxyisoflavanone + H₂O + [oxidized NADPH—hemoprotein reductase]
Other name(s): CYP93C; IFS; isoflavonoid synthase
Systematic name: liquiritigenin, [reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (hydroxylating, aryl migration)
Comments: A cytochrome *P*-450 (heme thiolate) protein found in plants. The reaction involves the migration of the 2-phenyl group of the flavanone to the 3-position of the isoflavanone. The 2-hydroxyl group is derived from the oxygen molecule. EC 4.2.1.105, 2-hydroxyisoflavanone dehydratase, acts on the products with loss of water and formation of genistein and daidzein, respectively.
References: [1987, 1409, 3626, 3334, 3333]

[EC 1.14.14.87 created 2011 as EC 1.14.13.136, modified 2013, transferred 2018 to EC 1.14.14.87]

EC 1.14.14.88

Accepted name: isoflavone 3'-hydroxylase
Reaction: formononetin + [reduced NADPH—hemoprotein reductase] + O₂ = calycosin + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): isoflavone 3'-monooxygenase; CYP81E9
Systematic name: formononetin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3'-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Also acts on biochanin A and other isoflavones with a 4'-methoxy group. Involved in the biosynthesis of the pterocarpin phytoalexins medicarpin and maackiain.
References: [1509]

[EC 1.14.14.88 created 1992 as EC 1.14.13.52, transferred 2018 to EC 1.14.14.88]

EC 1.14.14.89

Accepted name: 4'-methoxyisoflavone 2'-hydroxylase
Reaction: formononetin + [reduced NADPH—hemoprotein reductase] + O₂ = 2'-hydroxyformononetin + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP81E1 (gene name); CYP81E3 (gene name); CYP81E7 (gene name); isoflavone 2'-monooxygenase (ambiguous); isoflavone 2'-hydroxylase (ambiguous)
Systematic name: formononetin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (2'-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Acts on isoflavones with a 4'-methoxy group, such as formononetin and biochanin A. Involved in the biosynthesis of the pterocarpin phytoalexins medicarpin and maackiain. EC 1.14.14.90, isoflavone 2'-hydroxylase, is less specific and acts on other isoflavones as well as 4'-methoxyisoflavones.
References: [1509, 45, 2276]

[EC 1.14.14.89 created 1992 as EC 1.14.13.53, modified 2005, transferred 2018 to EC 1.14.14.89]

EC 1.14.14.90

- Accepted name:** isoflavone 2'-hydroxylase
Reaction: an isoflavone + [reduced NADPH—hemoprotein reductase] + O₂ = a 2'-hydroxyisoflavone + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): isoflavone 2'-monooxygenase; CYP81E1; CYP Ge-3
Systematic name: isoflavone,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (2'-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Acts on daidzein, formononetin and genistein. EC 1.14.14.89, 4'-methoxyisoflavone 2'-hydroxylase, has the same reaction but is more specific as it requires a 4'-methoxyisoflavone.
References: [45]

[EC 1.14.14.90 created 2005 as EC 1.14.13.89, transferred 2018 to EC 1.14.14.90]

EC 1.14.14.91

- Accepted name:** *trans*-cinnamate 4-monooxygenase
Reaction: *trans*-cinnamate + [reduced NADPH—hemoprotein reductase] + O₂ = 4-hydroxycinnamate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): cinnamic acid 4-hydroxylase; CA4H; cytochrome P450 cinnamate 4-hydroxylase; cinnamate 4-hydroxylase; cinnamate 4-monooxygenase; cinnamate hydroxylase; cinnamic 4-hydroxylase; cinnamic acid 4-monooxygenase; cinnamic acid *p*-hydroxylase; *t*-cinnamic acid hydroxylase; *trans*-cinnamate 4-hydroxylase; *trans*-cinnamic acid 4-hydroxylase; CYP73A1 (gene name)
Systematic name: *trans*-cinnamate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (4-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. The enzyme is involved in flavonoid biosynthesis.
References: [3044, 3264, 3006]

[EC 1.14.14.91 created 1976 as EC 1.14.13.11, transferred 2018 to EC 1.14.14.91]

EC 1.14.14.92

- Accepted name:** benzoate 4-monooxygenase
Reaction: benzoate + [reduced NADPH—hemoprotein reductase] + O₂ = 4-hydroxybenzoate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): benzoic acid 4-hydroxylase; benzoate 4-hydroxylase; benzoic 4-hydroxylase; benzoate-*p*-hydroxylase; *p*-hydroxybenzoate hydroxylase; CYP53A1 (gene name)
Systematic name: benzoate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (4-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in *Aspergillus* fungi.
References: [3147, 977]

[EC 1.14.14.92 created 1976 as EC 1.14.13.12, transferred 2018 to EC 1.14.14.92]

EC 1.14.14.93

- Accepted name:** 3,9-dihydroxypterocarpan 6 α -monooxygenase
Reaction: (6 α R,11 α R)-3,9-dihydroxypterocarpan + [reduced NADPH—hemoprotein reductase] + O₂ = (6 α S,11 α S)-3,6 α ,9-trihydroxypterocarpan + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): 3,9-dihydroxypterocarpan 6 α -hydroxylase; 3,9-dihydroxypterocarpan 6 α -monooxygenase (erroneous); CYP93A1 (gene name)
Systematic name: (6 α R,11 α R)-3,9-dihydroxypterocarpan,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (6 α -hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in soybean. The product of the reaction is the biosynthetic precursor of the glyceollin phytoalexins.
References: [1341, 3391]

[EC 1.14.14.93 created 1989 as EC 1.14.13.28, transferred 2018 to EC 1.14.14.93]

EC 1.14.14.94

- Accepted name:** leukotriene-B₄ 20-monoxygenase
Reaction: (6Z,8E,10E,14Z)-(5S,12R)-5,12-dihydroxyicoso-6,8,10,14-tetraenoate + [reduced NADPH—hemoprotein reductase] + O₂ = (6Z,8E,10E,14Z)-(5S,12R)-5,12,20-trihydroxyicoso-6,8,10,14-tetraenoate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): leukotriene-B₄ 20-hydroxylase; leucotriene-B₄ ω-hydroxylase; LTB₄ 20-hydroxylase; LTB₄ ω-hydroxylase; CYP4F2 (gene name); CYP4F3 (gene name)
Systematic name: (6Z,8E,10E,14Z)-(5S,12R)-5,12-dihydroxyicoso-6,8,10,14-tetraenoate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (20-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in mammals.
References: [3225, 3457, 3569]

[EC 1.14.14.94 created 1989 as EC 1.14.13.30, transferred 2018 to EC 1.14.14.94]

EC 1.14.14.95

- Accepted name:** germacrene A hydroxylase
Reaction: (+)-germacrene A + 3 [reduced NADPH—hemoprotein reductase] + 3 O₂ = germacra-1(10),4,11(13)-trien-12-oate + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)
(1a) (+)-germacrene A + O₂ + [reduced NADPH—hemoprotein reductase] = germacra-1(10),4,11(13)-trien-12-ol + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) germacra-1(10),4,11(13)-trien-12-ol + O₂ + [reduced NADPH—hemoprotein reductase] = germacra-1(10),4,11(13)-trien-12-al + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
(1c) germacra-1(10),4,11(13)-trien-12-al + O₂ + [reduced NADPH—hemoprotein reductase] = germacra-1(10),4,11(13)-trien-12-oate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): GAO (gene name)
Systematic name: (+)-germacrene-A,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (12-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. This plant enzyme catalyses three steps in a pathway that leads to the biosynthesis of many sesquiterpenoid lactones.
References: [2776, 2283]

[EC 1.14.14.95 created 2011 as EC 1.14.13.123, transferred 2018 to EC 1.14.14.95]

EC 1.14.14.96

- Accepted name:** 5-*O*-(4-coumaroyl)-D-quinic acid 3'-monoxygenase
Reaction: *trans*-5-*O*-(4-coumaroyl)-D-quinic acid + [reduced NADPH—hemoprotein reductase] + O₂ = *trans*-5-*O*-caffeoyl-D-quinic acid + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): 5-*O*-(4-coumaroyl)-D-quinic acid/shikimate 3'-hydroxylase; coumaroylquinic acid(coumaroylshikimate) 3'-monoxygenase; CYP98A3 (gene name)
Systematic name: *trans*-5-*O*-(4-coumaroyl)-D-quinic acid,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3'-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein, found in plants. It also acts on *trans*-5-*O*-(4-coumaroyl)shikimate.
References: [2072, 3387, 1054, 2453]

[EC 1.14.14.96 created 1990 as EC 1.14.13.36, transferred 2018 to EC 1.14.14.96]

EC 1.14.14.97

- Accepted name:** methyltetrahydroprotoberberine 14-monoxygenase
Reaction: (*S*)-*N*-methylcanadine + [reduced NADPH—hemoprotein reductase] + O₂ = allocryptopine + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): methyltetrahydroprotoberberine 14-hydroxylase; (*S*)-*cis*-*N*-methyltetrahydroprotoberberine 14-monoxygenase; (*S*)-*cis*-*N*-methyltetrahydroprotoberberine-14-hydroxylase; CYP82N4 (gene name)

Systematic name: (*S*)-*N*-methylcanadine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (14-hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants.

References: [3254, 233]

[EC 1.14.14.97 created 1990 as EC 1.14.13.37, transferred 2018 to EC 1.14.14.97]

EC 1.14.14.98

Accepted name: protopine 6-monooxygenase

Reaction: protopine + [reduced NADPH—hemoprotein reductase] + O₂ = 6-hydroxyprotopine + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): protopine 6-hydroxylase; CYP82N2 (gene name)

Systematic name: protopine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (6-hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein involved in benzophenanthridine alkaloid synthesis in higher plants.

References: [3801, 3791]

[EC 1.14.14.98 created 1999 as EC 1.14.13.55, transferred 2018 to EC 1.14.14.98]

EC 1.14.14.99

Accepted name: (*S*)-limonene 3-monooxygenase

Reaction: (*S*)-limonene + [reduced NADPH—hemoprotein reductase] + O₂ = (–)-*trans*-isopiperitenol + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): (–)-limonene 3-hydroxylase; (–)-limonene 3-monooxygenase; CYP71D15 (gene name)

Systematic name: (*S*)-limonene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3-hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein from peppermint (*Mentha piperita*).

References: [1816, 2324, 4269]

[EC 1.14.14.99 created 1992 as EC 1.14.13.47, modified 2003, transferred 2018 1.14.14.99]

EC 1.14.14.100

Accepted name: dihydrosanguinarine 10-monooxygenase

Reaction: dihydrosanguinarine + [reduced NADPH—hemoprotein reductase] + O₂ = 10-hydroxydihydrosanguinarine + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): dihydrosanguinarine 10-hydroxylase

Systematic name: dihydrosanguinarine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (10-hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein involved in benzophenanthridine alkaloid synthesis in higher plants.

References: [759]

[EC 1.14.14.100 created 1999 as EC 1.14.13.56, transferred 2018 to EC 1.14.14.100]

EC 1.14.14.101

Accepted name: dihydrochelirubine 12-monooxygenase

Reaction: dihydrochelirubine + [reduced NADPH—hemoprotein reductase] + O₂ = 12-hydroxydihydrochelirubine + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): dihydrochelirubine 12-hydroxylase

Systematic name: dihydrochelirubine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (12-hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein from the plant *Thalictrum bulgaricum*.

References: [1806]

[EC 1.14.14.101 created 1999 as EC 1.14.13.57, transferred 2018 to EC 1.14.14.101]

EC 1.14.14.102

Accepted name: *N*-methylcoclaurine 3'-monoxygenase
Reaction: (*S*)-*N*-methylcoclaurine + [reduced NADPH—hemoprotein reductase] + O₂ = (*S*)-3'-hydroxy-*N*-methylcoclaurine + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): *N*-methylcoclaurine 3'-hydroxylase; CYP80B1 (gene name)
Systematic name: (*S*)-*N*-methylcoclaurine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3'-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein involved in benzyloisoquinoline alkaloid synthesis in higher plants.
References: [2965]

[EC 1.14.14.102 created 2001 as 1.14.13.71, transferred 2018 to EC 1.14.14.102]

EC 1.14.14.103

Accepted name: tabersonine 16-hydroxylase
Reaction: tabersonine + [reduced NADPH—hemoprotein reductase] + O₂ = 16-hydroxytabersonine + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): tabersonine-11-hydroxylase; T11H; CYP71D12 (gene name)
Systematic name: tabersonine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (16-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein from the plant Madagascar periwinkle (*Catharanthus roseus*).
References: [3611, 287]

[EC 1.14.14.103 created 2002 as EC 1.14.13.73, transferred 2018 to EC 1.14.14.103]

EC 1.14.14.104

Accepted name: vinorine hydroxylase
Reaction: vinorine + [reduced NADPH—hemoprotein reductase] + O₂ = vomilenine + [oxidized NADPH—hemoprotein reductase] + H₂O
Systematic name: vinorine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (21 α -hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein from the plant *Rauvolfia serpentina*. Forms a stage in the biosynthesis of the indole alkaloid ajmaline.
References: [980]

[EC 1.14.14.104 created 2002 as EC 1.14.13.75, transferred 2018 to EC 1.14.14.104]

EC 1.14.14.105

Accepted name: taxane 10 β -hydroxylase
Reaction: taxa-4(20),11-dien-5 α -yl acetate + [reduced NADPH—hemoprotein reductase] + O₂ = 10 β -hydroxytaxa-4(20),11-dien-5 α -yl acetate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP725A1 (gene name); 5- α -taxadienol-10- β -hydroxylase
Systematic name: taxa-4(20),11-dien-5 α -yl acetate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (10 β -hydroxylating)
Comments: This microsomal cytochrome-*P*-450 (heme-thiolate) enzyme from the plant *Taxus cuspidata* is involved in the biosynthesis of the diterpenoid antineoplastic drug taxol (paclitaxel).
References: [4185, 1732, 3389]

[EC 1.14.14.105 created 2002 as EC 1.14.13.76, transferred 2018 to EC 1.14.14.105]

EC 1.14.14.106

Accepted name: taxane 13 α -hydroxylase
Reaction: taxa-4(20),11-dien-5 α -ol + [reduced NADPH—hemoprotein reductase] + O₂ = taxa-4(20),11-dien-5 α ,13 α -diol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP725A2 (gene name)
Systematic name: taxa-4(20),11-dien-5 α -ol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (13 α -hydroxylating)
Comments: This cytochrome-*P*-450(heme-thiolate) enzyme from the plant *Taxus cuspidata* is involved in the biosynthesis of the diterpenoid antineoplastic drug taxol (paclitaxel).
References: [4185, 1732]

[EC 1.14.14.106 created 2002 as EC 1.14.13.77, transferred 2018 to EC 1.14.14.106]

EC 1.14.14.107

Accepted name: *ent*-kaurenoic acid monooxygenase
Reaction: *ent*-kaur-16-en-19-oate + 3 [reduced NADPH—hemoprotein reductase] + 3 O₂ = gibberellin A₁₂ + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)
(1a) *ent*-kaur-16-en-19-oate + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-7 α -hydroxykaur-16-en-19-oate + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) *ent*-7 α -hydroxykaur-16-en-19-oate + [reduced NADPH—hemoprotein reductase] + O₂ = gibberellin A₁₂ aldehyde + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
(1c) gibberellin A₁₂ aldehyde + [reduced NADPH—hemoprotein reductase] + O₂ = gibberellin A₁₂ + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): KAO1 (gene name); CYP88A3 (gene name); *ent*-kaurenoic acid oxidase
Systematic name: *ent*-kaur-16-en-19-oate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein from plants. Catalyses three successive oxidations of *ent*-kaurenoic acid. The second step includes a ring-B contraction giving the gibbane skeleton. In pumpkin (*Cucurbita maxima*) *ent*-6 α ,7 α -dihydroxykaur-16-en-19-oate is also formed.
References: [1470]

[EC 1.14.14.107 created 2002 as EC 1.14.13.79, transferred 2018 to EC 1.14.14.107]

EC 1.14.14.108

Accepted name: 2,5-diketocamphane 1,2-monooxygenase
Reaction: (+)-bornane-2,5-dione + FMNH₂ + O₂ = (+)-5-oxo-1,2-campholide + FMN + H₂O
Other name(s): 2,5-diketocamphane lactonizing enzyme; ketolactonase I (ambiguous); 2,5-diketocamphane 1,2-monooxygenase oxygenating component; 2,5-DKCMO; *camP* (gene name); camphor 1,2-monooxygenase; camphor ketolactonase I
Systematic name: (+)-bornane-2,5-dione,FMNH₂:oxygen oxidoreductase (1,2-lactonizing)
Comments: A Baeyer-Villiger monooxygenase isolated from camphor-grown strains of *Pseudomonas putida* and encoded on the cam plasmid. Involved in the degradation of (+)-camphor. Requires a dedicated NADH-FMN reductase [*cf.* EC 1.5.1.42, FMN reductase (NADH)] [650, 4398, 3833]. Can accept several bicyclic ketones including (+)- and (–)-camphor [1793] and adamantanone [3438]. The product spontaneously converts to [(1*R*)-2,2,3-trimethyl-5-oxocyclopent-3-enyl]acetate.
References: [650, 4398, 3833, 3438, 1772, 1793, 1693]

[EC 1.14.14.108 created 1972 as EC 1.14.15.2, transferred 2012 to EC 1.14.13.162, transferred 2018 to EC 1.14.14.108]

EC 1.14.14.109

Accepted name: 3-hydroxyindolin-2-one monooxygenase
Reaction: 3-hydroxyindolin-2-one + [reduced NADPH—hemoprotein reductase] + O₂ = 2-hydroxy-2*H*-1,4-benzoxazin-3(4*H*)-one [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): BX4 (gene name); CYP71C1 (gene name)

Systematic name: 3-hydroxyindolin-2-one,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (2-hydroxy-2*H*-1,4-benzoxazin-3(4*H*)-one-forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme is involved in the biosynthesis of protective and allelopathic benzoxazinoids in some plants, most commonly from the family of Poaceae (grasses).
References: [1220, 1063, 3605]

[EC 1.14.14.109 created 2012 as EC 1.14.13.139, transferred 2018 to EC 1.14.14.109]

EC 1.14.14.110

Accepted name: 2-hydroxy-1,4-benzoxazin-3-one monooxygenase
Reaction: 2-hydroxy-2*H*-1,4-benzoxazin-3(4*H*)-one + [reduced NADPH—hemoprotein reductase] + O₂ = 2,4-dihydroxy-2*H*-1,4-benzoxazin-3(4*H*)-one + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): BX5 (gene name); CYP71C3 (gene name)
Systematic name: 2-hydroxy-2*H*-1,4-benzoxazin-3(4*H*)-one,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*N*-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme is involved in the biosynthesis of protective and allelopathic benzoxazinoids in some plants, most commonly from the family of Poaceae (grasses).
References: [164, 1220]

[EC 1.14.14.110 created 2012 as EC 1.14.13.140, transferred 2018 to EC 1.14.14.110]

EC 1.14.14.111

Accepted name: 9β-pimara-7,15-diene oxidase
Reaction: 9β-pimara-7,15-diene + 3 O₂ + 3 [reduced NADPH—hemoprotein reductase] = 9β-pimara-7,15-dien-19-oate + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)
(1a) 9β-pimara-7,15-diene + O₂ + [reduced NADPH—hemoprotein reductase] = 9β-pimara-7,15-dien-19-ol + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) 9β-pimara-7,15-dien-19-ol + O₂ + [reduced NADPH—hemoprotein reductase] = 9β-pimara-7,15-dien-19-al + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
(1c) 9β-pimara-7,15-dien-19-al + O₂ + [reduced NADPH—hemoprotein reductase] = 9β-pimara-7,15-dien-19-oate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP99A3; 9β-pimara-7,15-diene monooxygenase
Systematic name: 9β-pimara-7,15-diene,[reduced NADPH—hemoprotein reductase]:oxygen 19-oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme from rice (*Oryza sativa*) is involved in the biosynthesis of the phytoalexin momilactone. It also acts similarly on 9β-stemod-13(17)-ene.
References: [4115]

[EC 1.14.14.111 created 2012 as EC 1.14.13.144, transferred 2018 to EC 1.14.14.111]

EC 1.14.14.112

Accepted name: *ent*-cassa-12,15-diene 11-hydroxylase
Reaction: *ent*-cassa-12,15-diene + O₂ + [reduced NADPH—hemoprotein reductase] = *ent*-11β-hydroxycassa-12,15-diene + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): *ent*-cassadiene C11α-hydroxylase; CYP76M7
Systematic name: *ent*-cassa-12,15-diene,[reduced NADPH—hemoprotein reductase]:oxygen 11-oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme from rice (*Oryza sativa*) is involved in the biosynthesis of the antifungal phytocassanes.
References: [3760]

[EC 1.14.14.112 created 2012 as EC 1.14.13.145, transferred 2018 to EC 1.14.14.112]

EC 1.14.14.113

- Accepted name:** α -humulene 10-hydroxylase
Reaction: α -humulene + O₂ + [reduced NADPH—hemoprotein reductase] = 10-hydroxy- α -humulene + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP71BA1
Systematic name: α -humulene,[reduced NADPH—hemoprotein reductase]:oxygen 10-oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The recommended numbering of humulene gives 10-hydroxy- α -humulene as the product rather than 8-hydroxy- α -humulene as used by the reference. See Section F: Natural Product Nomenclature.
References: [4400]

[EC 1.14.14.113 created 2012 as EC 1.14.13.150, transferred 2018 to EC 1.14.14.113]

EC 1.14.14.114

- Accepted name:** amorpha-4,11-diene 12-monooxygenase
Reaction: amorpha-4,11-diene + 3 O₂ + 3 [reduced NADPH—hemoprotein reductase] = artemisinate + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)
(1a) amorpha-4,11-diene + O₂ + [reduced NADPH—hemoprotein reductase] = artemisinic alcohol + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) artemisinic alcohol + O₂ + [reduced NADPH—hemoprotein reductase] = artemisinic aldehyde + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
(1c) artemisinic aldehyde + O₂ + [reduced NADPH—hemoprotein reductase] = artemisinate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP71AV1
Systematic name: amorpha-4,11-diene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (12-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Cloned from the plant *Artemisia annua* (sweet wormwood). Part of the biosynthetic pathway of artemisinin.
References: [3847]

[EC 1.14.14.114 created 2012 as EC 1.14.13.158, transferred 2018 to EC 1.14.14.114]

EC 1.14.14.115

- Accepted name:** 11-oxo- β -amyrin 30-oxidase
Reaction: 11-oxo- β -amyrin + 3 O₂ + 3 [reduced NADPH—hemoprotein reductase] = glycyrrhetinate + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)
(1a) 11-oxo- β -amyrin + O₂ + [reduced NADPH—hemoprotein reductase] = 30-hydroxy-11-oxo- β -amyrin + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) 30-hydroxy-11-oxo- β -amyrin + O₂ + [reduced NADPH—hemoprotein reductase] = glycyrrhetaldehyde + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
(1c) glycyrrhetaldehyde + O₂ + [reduced NADPH—hemoprotein reductase] = glycyrrhetinate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP72A; CYP72A154; 11-oxo- β -amyrin 30-monooxygenase
Systematic name: 11-oxo- β -amyrin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (30-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme from the plant *Glycyrrhiza uralensis* (licorice) is involved in the biosynthesis of the triterpenoid saponin glycyrrhizin. The enzyme from the plant *Medicago truncatula* can also hydroxylate β -amyrin.
References: [3434]

[EC 1.14.14.115 created 2013 as EC 1.14.13.173, transferred 2018 to EC 1.14.14.115]

EC 1.14.14.116

- Accepted name:** averantin hydroxylase

Reaction: (1) (1'*S*)-averantin + [reduced NADPH—hemoprotein reductase] + O₂ = (1'*S*,5'*S*)-5'-hydroxyaverantin + [oxidized NADPH—hemoprotein reductase] + H₂O
(2) (1'*S*)-averantin + [reduced NADPH—hemoprotein reductase] + O₂ = (1'*S*,5'*R*)-5'-hydroxyaverantin + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): AVN hydroxylase; *avnA* (gene name); CYP60A1
Systematic name: (1'*S*)-averantin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (5'-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the saprophytic mold *Aspergillus parasiticus*. Involved in aflatoxin biosynthesis. Does not react with (1'*R*)-averantin.
References: [4295, 4402]

[EC 1.14.14.116 created 2013 as EC 1.14.13.174, transferred 2018 to EC 1.14.14.116]

EC 1.14.14.117

Accepted name: aflatoxin B synthase
Reaction: (1) 8-*O*-methylsterigmatocystin + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = aflatoxin B₁ + 2 [oxidized NADPH—hemoprotein reductase] + H₂O + methanol + CO₂
(2) 8-*O*-methylidihydrosterigmatocystin + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = aflatoxin B₂ + 2 [oxidized NADPH—hemoprotein reductase] + H₂O + methanol + CO₂
Other name(s): *ordA* (gene name)
Systematic name: 8-*O*-methylsterigmatocystin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (aflatoxin-B forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Isolated from the mold *Aspergillus parasiticus*.
References: [292, 4403, 3959]

[EC 1.14.14.117 created 2013 as EC 1.14.13.175, transferred 2018 to EC 1.14.14.117]

EC 1.14.14.118

Accepted name: tryprostatin B 6-hydroxylase
Reaction: tryprostatin B + [reduced NADPH—hemoprotein reductase] + O₂ = 6-hydroxytryprostatin B + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): *ftmC* (gene name)
Systematic name: tryprostatin B,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (6-hydroxytryprostatin B-forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Involved in the biosynthetic pathways of several indole alkaloids such as tryprostatins, fumitremorgins and verruculogen.
References: [1838]

[EC 1.14.14.118 created 2013 as EC 1.14.13.176, transferred 2018 to EC 1.14.14.118]

EC 1.14.14.119

Accepted name: fumitremorgin C monooxygenase
Reaction: fumitremorgin C + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = 12 α ,13 α -dihydroxyfumitremorgin C + 2 [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): *ftmG* (gene name)
Systematic name: fumitremorgin C,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (12 α ,13 α -dihydroxyfumitremorgin C-forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Involved in the biosynthetic pathway of the indole alkaloid verruculogen.
References: [1838]

[EC 1.14.14.119 created 2013 as EC 1.14.13.177, transferred 2018 to EC 1.14.14.119]

EC 1.14.14.120

Accepted name: dammarenediol 12-hydroxylase
Reaction: dammarenediol-II + [reduced NADPH—hemoprotein reductase] + O₂ = protopanaxadiol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): protopanaxadiol synthase; CYP716A47
Systematic name: dammarenediol-II,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (12β-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from ginseng (*Panax ginseng*). Involved in the biosynthetic pathway of ginsenosides.
References: [1362]

[EC 1.14.14.120 created 2013 as EC 1.14.13.183, transferred 2018 to EC 1.14.14.120]

EC 1.14.14.121

Accepted name: protopanaxadiol 6-hydroxylase
Reaction: protopanaxadiol + [reduced NADPH—hemoprotein reductase] + O₂ = protopanaxatriol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): protopanaxatriol synthase; P6H; CYP716A53v2
Systematic name: protopanaxadiol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (6α-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the rhizomes of ginseng (*Panax ginseng*). Involved in the biosynthetic pathway of ginsenosides.
References: [4411, 1361]

[EC 1.14.14.121 created 2013 as EC 1.14.13.184, transferred 2018 to EC 1.14.14.121]

EC 1.14.14.122

Accepted name: oryzalexin E synthase
Reaction: *ent*-sandaracopimaradien-3β-ol + [reduced NADPH—hemoprotein reductase] + O₂ = oryzalexin E + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP76M6
Systematic name: *ent*-sandaracopimaradien-3β-ol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (oryzalexin E forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Isolated from *Oryza sativa* (rice). Oryzalexin E is a phytoalexin.
References: [4266]

[EC 1.14.14.122 created 2014 as EC 1.14.13.192, transferred 2018 to EC 1.14.14.122]

EC 1.14.14.123

Accepted name: oryzalexin D synthase
Reaction: *ent*-sandaracopimaradien-3β-ol + [reduced NADPH—hemoprotein reductase] + O₂ = oryzalexin D + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP76M8
Systematic name: *ent*-sandaracopimaradien-3β-ol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (oryzalexin D forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Isolated from *Oryza sativa* (rice). Oryzalexin D is a phytoalexin.
References: [4266]

[EC 1.14.14.123 created 2014 as EC 1.14.13.193, transferred 2018 to EC 1.14.14.123]

EC 1.14.14.124

Accepted name: dihydromonacolin L hydroxylase

Reaction: dihydromonacolin L acid + O₂ + [reduced NADPH—hemoprotein reductase] = monacolin L acid + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(1a) dihydromonacolin L acid + O₂ + [reduced NADPH—hemoprotein reductase] = 3 α -hydroxy-3,5-dihydromonacolin L acid + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) 3 α -hydroxy-3,5-dihydromonacolin L acid = monacolin L acid + H₂O (spontaneous)

Other name(s): LovA (ambiguous)
Systematic name: dihydromonacolin L acid,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3-hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein. The dehydration of 3 α -hydroxy-3,5-dihydromonacolin L acid is believed to be spontaneous [3926, 2706]. The enzyme from fungi also catalyses the reaction of EC 1.14.14.125, monacolin L hydroxylase [205].

References: [3926, 2706, 205]

[EC 1.14.14.124 created 2014 as EC 1.14.13.197, transferred 2018 to EC 1.14.14.124]

EC 1.14.14.125

Accepted name: monacolin L hydroxylase

Reaction: monacolin L acid + O₂ + [reduced NADPH—hemoprotein reductase] = monacolin J acid + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): LovA (ambiguous)
Systematic name: monacolin L acid,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (8-hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme from fungi also catalyses the reaction of EC 1.14.14.124, dihydromonacolin L hydroxylase.

References: [205]

[EC 1.14.14.125 created 2014 as EC 1.14.13.198, transferred 2018 to EC 1.14.14.125]

EC 1.14.14.126

Accepted name: β -amyrin 28-monooxygenase

Reaction: β -amyrin + 3 O₂ + 3 [reduced NADPH—hemoprotein reductase] = oleanolate + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)

(1a) β -amyrin + O₂ + [reduced NADPH—hemoprotein reductase] = erythrodiol + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) erythrodiol + O₂ + [reduced NADPH—hemoprotein reductase] = oleanolic aldehyde + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1c) oleanolic aldehyde + O₂ + [reduced NADPH—hemoprotein reductase] = oleanolate + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP716A52v2; CYP716A12; CYP16A75; β -amyrin 28-oxidase
Systematic name: β -amyrin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (28-hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. The enzyme is involved in the biosynthesis of oleanane-type triterpenoids, such as ginsenoside Ro. The enzyme from *Medicago truncatula* (barrel medic) (CYP716A12) can also convert α -amyrin and lupeol to ursolic acid and betulinic acid, respectively. The enzyme from *Maesa lanceolata* (false assegai) (CYP16A75) does not catalyse the reaction to completion, resulting in accumulation of both intermediates.

References: [1111, 1363, 2637]

[EC 1.14.14.126 created 2015 as EC 1.14.13.201, transferred 2018 to EC 1.14.14.126]

EC 1.14.14.127

Accepted name: methyl farnesoate epoxidase

Reaction: methyl (2*E*,6*E*)-farnesoate + [reduced NADPH—hemoprotein reductase] + O₂ = juvenile hormone III + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP15A1

Systematic name: methyl (2*E*,6*E*)-farnesoate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme, found in insects except for Lepidoptera (moths and butterflies) is specific for methyl farnesoate (*cf.* EC 1.14.14.128, farnesoate epoxidase) [1473, 729].
References: [1473, 729]

[EC 1.14.14.127 created 2015 as EC 1.14.13.202, transferred 2018 to EC 1.14.14.127]

EC 1.14.14.128

Accepted name: farnesoate epoxidase
Reaction: (2*E*,6*E*)-farnesoate + [reduced NADPH—hemoprotein reductase] + O₂ = juvenile-hormone-III carboxylate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP15C1
Systematic name: (2*E*,6*E*)-farnesoate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme, found in Lepidoptera (moths and butterflies), is specific for farnesoate (*cf.* EC 1.14.14.127, methyl farnesoate epoxidase) [728, 729]. It is involved in the synthesis of juvenile hormone.
References: [728, 729]

[EC 1.14.14.128 created 2015 as EC 1.14.13.203, transferred 2018 to EC 1.14.14.128]

EC 1.14.14.129

Accepted name: long-chain acyl-CoA ω-monooxygenase
Reaction: (1) oleoyl-CoA + [reduced NADPH—hemoprotein reductase] + O₂ = 18-hydroxyoleoyl-CoA + [oxidized NADPH—hemoprotein reductase] + H₂O
(2) linoleoyl-CoA + [reduced NADPH—hemoprotein reductase] + O₂ = 18-hydroxylinoleoyl-CoA + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): long-chain acyl-CoA ω-hydroxylase; CYP86A22 (gene name); CYP52M1 (gene name)
Systematic name: long-chain acyl-CoA,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (ω-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzymes from solanaceous plants are involved in the biosynthesis of stigmatic estolide, a lipid-based polyester that forms a major component of the exudate.
References: [1359]

[EC 1.14.14.129 created 2015 as EC 1.14.13.204, transferred 2018 to EC 1.14.14.129]

EC 1.14.14.130

Accepted name: laurate 7-monooxygenase
Reaction: dodecanoate + [reduced NADPH—hemoprotein reductase] + O₂ = 7-hydroxydodecanoate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP703A2 (gene name)
Systematic name: dodecanoate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (7-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. The enzyme is involved in the synthesis of sporopollenin - a complex polymer found at the outer layer of spores and pollen. It can also act on decanoate (C₁₀), myristate (C₁₄), and palmitate (C₁₆) with lower activity. The enzyme also produces a small amount of products that are hydroxylated at neighboring positions (C-6, C-8 and C-9).
References: [2611]

[EC 1.14.14.130 created 2015 as EC 1.14.13.206, transferred 2018 to EC 1.14.14.130]

EC 1.14.14.131

Accepted name: bursehernin 5'-monooxygenase

Reaction: (–)-burshehnerin + [reduced NADPH—hemoprotein reductase] + O₂ = (–)-5′-demethylatein + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP71CU1 (gene name); burshehnerin 5′-hydroxylase
Systematic name: (–)-burshehnerin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (5′-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein characterized from the plant *Sinopodophyllum hexandrum*. The enzyme is involved in the biosynthetic pathway of podophyllotoxin, a non-alkaloid toxin lignan whose derivatives are important anticancer drugs.
References: [2151]

[EC 1.14.14.131 created 2016 as EC 1.14.13.213, transferred 2018 to EC 1.14.14.131]

EC 1.14.14.132

Accepted name: (–)-4′-demethyl-deoxypodophyllotoxin 4-hydroxylase
Reaction: (–)-4′-demethyldeoxypodophyllotoxin + [reduced NADPH—hemoprotein reductase] + O₂ = (–)-4′-demethylepipodophyllotoxin + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP82D61 (gene name)
Systematic name: (–)-deoxypodophyllotoxin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (4-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein characterized from the plant *Sinopodophyllum hexandrum*. The enzyme produces the direct precursor to etoposide, a potent anticancer drug. It can also act on (–)-deoxypodophyllotoxin with lower efficiency.
References: [2151]

[EC 1.14.14.132 created 2016 as EC 1.14.13.214, transferred 2018 to EC 1.14.14.132]

EC 1.14.14.133

Accepted name: 1,8-cineole 2-*endo*-monooxygenase
Reaction: 1,8-cineole + [reduced flavodoxin] + O₂ = 2-*endo*-hydroxy-1,8-cineole + [oxidized flavodoxin] + H₂O
Other name(s): P450_{cin}; CYP176A; CYP176A1
Systematic name: 1,8-cineole,[reduced flavodoxin]:oxygen oxidoreductase (2-*endo*-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein that uses a flavodoxin-like redox partner to reduce the heme iron. Isolated from the bacterium *Citrobacter braakii*, which can use 1,8-cineole as the sole source of carbon.
References: [1429, 2497, 1931, 2498]

[EC 1.14.14.133 created 2012 as EC 1.14.13.156, transferred 2018 to EC 1.14.14.133]

EC 1.14.14.134

Accepted name: β-amyrin 24-hydroxylase
Reaction: (1) β-amyrin + [reduced NADPH—hemoprotein reductase] + O₂ = 24-hydroxy-β-amyrin + [oxidized NADPH—hemoprotein reductase] + H₂O
(2) sophoradiol + [reduced NADPH—hemoprotein reductase] + O₂ = 24-hydroxysophoradiol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): sophoradiol 24-hydroxylase; CYP93E1
Systematic name: β-amyrin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (24-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Found in plants and participates in the biosynthesis of soybean saponins.
References: [3485]

[EC 1.14.14.134 created 2011 as EC 1.14.99.43, transferred 2018 to EC 1.14.14.134]

EC 1.14.14.135

Accepted name: glyceollin synthase
Reaction: (1) 2-dimethylallyl-(6a*S*,11a*S*)-3,6a,9-trihydroxypterocarpan + [reduced NADPH—hemoprotein reductase] + O₂ = glyceollin II + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
(2) 2-dimethylallyl-(6a*S*,11a*S*)-3,6a,9-trihydroxypterocarpan + [reduced NADPH—hemoprotein reductase] + O₂ = glyceollin III + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
(3) 4-dimethylallyl-(6a*S*,11a*S*)-3,6a,9-trihydroxypterocarpan + [reduced NADPH—hemoprotein reductase] + O₂ = glyceollin I + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): dimethylallyl-3,6a,9-trihydroxypterocarpan cyclase
Systematic name: 2-dimethylallyl-(6a*S*,11a*S*)-3,6a,9-trihydroxypterocarpan,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (cyclizing)
Comments: A cytochrome *P*-450 (heme-thiolate) protein purified from soybean.
References: [4168]

[EC 1.14.14.135 created 2004 as EC 1.14.13.85, transferred 2018 to EC 1.14.14.135]

EC 1.14.14.136

Accepted name: deoxysarpagine hydroxylase
Reaction: 10-deoxysarpagine + [reduced NADPH—hemoprotein reductase] + O₂ = sarpagine + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): DOSH
Systematic name: 10-deoxysarpagine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (10-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Rauvolfia serpentina*.
References: [4397]

[EC 1.14.14.136 created 2005 as EC 1.14.13.91, transferred 2018 to EC 1.14.14.136]

EC 1.14.14.137

Accepted name: (+)-abscisic acid 8'-hydroxylase
Reaction: (+)-abscisate + [reduced NADPH—hemoprotein reductase] + O₂ = 8'-hydroxyabscisate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): (+)-ABA 8'-hydroxylase; ABA 8'-hydroxylase; CYP707A1 (gene name)
Systematic name: abscisate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (8'-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. Catalyses the first step in the oxidative degradation of abscisic acid and is considered to be the pivotal enzyme in controlling the rate of degradation of this plant hormone [713]. CO inhibits the reaction, but its effects can be reversed by the presence of blue light [713]. The 8'-hydroxyabscisate formed can be converted into (–)-phaseic acid, most probably spontaneously.
References: [713, 2061, 3285]

[EC 1.14.14.137 created 2005 as EC 1.14.13.93, transferred 2018 EC 1.14.14.137]

EC 1.14.14.138

Accepted name: lithocholate 6β-hydroxylase
Reaction: lithocholate + [reduced NADPH—hemoprotein reductase] + O₂ = 6β-hydroxylithocholate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): lithocholate 6β-monooxygenase; CYP3A10; 6β-hydroxylase; cytochrome P450 3A10; lithocholic acid 6β-hydroxylase
Systematic name: lithocholate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (6β-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein from *Mesocricetus auratus* (golden hamster). Expression of the gene for this enzyme is 50-fold higher in male compared to female hamsters [3842].
References: [3842, 542, 3701, 3263]

[EC 1.14.14.138 created 2005 as EC 1.14.13.94, transferred 2018 to EC 1.14.14.138]

EC 1.14.14.139

- Accepted name:** 5 β -cholestane-3 α ,7 α -diol 12 α -hydroxylase
Reaction: 5 β -cholestane-3 α ,7 α -diol + [reduced NADPH—hemoprotein reductase] + O₂ = 5 β -cholestane-3 α ,7 α ,12 α -triol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): 5 β -cholestane-3 α ,7 α -diol 12 α -monooxygenase; sterol 12 α -hydroxylase (ambiguous); CYP8B1; cytochrome P450 8B1
Systematic name: 5 β -cholestane-3 α ,7 α -diol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (12 α -hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in mammals. This is the key enzyme in the biosynthesis of the bile acid cholic acid (3 α ,7 α ,12 α -trihydroxy-5 β -cholanoic acid). The activity of this enzyme determines the biosynthetic ratio between cholic acid and chenodeoxycholic acid [2322]. The enzyme can also hydroxylate the substrate at the 25 and 26 position, but to a lesser extent [1378].
References: [1378, 1377, 2322, 784, 4341, 3263]

[EC 1.14.14.139 created 2005 as EC 1.14.13.96, transferred 2018 to EC 1.14.14.139]

[1.14.14.140 *Transferred entry. licodione synthase. Now included with EC 1.14.14.162, flavanone 2-hydroxylase*]

[EC 1.14.14.140 created 2004 as EC 1.14.13.87, transferred 2018 to EC 1.14.14.140, transferred 2018 to EC 1.14.14.162, deleted 2018]

EC 1.14.14.141

- Accepted name:** psoralen synthase
Reaction: (+)-marmesin + [reduced NADPH—hemoprotein reductase] + O₂ = psoralen + [oxidized NADPH—hemoprotein reductase] + acetone + 2 H₂O
Other name(s): CYP71AJ1
Systematic name: (+)-marmesin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: This microsomal cytochrome *P*-450 (heme-thiolate) enzyme is rather specific for (+)-marmesin, although it can also accept 5-hydroxymarmesin to a much lesser extent. Furanocoumarins protect plants from fungal invasion and herbivore attack. (+)-Columbianetin, the angular furanocoumarin analogue of the linear furanocoumarin (+)-marmesin, acts as a competitive inhibitor even though it is not a substrate.
References: [2137]

[EC 1.14.14.141 created 2007 as EC 1.14.13.102, transferred 2018 to EC 1.14.14.141]

EC 1.14.14.142

- Accepted name:** 8-dimethylallylnaringenin 2'-hydroxylase
Reaction: sophoraflavanone B + [reduced NADPH—hemoprotein reductase] + O₂ = leachianone G + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): 8-DMAN 2'-hydroxylase
Systematic name: sophoraflavanone-B,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (2'-hydroxylating)
Comments: A membrane-bound cytochrome *P*-450 (heme-thiolate) protein that is associated with the endoplasmic reticulum [4314, 4460]. This enzyme is specific for sophoraflavanone B as substrate. Along with EC 2.5.1.70 (naringenin 8-dimethylallyltransferase) and EC 2.5.1.71 (leachianone G 2''-dimethylallyltransferase), this enzyme forms part of the sophoraflavanone G biosynthetic pathway.
References: [4314, 4460]

[EC 1.14.14.142 created 2007 as EC 1.14.13.103, transferred 2018 to EC 1.14.14.142]

EC 1.14.14.143

- Accepted name:** (+)-menthofuran synthase
Reaction: (+)-pulegone + [reduced NADPH—hemoprotein reductase] + O₂ = (+)-menthofuran + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): menthofuran synthase; (+)-pulegone 9-hydroxylase; (+)-MFS; cytochrome P450 menthofuran synthase
Systematic name: (+)-pulegone,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (9-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The conversion of substrate into product involves the hydroxylation of the *syn*-methyl (C₉), intramolecular cyclization to the hemiketal and dehydration to the furan [278]. This is the second cytochrome *P*-450-mediated step of monoterpene metabolism in peppermint, with the other step being catalysed by EC 1.14.14.99, (*S*)-limonene 3-monooxygenase [278].
References: [278, 2370]

[EC 1.14.14.143 created 2008 as EC 1.14.13.104, transferred 2018 to EC 1.14.14.143]

EC 1.14.14.144

Accepted name: abieta-7,13-diene hydroxylase
Reaction: abieta-7,13-diene + [reduced NADPH—hemoprotein reductase] + O₂ = abieta-7,13-dien-18-ol + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): abietadiene hydroxylase (ambiguous)
Systematic name: abieta-7,13-diene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (18-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. This enzyme catalyses a step in the pathway of abietic acid biosynthesis. The activity has been demonstrated in cell-free stem extracts of *Abies grandis* (grand fir) and *Pinus contorta* (lodgepole pine). Activity is induced by wounding of the plant tissue [1117].
References: [1115, 1117]

[EC 1.14.14.144 created 2009 as EC 1.14.13.108, modified 2012, transferred 2018 to EC 1.14.14.144]

EC 1.14.14.145

Accepted name: abieta-7,13-dien-18-ol hydroxylase
Reaction: abieta-7,13-dien-18-ol + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = abieta-7,13-dien-18-oate + 2 [oxidized NADPH—hemoprotein reductase] + 3 H₂O (overall reaction)
(1a) abieta-7,13-dien-18-ol + [reduced NADPH—hemoprotein reductase] + O₂ = abieta-7,13-dien-18,18-diol + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) abieta-7,13-dien-18,18-diol = abieta-7,13-dien-18-al + H₂O (spontaneous)
(1c) abieta-7,13-dien-18-al + [reduced NADPH—hemoprotein reductase] + O₂ = abieta-7,13-dien-18-oate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP720B1; PtAO; abietadienol hydroxylase (ambiguous)
Systematic name: abieta-7,13-dien-18-ol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (18-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. This enzyme catalyses a step in the pathway of abietic acid biosynthesis. The activity has been demonstrated in cell-free stem extracts of *Abies grandis* (grand fir) and *Pinus contorta* (lodgepole pine) [1115], and the gene encoding the enzyme has been identified in *Pinus taeda* (loblolly pine) [3198]. The recombinant enzyme catalyses the oxidation of multiple diterpene alcohol and aldehydes, including levopimaradienol, isopimara-7,15-dienol, isopimara-7,15-dienal, dehydroabietadienol and dehydroabietadienal. It is not able to oxidize abietadiene.
References: [1115, 1117, 3198]

[EC 1.14.14.145 created 2009 as EC 1.14.13.109, modified 2012, transferred 2018 to EC 1.14.14.145]

EC 1.14.14.146

Accepted name: geranylgeraniol 18-hydroxylase
Reaction: geranylgeraniol + [reduced NADPH—hemoprotein reductase] + O₂ = 18-hydroxygeranylgeraniol + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): GGOH-18-hydroxylase
Systematic name: geranylgeraniol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (18-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Croton sublyratus*.
References: [3820]

[EC 1.14.14.146 created 2009 as EC 1.14.13.110, transferred 2018 to EC 1.14.14.146]

EC 1.14.14.147

Accepted name: 3-*epi*-6-deoxocathasterone 23-monooxygenase
Reaction: (1) 3-*epi*-6-deoxocathasterone + [reduced NADPH—hemoprotein reductase] + O₂ = 6-deoxotyphasterol + [oxidized NADPH—hemoprotein reductase] + H₂O
(2) (22*S*,24*R*)-22-hydroxy-5α-ergostan-3-one + [reduced NADPH—hemoprotein reductase] + O₂ = 3-dehydro-6-deoxoteasterone + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): cytochrome P450 90C1; CYP90D1; CYP90C1
Systematic name: 3-*epi*-6-deoxocathasterone,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*C*-23-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein involved in brassinosteroid biosynthesis. *C*-23 hydroxylation shortcuts bypass campestanol, 6-deoxocathasterone, and 6-deoxoteasterone and lead directly from (22*S*,24*R*)-22-hydroxy-5α-ergostan-3-one and 3-*epi*-6-deoxocathasterone to 3-dehydro-6-deoxoteasterone and 6-deoxotyphasterol [2850].
References: [2850]

[EC 1.14.14.147 created 2010 as EC 1.14.13.112, transferred 2018 to EC 1.14.14.147]

EC 1.14.14.148

Accepted name: angelicin synthase
Reaction: (+)-columbianetin + [reduced NADPH—hemoprotein reductase] + O₂ = angelicin + [oxidized NADPH—hemoprotein reductase] + acetone + 2 H₂O
Other name(s): CYP71AJ4 (gene name)
Systematic name: (+)-columbianetin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase
Comments: This cytochrome *P*-450 (heme-thiolate) enzyme from wild parsnip is involved in the formation of angular furanocoumarins. Attacks its substrate by *syn*-elimination of hydrogen from *C*-3'.
References: [2136]

[EC 1.14.14.148 created 2010 as EC 1.14.13.115, transferred 2018 to EC 1.14.14.148]

EC 1.14.14.149

Accepted name: 5-epiaristolochene 1,3-dihydroxylase
Reaction: 5-epiaristolochene + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = capsidiol + 2 [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): 5-*epi*-aristolochene 1,3-dihydroxylase; EAH; CYP71D20
Systematic name: 5-epiaristolochene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (1- and 3-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Kinetic studies suggest that 1β-hydroxyepiaristolochene is mainly formed first followed by hydroxylation at *C*-3. However the reverse order via 3α-hydroxyepiaristolochene does occur.
References: [3114, 3782]

[EC 1.14.14.149 created 2011 as EC 1.14.13.119, transferred 2018 to EC 1.14.14.149]

EC 1.14.14.150

Accepted name: costunolide synthase

Reaction: germacra-1(10),4,11(13)-trien-12-oate + [reduced NADPH—hemoprotein reductase] + O₂ = (+)-costunolide + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(1a) germacra-1(10),4,11(13)-trien-12-oate + [reduced NADPH—hemoprotein reductase] + O₂ = 6 α -hydroxygermacra-1(10),4,11(13)-trien-12-oate + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) 6 α -hydroxygermacra-1(10),4,11(13)-trien-12-oate = (+)-costunolide + H₂O (spontaneous)

Other name(s): CYP71BL2

Systematic name: germacra-1(10),4,11(13)-trien-12-oate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (6 α -hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein from chicory plants. The enzyme hydroxylates carbon C-6 of germacra-1(10),4,11(13)-trien-12-oate to give 6 α -hydroxygermacra-1(10),4,11(13)-trien-12-oate, which spontaneously cyclises to form the lactone ring.

References: [763]

[EC 1.14.14.150 created 2011 as EC 1.14.13.120, transferred 2018 to EC 1.14.14.150]

EC 1.14.14.151

Accepted name: premnaspirodiene oxygenase

Reaction: (–)-vetispiradiene + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = solavetivone + 2 [oxidized NADPH—hemoprotein reductase] + 3 H₂O (overall reaction)

(1a) (–)-vetispiradiene + [reduced NADPH—hemoprotein reductase] + O₂ = solavetivol + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) solavetivol + [reduced NADPH—hemoprotein reductase] + O₂ = solavetivone + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

Other name(s): HPO; *Hyoscyamus muticus* premnaspirodiene oxygenase; CYP71D55

Systematic name: (–)-vetispiradiene,[reduced NADPH—hemoprotein reductase]:oxygen 2 α -oxidoreductase

Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme from the plant *Hyoscyamus muticus* also hydroxylates valencene at C-2 to give the α -hydroxy compound, nootkatol, and this is converted into nootkatone. 5-Epiaristolochene and epieremophilene are hydroxylated at C-2 to give a 2 β -hydroxy derivatives that are not oxidized further.

References: [3781]

[EC 1.14.14.151 created 2011 as EC 1.14.13.121, transferred 2018 to EC 1.14.14.151]

EC 1.14.14.152

Accepted name: β -amyrin 11-oxidase

Reaction: β -amyrin + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = 11-oxo- β -amyrin + 2 [oxidized NADPH—hemoprotein reductase] + 3 H₂O (overall reaction)

(1a) β -amyrin + [reduced NADPH—hemoprotein reductase] + O₂ = 11 α -hydroxy- β -amyrin + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) 11 α -hydroxy- β -amyrin + [reduced NADPH—hemoprotein reductase] + O₂ = 11-oxo- β -amyrin + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

Other name(s): CYP88D6

Systematic name: β -amyrin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein from the plant *Glycyrrhiza uralensis* (Chinese licorice) that participates in the glycyrrhizin biosynthesis pathway. The enzyme is also able to oxidize 30-hydroxy- β -amyrin to 11 α ,30-dihydroxy- β -amyrin but this is not thought to be part of glycyrrhizin biosynthesis.

References: [3433]

[EC 1.14.14.152 created 2011 as EC 1.14.13.134, transferred 2018 to EC 1.14.14.152]

EC 1.14.14.153

Accepted name: indole-2-monooxygenase

Reaction: indole + [reduced NADPH—hemoprotein reductase] + O₂ = indolin-2-one + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): BX2 (gene name); CYP71C4 (gene name)
Systematic name: indole,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (2-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme is involved in the biosynthesis of protective and allelopathic benzoxazinoids in some plants, most commonly from the family of Poaceae (grasses).
References: [1063, 1220]

[EC 1.14.14.153 created 2012 as EC 1.14.13.137, transferred 2018 to EC 1.14.14.153]

EC 1.14.14.154

Accepted name: sterol 14 α -demethylase
Reaction: a 14 α -methylsteroid + 3 [reduced NADPH—hemoprotein reductase] + 3 O₂ = a Δ^{14} -steroid + formate + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)
(1a) a 14 α -methylsteroid + [reduced NADPH—hemoprotein reductase] + O₂ = a 14 α -hydroxymethylsteroid + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) a 14 α -hydroxysteroid + [reduced NADPH—hemoprotein reductase] + O₂ = a 14 α -formylsteroid + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
(1c) a 14 α -formylsteroid + [reduced NADPH—hemoprotein reductase] + O₂ = a Δ^{14} -steroid + formate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): obtusifoliol 14-demethylase; lanosterol 14-demethylase; lanosterol 14 α -demethylase; sterol 14-demethylase; CYP51 (gene name); ERG11 (gene name)
Systematic name: sterol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (14-methyl cleaving)
Comments: This cytochrome *P*-450 (heme-thiolate) enzyme acts on a range of steroids with a 14 α -methyl group, such as obtusifoliol and lanosterol. The enzyme catalyses a hydroxylation and a reduction of the 14 α -methyl group, followed by a second hydroxylation, resulting in the elimination of formate and formation of a 14(15) double bond.
References: [59, 4381, 104, 102, 103, 168]

[EC 1.14.14.154 created 2001 as EC 1.14.13.70, modified 2013, transferred 2018 EC 1.14.14.154]

EC 1.14.14.155

Accepted name: 3,6-diketocamphane 1,2-monooxygenase
Reaction: (-)-bornane-2,5-dione + O₂ + FMNH₂ = (-)-5-oxo-1,2-campholide + FMN + H₂O
Other name(s): 3,6-diketocamphane lactonizing enzyme; 3,6-DKCMO
Systematic name: (-)-bornane-2,5-dione,FMNH₂:oxygen oxidoreductase (1,2-lactonizing)
Comments: A Baeyer-Villiger monooxygenase isolated from camphor-grown strains of *Pseudomonas putida* and encoded on the cam plasmid. Involved in the degradation of (-)-camphor. Requires a dedicated NADH—FMN reductase [*cf.* EC 1.5.1.42, FMN reductase (NADH)] [1693, 1678]. The product spontaneously converts to [(1*R*)-2,2,3-trimethyl-5-oxocyclopent-3-enyl]acetate.
References: [1693, 1678]

[EC 1.14.14.155 created 2018]

EC 1.14.14.156

Accepted name: tryptophan *N*-monooxygenase
Reaction: L-tryptophan + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = (*E*)-indol-3-ylacetaldoxime + 2 [oxidized NADPH—hemoprotein reductase] + CO₂ + 3 H₂O (overall reaction)
(1a) L-tryptophan + [reduced NADPH—hemoprotein reductase] + O₂ = *N*-hydroxy-L-tryptophan + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) *N*-hydroxy-L-tryptophan + [reduced NADPH—hemoprotein reductase] + O₂ = *N,N*-dihydroxy-L-tryptophan + [oxidized NADPH—hemoprotein reductase] + H₂O

(1c) *N,N*-dihydroxy-L-tryptophan = (*E*)-indol-3-ylacetaldoxime + CO₂ + H₂O
Other name(s): tryptophan *N*-hydroxylase; CYP79B1; CYP79B2; CYP79B3
Systematic name: L-tryptophan,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*N*-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein from the plant *Arabidopsis thaliana*. This enzyme catalyses two successive *N*-hydroxylations of L-tryptophan, the first steps in the biosynthesis of both auxin and the indole alkaloid phytoalexin camalexin. The product of the two hydroxylations, *N,N*-dihydroxy-L-tryptophan, is extremely labile and dehydrates spontaneously. The dehydrated product is then subject to a decarboxylation that produces an oxime. It is still not known whether the decarboxylation is spontaneous or catalysed by the enzyme.
References: [2538, 1608, 4466, 2744]

[EC 1.14.14.156 created 2011 as EC 1.14.13.125, transferred 2018 to EC 1.14.14.156]

EC 1.14.14.157

Accepted name: indolin-2-one monooxygenase
Reaction: indolin-2-one + [reduced NADPH—hemoprotein reductase] + O₂ = 3-hydroxyindolin-2-one + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): BX3 (gene name); CYP71C2 (gene name)
Systematic name: indolin-2-one,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme is involved in the biosynthesis of protective and allelopathic benzoxazinoids in some plants, most commonly from the family of Poaceae (grasses).
References: [1063, 1220]

[EC 1.14.14.157 created 2012 as EC 1.14.13.138, transferred 2018 to EC 1.14.14.157]

EC 1.14.14.158

Accepted name: carotenoid ϵ hydroxylase
Reaction: (1) α -carotene + [reduced NADPH-hemoprotein reductase] + O₂ = α -cryptoxanthin + [oxidized NADPH-hemoprotein reductase] + H₂O
(2) zeinoxanthin + [reduced NADPH-hemoprotein reductase] + O₂ = lutein + [oxidized NADPH-hemoprotein reductase] + H₂O
Other name(s): CYP97C1; LUT1; CYP97C; carotene ϵ -monooxygenase
Systematic name: α -carotene,[reduced NADPH-hemoprotein reductase]:oxygen oxidoreductase (3-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein.
References: [3025, 3887, 3647, 539, 3148]

[EC 1.14.14.158 created 2011 as EC 1.14.99.45, transferred 2018 to EC 1.14.14.158]

EC 1.14.14.159

Accepted name: dolabradiene monooxygenase
Reaction: (1) dolabradiene + O₂ + [reduced NADPH—hemoprotein reductase] = 15,16-epoxydolabrene + H₂O + [oxidized NADPH—hemoprotein reductase]
(2) 15,16-epoxydolabrene + O₂ + [reduced NADPH—hemoprotein reductase] = 3 β -hydroxy-15,16-epoxydolabrene + H₂O + [oxidized NADPH—hemoprotein reductase]
Other name(s): CYP71Z16 (gene name)
Systematic name: dolabradiene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3 β -hydroxy-15,16-epoxydolabrene-forming)
Comments: A cytochrome *P*-450 (heme thiolate) enzyme characterized from maize. The enzyme catalyses the epoxidation of dolabradiene at C-16, followed by hydroxylation at C-3.
References: [2357]

[EC 1.14.14.159 created 2018]

EC 1.14.14.160

- Accepted name:** zealexin A1 synthase
- Reaction:** (S)- β -macrocarpene + 3 O₂ + 3 [reduced NADPH—hemoprotein reductase] = zealexin A1 + 4 H₂O + 3 [oxidized NADPH—hemoprotein reductase] (overall reaction)
(1a) (S)- β -macrocarpene + O₂ + [reduced NADPH—hemoprotein reductase] = [(4S)-4-(5,5-dimethylcyclohex-1-en-1-yl)-cyclohex-1-en-1-yl]methanol + H₂O + [oxidized NADPH—hemoprotein reductase]
(1b) [(4S)-4-(5,5-dimethylcyclohex-1-en-1-yl)-cyclohex-1-en-1-yl] methanol + O₂ + [reduced NADPH—hemoprotein reductase] = (4S)-4-(5,5-dimethylcyclohex-1-en-1-yl)cyclohex-1-ene-1-carbaldehyde + 2 H₂O + [oxidized NADPH—hemoprotein reductase]
(1c) (4S)-4-(5,5-dimethylcyclohex-1-en-1-yl)cyclohex-1-ene-1-carbaldehyde + O₂ + [reduced NADPH—hemoprotein reductase] = zealexin A1 + H₂O + [oxidized NADPH—hemoprotein reductase]
- Other name(s):** CYP71Z18 (gene name)
- Systematic name:** (S)- β -macrocarpene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (zealexin A1-forming)
- Comments:** A cytochrome *P*-450 (heme thiolate) enzyme characterized from maize. The enzyme sequentially oxidizes(S)- β -macrocarpene via alcohol and aldehyde intermediates to form zealexin A1, a maize phytoalexin that provides biochemical protection against fungal infection.
- References:** [2389]

[EC 1.14.14.160 created 2018]

EC 1.14.14.161

- Accepted name:** nepetalactol monooxygenase
- Reaction:** (+)-*cis,trans*-nepetalactol + 3 [reduced NADPH—hemoprotein reductase] + 3 O₂ = 7-deoxyloganetate + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)
(1a) (+)-*cis,trans*-nepetalactol + [reduced NADPH—hemoprotein reductase] + O₂ = 7-deoxyloganic alcohol + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) 7-deoxyloganic alcohol + [reduced NADPH—hemoprotein reductase] + O₂ = iridotrial + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
(1c) iridotrial + [reduced NADPH—hemoprotein reductase] + O₂ = 7-deoxyloganetate + [oxidized NADPH—hemoprotein reductase] + H₂O
- Other name(s):** CYP76A26 (gene name); iridoid oxidase (misleading)
- Systematic name:** (+)-*cis,trans*-nepetalactol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (hydroxylating)
- Comments:** The enzyme, characterized from the plant *Catharanthus roseus*, is a cytochrome *P*-450 (heme thiolate) protein. It catalyses three successive reactions in the pathway leading to biosynthesis of monoterpenoid indole alkaloids.
- References:** [2531]

[EC 1.14.14.161 created 2018]

EC 1.14.14.162

- Accepted name:** flavanone 2-hydroxylase
- Reaction:** a flavanone + [reduced NADPH—hemoprotein reductase] + O₂ = a 2-hydroxyflavanone + [oxidized NADPH—hemoprotein reductase] + H₂O
- Other name(s):** CYP93G2 (gene name); CYP93B1 (gene name); (2S)-flavanone 2-hydroxylase; licodione synthase
- Systematic name:** flavanone,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (2-hydroxylating)
- Comments:** A cytochrome *P*-450 (heme thiolate) plant enzyme that catalyses the 2-hydroxylation of multiple flavanones such as (2S)-naringenin, (2S)-eriodictyol, (2S)-pinocembrin, and (2S)-liquiritigenin. The products are *meta*-stable and exist in an equilibrium with open forms such as 1-(4-hydroxyphenyl)-3-(2,4,6-trihydroxyphenyl)propane-1,3-dione.
- References:** [2908, 44, 877]

[EC 1.14.14.162 created 2018. EC 1.14.14.140 created 2004 as EC 1.14.13.87, transferred 2018 to EC 1.14.14.140, transferred 2018 to EC 1.14.14.162]

EC 1.14.14.163

Accepted name: (*S*)-1-hydroxy-*N*-methylcanadine 13-hydroxylase
Reaction: (*S*)-1-hydroxy-*N*-methylcanadine + [reduced NADPH—hemoprotein reductase] + O₂ = (1*S*,14*R*)-1,13-dihydroxy-*N*-methylcanadine + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP82X2 (gene name)
Systematic name: (*S*)-1-hydroxy-*N*-methylcanadine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (13-hydroxylating)
Comments: The enzyme, characterized from the plant *Papaver somniferum* (opium poppy), participates in the biosynthesis of the isoquinoline alkaloid noscapine.
References: [737, 2239, 2237]

[EC 1.14.14.163 created 2018]

EC 1.14.14.164

Accepted name: fraxetin 5-hydroxylase
Reaction: fraxetin + [reduced NADPH—hemoprotein reductase] + O₂ = sideretin (reduced form) + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP82C4; fraxetin 5-monooxygenase
Systematic name: fraxetin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (5-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein involved in biosynthesis of iron(III)-chelating coumarins in higher plants.
References: [3113]

[EC 1.14.14.164 created 2018]

EC 1.14.14.165

Accepted name: indole-3-carbonyl nitrile 4-hydroxylase
Reaction: indole-3-carbonyl nitrile + [reduced NADPH—hemoprotein reductase] + O₂ = 4-hydroxyindole-3-carbonyl nitrile + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP82C2
Systematic name: indole-3-carbonyl nitrile,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (4-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein characterized from the plant *Arabidopsis thaliana*. Involved in biosynthesis of small cyanogenic compounds that take part in pathogen defense. The enzyme also catalyses the 5-hydroxylation of xanthotoxin [2063].
References: [2063, 3112]

[EC 1.14.14.165 created 2018]

EC 1.14.14.166

Accepted name: (*S*)-*N*-methylcanadine 1-hydroxylase
Reaction: (*S*)-*N*-methylcanadine + [reduced NADPH—hemoprotein reductase] + O₂ = (*S*)-1-hydroxy-*N*-methylcanadine + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP82Y1 (gene name)
Systematic name: (*S*)-*N*-methylcanadine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (1-hydroxylating)
Comments: This cytochrome *P*-450 (heme-thiolate) enzyme, characterized from the plant *Papaver somniferum* (opium poppy), participates in the biosynthesis of the isoquinoline alkaloid noscapine.
References: [739, 2237]

[EC 1.14.14.166 created 2018]

EC 1.14.14.167

Accepted name: (13*S*,14*R*)-13-*O*-acetyl-1-hydroxy-*N*-methylcanadine 8-hydroxylase
Reaction: (13*S*,14*R*)-13-*O*-acetyl-1-hydroxy-*N*-methylcanadine + [reduced NADPH—hemoprotein reductase] + O₂ = (13*S*,14*R*)-13-*O*-acetyl-1,8-dihydroxy-*N*-methylcanadine + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): CYP82X1 (gene name)
Systematic name: (13*S*,14*R*)-13-*O*-acetyl-1-hydroxy-*N*-methylcanadine 8-hydroxylase,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (8-hydroxylating)
Comments: This cytochrome *P*-450 (heme-thiolate) enzyme, characterized from the plant *Papaver somniferum* (opium poppy), participates in the biosynthesis of the isoquinoline alkaloid noscapine.
References: [737, 2239, 2237]

[EC 1.14.14.167 created 2018]

EC 1.14.14.168

Accepted name: germacrene A acid 8β-hydroxylase
Reaction: germacra-1(10),4,11(13)-trien-12-oate + [reduced NADPH—hemoprotein reductase] + O₂ = 8β-hydroxygermacra-1(10),4,11(13)-trien-12-oate + [oxidized NADPH—hemoprotein reductase] + H₂O
Other name(s): HaG8H; CYP71BL1; CYP71BL6
Systematic name: germacra-1(10),4,11(13)-trien-12-oate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (8β-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein from the plant *Helianthus annuus* (common sunflower). The cyclisation of 8β-hydroxygermacra-1(10),4,11(13)-triene-12-oate to inunolide (12,8β) does not seem to occur spontaneously. The enzyme from *Inula hupehensis* also forms some 8α-hydroxygermacra-1(10),4,11(13)-triene-12-oate, which spontaneously cyclises to 8-*epi*-inunolide (12,8α) (*cf.* EC 1.14.14.170 8-*epi*-inunolide synthase).
References: [1065, 1250]

[EC 1.14.14.168 created 2018]

EC 1.14.14.169

Accepted name: eupatolide synthase
Reaction: 8β-hydroxygermacra-1(10),4,11(13)-trien-12-oate + [reduced NADPH—hemoprotein reductase] + O₂ = eupatolide + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(1a) 8β-hydroxygermacra-1(10),4,11(13)-trien-12-oate + [reduced NADPH—hemoprotein reductase] + O₂ = 6α,8β-dihydroxygermacra-1(10),4,11(13)-trien-12-oate + [oxidized NADPH—hemoprotein reductase] + H₂O
(1b) 6α,8β-dihydroxygermacra-1(10),4,11(13)-trien-12-oate = eupatolide + H₂O (spontaneous)
Other name(s): CYP71DD6; HaES
Systematic name: 8β-hydroxygermacra-1(10),4,11(13)-trien-12-oate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (6α-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein from the plant *Helianthus annuus* (common sunflower).
References: [1065]

[EC 1.14.14.169 created 2018]

EC 1.14.14.170

Accepted name: 8-*epi*-inunolide synthase
Reaction: germacra-1(10),4,11(13)-trien-12-oate + [reduced NADPH—hemoprotein reductase] + O₂ = 8-*epi*-inunolide + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)
(1a) germacra-1(10),4,11(13)-trien-12-oate + [reduced NADPH—hemoprotein reductase] + O₂ = 8α-hydroxygermacra-1(10),4,11(13)-trien-12-oate + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) 8 α -hydroxygermacra-1(10),4,11(13)-trien-12-oate = 8-*epi*-inunolide + H₂O (spontaneous)
Other name(s): CYP71BL1
Systematic name: germacra-1(10),4,11(13)-trien-12-oate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (8 α -hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein from the plant *Inula hupehensis*. The enzyme also produces 8 β -hydroxygermacra-1(10),4,11(13)-triene-12-oate (EC 1.14.14.168, germacrene A acid 8 β -hydroxylase).
References: [1250]

[EC 1.14.14.170 created 2018]

EC 1.14.15 With reduced iron-sulfur protein as one donor, and incorporation of one atom of oxygen into the other donor

EC 1.14.15.1

Accepted name: camphor 5-monooxygenase
Reaction: (+)-camphor + reduced putidaredoxin + O₂ = (+)-*exo*-5-hydroxycamphor + oxidized putidaredoxin + H₂O
Other name(s): camphor 5-*exo*-methylene hydroxylase; 2-bornanone 5-*exo*-hydroxylase; bornanone 5-*exo*-hydroxylase; camphor 5-*exo*-hydroxylase; camphor 5-*exo*-hydroxylase; camphor hydroxylase; *d*-camphor monooxygenase; methylene hydroxylase; methylene monooxygenase; D-camphor-*exo*-hydroxylase; camphor methylene hydroxylase
Systematic name: (+)-camphor, reduced putidaredoxin:oxygen oxidoreductase (5-hydroxylating)
Comments: A heme-thiolate protein (*P*-450). Also acts on (-)-camphor and 1,2-campholide, forming 5-*exo*-hydroxy-1,2-campholide.
References: [1453, 3954]

[EC 1.14.15.1 created 1972, modified 1986]

[1.14.15.2 Transferred entry. camphor 1,2-monooxygenase. Now EC 1.14.13.162, 2,5-diketocamphane 1,2-monooxygenase.]

[EC 1.14.15.2 created 1972, deleted 2012]

EC 1.14.15.3

Accepted name: alkane 1-monooxygenase
Reaction: octane + 2 reduced rubredoxin + O₂ + 2 H⁺ = 1-octanol + 2 oxidized rubredoxin + H₂O
Other name(s): alkane 1-hydroxylase; ω -hydroxylase; fatty acid ω -hydroxylase; alkane monooxygenase; 1-hydroxylase; alkane hydroxylase
Systematic name: alkane, reduced-rubredoxin:oxygen 1-oxidoreductase
Comments: Some enzymes in this group are heme-thiolate proteins (*P*-450). Also hydroxylates fatty acids in the ω -position.
References: [502, 2488, 2988]

[EC 1.14.15.3 created 1972]

EC 1.14.15.4

Accepted name: steroid 11 β -monooxygenase
Reaction: a steroid + 2 reduced adrenodoxin + O₂ + 2 H⁺ = an 11 β -hydroxysteroid + 2 oxidized adrenodoxin + H₂O
Other name(s): steroid 11 β -hydroxylase; steroid 11 β /18-hydroxylase
Systematic name: steroid, reduced-adrenodoxin:oxygen oxidoreductase (11 β -hydroxylating)
Comments: A heme-thiolate protein (*P*-450). Also hydroxylates steroids at the 18-position, and converts 18-hydroxycorticosterone into aldosterone.
References: [1259, 1438, 3907, 4335, 4495]

[EC 1.14.15.4 created 1961 as EC 1.99.1.7, transferred 1965 to EC 1.14.1.6, transferred 1972 to EC 1.14.15.4, modified 1989, modified 2014]

EC 1.14.15.5

Accepted name: corticosterone 18-monooxygenase
Reaction: corticosterone + 2 reduced adrenodoxin + O₂ + 2 H⁺ = 18-hydroxycorticosterone + 2 oxidized adrenodoxin + H₂O
Other name(s): corticosterone 18-hydroxylase; corticosterone methyl oxidase
Systematic name: corticosterone, reduced-adrenodoxin:oxygen oxidoreductase (18-hydroxylating)
References: [3119]

[EC 1.14.15.5 created 1972]

EC 1.14.15.6

Accepted name: cholesterol monooxygenase (side-chain-cleaving)
Reaction: cholesterol + 6 reduced adrenodoxin + 3 O₂ + 6 H⁺ = pregnenolone + 4-methylpentanal + 6 oxidized adrenodoxin + 4 H₂O (overall reaction)
(1a) cholesterol + 2 reduced adrenodoxin + O₂ + 2 H⁺ = (22*R*)-22-hydroxycholesterol + 2 oxidized adrenodoxin + H₂O
(1b) (22*R*)-22-hydroxycholesterol + 2 reduced adrenodoxin + O₂ + 2 H⁺ = (20*R*,22*R*)-20,22-dihydroxycholesterol + 2 oxidized adrenodoxin + H₂O
(1c) (20*R*,22*R*)-20,22-dihydroxy-cholesterol + 2 reduced adrenodoxin + O₂ + 2 H⁺ = pregnenolone + 4-methylpentanal + 2 oxidized adrenodoxin + 2 H₂O
Other name(s): cholesterol desmolase; cytochrome *P*-450_{sc}; C₂₇-side chain cleavage enzyme; cholesterol 20-22-desmolase; cholesterol C₂₀₋₂₂ desmolase; cholesterol side-chain cleavage enzyme; cholesterol side-chain-cleaving enzyme; steroid 20-22 desmolase; steroid 20-22-lyase; CYP11A1 (gene name)
Systematic name: cholesterol, reduced-adrenodoxin:oxygen oxidoreductase (side-chain-cleaving)
Comments: A heme-thiolate protein (cytochrome *P*-450). The reaction proceeds in three stages, with two hydroxylations at C-22 and C-20 preceding scission of the side-chain between carbons 20 and 22. The initial source of the electrons is NADPH, which transfers the electrons to the adrenodoxin via EC 1.18.1.6, adrenodoxin-NADP⁺ reductase.
References: [453, 1382, 1380, 3689, 2435]

[EC 1.14.15.6 created 1983, modified 2013, modified 2014]

EC 1.14.15.7

Accepted name: choline monooxygenase
Reaction: choline + O₂ + 2 reduced ferredoxin + 2 H⁺ = betaine aldehyde hydrate + H₂O + 2 oxidized ferredoxin
Systematic name: choline, reduced-ferredoxin:oxygen oxidoreductase
Comments: The spinach enzyme, which is located in the chloroplast, contains a Rieske-type [2Fe-2S] cluster, and probably also a mononuclear Fe centre. Requires Mg²⁺. Catalyses the first step of glycine betaine synthesis. In many bacteria, plants and animals, betaine is synthesized in two steps: (1) choline to betaine aldehyde and (2) betaine aldehyde to betaine. Different enzymes are involved in the first reaction. In plants, the reaction is catalysed by this enzyme whereas in animals and many bacteria it is catalysed by either membrane-bound EC 1.1.99.1 (choline dehydrogenase) or soluble EC 1.1.3.17 (choline oxidase) [4077]. The enzyme involved in the second step, EC 1.2.1.8 (betaine-aldehyde dehydrogenase), appears to be the same in plants, animals and bacteria. In some bacteria, betaine is synthesized from glycine through the actions of EC 2.1.1.156 (glycine/sarcosine *N*-methyltransferase) and EC 2.1.1.157 (sarcosine/dimethylglycine *N*-methyltransferase).
References: [414, 450, 3130, 3262, 2827, 2828, 4077]

[EC 1.14.15.7 created 2001, modified 2002 (EC 1.14.14.4 created 2000, incorporated 2002), modified 2005, modified 2011]

EC 1.14.15.8

- Accepted name:** steroid 15 β -monooxygenase
Reaction: progesterone + 2 reduced [2Fe-2S] ferredoxin + O₂ = 15 β -hydroxyprogesterone + 2 oxidized [2Fe-2S] ferredoxin + H₂O
Other name(s): cytochrome *P*-450_{meg}; cytochrome P450_{meg}; steroid 15 β -hydroxylase; CYP106A2; BmCYP106A2
Systematic name: progesterone, reduced-ferredoxin:oxygen oxidoreductase (15 β -hydroxylating)
Comments: The enzyme from the bacterium *Bacillus megaterium* hydroxylates a variety of 3-oxo- Δ^4 -steroids in position 15 β . Ring A-reduced, aromatic, and 3 β -hydroxy- Δ^4 -steroids do not serve as substrates [263].
References: [264, 263, 2271, 1238, 2272]

[EC 1.14.15.8 created 2010]

EC 1.14.15.9

- Accepted name:** spheroidene monooxygenase
Reaction: (1) spheroidene + 4 reduced ferredoxin [iron-sulfur] cluster + 2 O₂ + 4 H⁺ = spheroiden-2-one + 4 oxidized ferredoxin [iron-sulfur] cluster + 3 H₂O (overall reaction)
(1a) spheroidene + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = 2-hydroxyspheroidene + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(1b) 2-hydroxyspheroidene + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = 2,2-dihydroxyspheroidene + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(1c) 2,2-dihydroxyspheroidene = spheroiden-2-one + H₂O (spontaneous)
(2) spirilloxanthin + 4 reduced ferredoxin [iron-sulfur] cluster + 2 O₂ + 4 H⁺ = 2-oxospirilloxanthin + 4 oxidized ferredoxin [iron-sulfur] cluster + 3 H₂O (overall reaction)
(2a) spirilloxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = 2-hydroxyspirilloxanthin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(2b) 2-hydroxyspirilloxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = 2,2-dihydroxyspirilloxanthin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(2c) 2,2-dihydroxyspirilloxanthin = 2-oxospirilloxanthin + H₂O (spontaneous)
(3) 2-oxospirilloxanthin + 4 reduced ferredoxin [iron-sulfur] cluster + 2 O₂ + 4 H⁺ = 2,2'-dioxospirilloxanthin + 4 oxidized ferredoxin [iron-sulfur] cluster + 3 H₂O (overall reaction)
(3a) 2-oxospirilloxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = 2'-hydroxy-2-oxospirilloxanthin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(3b) 2'-hydroxy-2-oxospirilloxanthin + reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = 2',2'-dihydroxy-2-oxospirilloxanthin + oxidized ferredoxin [iron-sulfur] cluster + H₂O
(3c) 2',2'-dihydroxy-2-oxospirilloxanthin = 2,2'-dioxospirilloxanthin + H₂O (spontaneous)
Other name(s): CrtA; acyclic carotenoid 2-ketolase; spirilloxanthin monooxygenase; 2-oxo-spirilloxanthin monooxygenase
Systematic name: spheroidene, reduced-ferredoxin:oxygen oxidoreductase (spheroiden-2-one-forming)
Comments: The enzyme is involved in spheroidenone biosynthesis and in 2,2'-dioxospirilloxanthin biosynthesis. The enzyme from *Rhodobacter sphaeroides* contains heme at its active site [2173].
References: [2173, 1184]

[EC 1.14.15.9 created 2012, modified 2016]

EC 1.14.15.10

- Accepted name:** (+)-camphor 6-*endo*-hydroxylase
Reaction: (+)-camphor + reduced putidaredoxin + O₂ = (+)-6-*endo*-hydroxycamphor + oxidized putidaredoxin + H₂O
Other name(s): P450_{camr}
Systematic name: (+)-camphor, reduced putidaredoxin:oxygen oxidoreductase (6-*endo*-hydroxylating)
Comments: A cytochrome *P*-450 monooxygenase from the bacterium *Rhodococcus* sp. NCIMB 9784.
References: [1292]

[EC 1.14.15.10 created 2012]

EC 1.14.15.11

Accepted name: pentalenic acid synthase
Reaction: 1-deoxypentalenate + reduced ferredoxin + O₂ = pentalenate + oxidized ferredoxin + H₂O
Other name(s): CYP105D7; sav7469 (gene name); 1-deoxypentalenate, reduced ferredoxin:O₂ oxidoreductase
Systematic name: 1-deoxypentalenate, reduced ferredoxin:oxygen oxidoreductase
Comments: A heme-thiolate enzyme (*P*-450). Isolated from the bacterium *Streptomyces avermitilis*. The product, pentalenate, is a co-metabolite from pentalenolactone biosynthesis.
References: [3786]

[EC 1.14.15.11 created 2012]

[1.14.15.12 Transferred entry. pimeloyl-[acyl-carrier protein] synthase. Now EC 1.14.14.46, pimeloyl-[acyl-carrier protein] synthase]

[EC 1.14.15.12 created 2013, deleted 2017]

EC 1.14.15.13

Accepted name: pulcherriminic acid synthase
Reaction: cyclo(L-leucyl-L-leucyl) + 6 reduced ferredoxin + 3 O₂ = pulcherriminic acid + 6 oxidized ferredoxin + 4 H₂O
Other name(s): cyclo-L-leucyl-L-leucyl dipeptide oxidase; CYP134A1; CypX (ambiguous)
Systematic name: cyclo(L-leucyl-L-leucyl), reduced-ferredoxin:oxygen oxidoreductase (*N*-hydroxylating, aromatizing)
Comments: A heme-thiolate (*P*-450) enzyme from the bacterium *Bacillus subtilis*. The order of events during the overall reaction is unknown. Pulcherriminic acid spontaneously forms an iron chelate with Fe(3+) to form the red pigment pulcherrimin [700].
References: [2342, 700]

[EC 1.14.15.13 created 2013]

EC 1.14.15.14

Accepted name: methyl-branched lipid ω-hydroxylase
Reaction: a methyl-branched lipid + O₂ + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ = an ω-hydroxy-methyl-branched lipid + H₂O + 2 oxidized ferredoxin [iron-sulfur] cluster
Other name(s): CYP124
Systematic name: methyl-branched lipid, reduced-ferredoxin:oxygen oxidoreductase (ω-hydroxylating)
Comments: The enzyme, found in pathogenic and nonpathogenic mycobacteria species, actinomycetes, and some proteobacteria, hydroxylates the ω-carbon of a number of methyl-branched lipids, including (*2E,6E*)-farnesol, phytanate, geranylgeraniol, 15-methylpalmitate and (*2E,6E*)-farnesyl diphosphate. It is a *P*-450 heme-thiolate enzyme.
References: [1765]

[EC 1.14.15.14 created 2015]

EC 1.14.15.15

Accepted name: cholestanetriol 26-monooxygenase
Reaction: 5β-cholestane-3α,7α,12α-triol + 6 reduced adrenodoxin + 6 H⁺ + 3 O₂ = (25*R*)-3α,7α,12α-trihydroxy-5β-cholestan-26-oate + 6 oxidized adrenodoxin + 4 H₂O (overall reaction)
(1a) 5β-cholestane-3α,7α,12α-triol + 2 reduced adrenodoxin + 2 H⁺ + O₂ = (25*R*)-5β-cholestan-3α,7α,12α,26-tetraol + 2 oxidized adrenodoxin + H₂O
(1b) (25*R*)-5β-cholestan-3α,7α,12α,26-tetraol + 2 reduced adrenodoxin + 2 H⁺ + O₂ = (25*R*)-3α,7α,12α-trihydroxy-5β-cholestan-26-al + 2 oxidized adrenodoxin + 2 H₂O

(1c) (25*R*)-3 α ,7 α ,12 α -trihydroxy-5 β -cholestan-26-al + 2 reduced adrenodoxin + 2 H⁺ + O₂ = (25*R*)-3 α ,7 α ,12 α -trihydroxy-5 β -cholestan-26-oate + 2 oxidized adrenodoxin + H₂O

- Other name(s):** 5 β -cholestane-3 α ,7 α ,12 α -triol 26-hydroxylase; 5 β -cholestane-3 α ,7 α ,12 α -triol hydroxylase; cholestanetriol 26-hydroxylase; sterol 27-hydroxylase; sterol 26-hydroxylase; cholesterol 27-hydroxylase; CYP27A; CYP27A1; cytochrome P450 27A1'
- Systematic name:** 5 β -cholestane-3 α ,7 α ,12 α -triol,adrenodoxin:oxygen oxidoreductase (26-hydroxylating)
- Comments:** This mitochondrial cytochrome *P*-450 enzyme requires adrenodoxin. It catalyses the first three sterol side chain oxidations in bile acid biosynthesis via the neutral (classic) pathway. Can also act on cholesterol, cholest-5-ene-3 β ,7 α -diol, 7 α -hydroxycholest-4-en-3-one, and 5 β -cholestane-3 α ,7 α -diol. The enzyme can also hydroxylate cholesterol at positions 24 and 25. The initial source of the electrons is NADPH, which transfers the electrons to the adrenodoxin via EC 1.18.1.6, adrenodoxin-NADP⁺ reductase.
- References:** [2440, 2868, 4211, 85, 719, 1545, 3011, 1119, 3012]

[EC 1.14.15.15 created 1976 as EC 1.14.13.15, modified 2005, modified 2012, transferred 2016 to EC 1.14.15.15]

EC 1.14.15.16

- Accepted name:** vitamin D₃ 24-hydroxylase
- Reaction:** (1) calcitriol + 2 reduced adrenodoxin + 2 H⁺ + O₂ = calcitrol + 2 oxidized adrenodoxin + H₂O
(2) calcidiol + 2 reduced adrenodoxin + 2 H⁺ + O₂ = secalciferol + 2 oxidized adrenodoxin + H₂O
- Other name(s):** CYP24A1
- Systematic name:** calcitriol,adrenodoxin:oxygen oxidoreductase (24-hydroxylating)
- Comments:** This mitochondrial cytochrome *P*-450 enzyme requires adrenodoxin. The enzyme can perform up to 6 rounds of hydroxylation of the substrate calcitriol leading to calcitroic acid. The human enzyme also shows 23-hydroxylating activity leading to 1,25 dihydroxyvitamin D₃-26,23-lactone as end product while the mouse and rat enzymes do not. The initial source of the electrons is NADPH, which transfers the electrons to the adrenodoxin via EC 1.18.1.6, adrenodoxin-NADP⁺ reductase.
- References:** [2439, 1351, 3291, 3069, 2098, 3330, 3068]

[EC 1.14.15.16 created 2011 as EC 1.14.13.126, transferred 2016 to EC 1.14.15.16]

EC 1.14.15.17

- Accepted name:** pheophorbide *a* oxygenase
- Reaction:** pheophorbide *a* + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = red chlorophyll catabolite + 2 oxidized ferredoxin [iron-sulfur] cluster (overall reaction)
(1a) pheophorbide *a* + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = epoxypheophorbide *a* + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(1b) epoxypheophorbide *a* + H₂O = red chlorophyll catabolite (spontaneous)
- Other name(s):** pheide *a* monooxygenase; pheide *a* oxygenase; PaO; PAO
- Systematic name:** pheophorbide-*a*,ferredoxin:oxygen oxidoreductase (biladiene-forming)
- Comments:** This enzyme catalyses a key reaction in chlorophyll degradation, which occurs during leaf senescence and fruit ripening in higher plants. The enzyme from *Arabidopsis* contains a Rieske-type iron-sulfur cluster [3071] and requires reduced ferredoxin, which is generated either by NADPH through the pentose-phosphate pathway or by the action of photosystem I [3209]. While still attached to this enzyme, the product is rapidly converted into primary fluorescent chlorophyll catabolite by the action of EC 1.3.7.12, red chlorophyll catabolite reductase [3071, 3070]. Pheophorbide *b* acts as an inhibitor. In ¹⁸O₂ labelling experiments, only the aldehyde oxygen is labelled, suggesting that the other oxygen atom may originate from H₂O [1576].
- References:** [1576, 3071, 623, 3209, 1575, 3070]

[EC 1.14.15.17 created 2007 as EC 1.14.12.20, transferred 2016 to EC 1.14.15.17]

EC 1.14.15.18

- Accepted name:** calcidiol 1-monooxygenase

Reaction: (1) calcidiol + 2 reduced adrenodoxin + 2 H⁺ + O₂ = calcitriol + 2 oxidized adrenodoxin + H₂O
(2) secalciferol + 2 reduced adrenodoxin + 2 H⁺ + O₂ = calcitriol + 2 oxidized adrenodoxin + H₂O
Other name(s): 25-hydroxycholecalciferol 1-hydroxylase; 25-hydroxycholecalciferol 1-monooxygenase; 1-hydroxylase-25-hydroxyvitamin D₃; 25-hydroxy D₃-1 α -hydroxylase; 25-hydroxycholecalciferol 1 α -hydroxylase; 25-hydroxyvitamin D₃ 1 α -hydroxylase
Systematic name: calcidiol,adrenodoxin:oxygen oxidoreductase (1-hydroxylating)
Comments: A P-450 (heme-thiolate) enzyme found in mammals.
References: [1268, 3292, 3331]

[EC 1.14.15.18 created 1976 as EC 1.14.13.13, transferred 2016 to EC 1.14.15.18]

EC 1.14.15.19

Accepted name: C-19 steroid 1 α -hydroxylase
Reaction: testosterone + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = 1 α -hydroxytestosterone + H₂O + 2 oxidized ferredoxin [iron-sulfur] cluster
Other name(s): CYP260A1
Systematic name: testosterone,reduced-ferredoxin:oxygen oxidoreductase (1 α -hydroxylating)
Comments: The enzyme, characterized from the bacterium *Sorangium cellulosum*, is a class I cytochrome P-450, and uses ferredoxin as its electron donor [973]. It was shown to act on several C-19 steroid substrates, including testosterone, androstenedione, testosterone-acetate and 11-oxoandrostenedione [1897].
References: [973, 1897]

[EC 1.14.15.19 created 2016]

EC 1.14.15.20

Accepted name: heme oxygenase (biliverdin-producing, ferredoxin)
Reaction: protoheme + 6 reduced ferredoxin [iron-sulfur] cluster + 3 O₂ + 6 H⁺ = biliverdin + Fe²⁺ + CO + 6 oxidized ferredoxin [iron-sulfur] cluster + 3 H₂O
Other name(s): HO1 (gene name); HY1 (gene name); HO3 (gene name); HO4 (gene name); *pbsA1* (gene name)
Systematic name: protoheme,reduced ferredoxin:oxygen oxidoreductase (α -methene-oxidizing, hydroxylating)
Comments: The enzyme, found in plants, algae, and cyanobacteria, participates in the biosynthesis of phytylchromobilin and phytobilins. The terminal oxygen atoms that are incorporated into the carbonyl groups of pyrrole rings A and B of biliverdin are derived from two separate oxygen molecules. The third oxygen molecule provides the oxygen atom that converts the α -carbon to CO. Unlike this enzyme, which uses ferredoxin as its electron donor, the electron source for the related mammalian enzyme (EC 1.14.14.18) is EC 1.6.2.4, NADPH—hemoprotein reductase.
References: [2602, 3715, 734]

[EC 1.14.15.20 created 2016]

EC 1.14.15.21

Accepted name: zeaxanthin epoxidase
Reaction: zeaxanthin + 4 reduced ferredoxin [iron-sulfur] cluster + 4 H⁺ + 2 O₂ = violaxanthin + 4 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O (overall reaction)
(1a) zeaxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = antheraxanthin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(1b) antheraxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = violaxanthin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
Other name(s): Zea-epoxidase
Systematic name: zeaxanthin,reduced ferredoxin:oxygen oxidoreductase
Comments: A flavoprotein (FAD) that is active under conditions of low light. Along with EC 1.23.5.1, violaxanthin de-epoxidase, this enzyme forms part of the xanthophyll (or violaxanthin) cycle, which is involved in protecting the plant against damage by excess light. It will also epoxidize lutein in some higher-plant species.

References: [435, 443, 3871, 1493, 1083, 1082, 2442]

[EC 1.14.15.21 created 2005 as EC 1.14.13.90, transferred 2016 to EC 1.14.15.21]

EC 1.14.15.22

Accepted name: vitamin D 1,25-hydroxylase
Reaction: (1) calciol + O₂ + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ = calcidiol + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(2) calcidiol + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = calcitriol + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
Other name(s): CYP105A1; *Streptomyces griseolus* cytochrome P450SU-1
Systematic name: calciol,ferredoxin:oxygen oxidoreductase (1,25-hydroxylating)
Comments: A P-450 (heme-thiolate) enzyme found in the bacterium *Streptomyces griseolus*. cf. EC 1.14.14.24, vitamin D 25-hydroxylase and EC 1.14.15.18, calcidiol 1-monooxygenase.
References: [3332, 3711]

[EC 1.14.15.22 created 2016]

EC 1.14.15.23

Accepted name: chloroacetanilide *N*-alkylformylase
Reaction: butachlor + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ = 2-chloro-*N*-(2,6-diethylphenyl)acetamide + butyl formate + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
Other name(s): *cndA* (gene name)
Systematic name: butachlor,ferredoxin:oxygen oxidoreductase (butyl formate-releasing)
Comments: The enzyme, characterized from the bacterium *Sphingomonas* sp. DC-6, initiates the degradation of several chloroacetanilide herbicides, including alachlor, acetochlor, and butachlor. The enzyme is a Rieske non-heme iron oxygenase, and requires a ferredoxin and EC 1.18.1.3, ferredoxin—NAD⁺ reductase, for activity.
References: [574]

[EC 1.14.15.23 created 2017]

EC 1.14.15.24

Accepted name: β-carotene 3-hydroxylase
Reaction: β-carotene + 4 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + 2 O₂ = zeaxanthin + 4 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O (overall reaction)
(1a) β-carotene + 2 reduced ferredoxin [iron-sulfur] cluster + H⁺ + O₂ = β-cryptoxanthin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(1b) β-cryptoxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + H⁺ + O₂ = zeaxanthin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
Other name(s): β-carotene 3,3'-monooxygenase; CrtZ
Systematic name: β-carotene, reduced ferredoxin [iron-sulfur] cluster:oxygen 3-oxidoreductase
Comments: Requires ferredoxin and Fe(II). Also acts on other carotenoids with a β-end group. In some species canthaxanthin is the preferred substrate.
References: [3734, 1059, 1060, 367, 2261, 4476, 610]

[EC 1.14.15.24 created 2011 as EC 1.14.13.129, transferred 2017 to EC 1.14.15.24]

EC 1.14.15.25

Accepted name: *p*-cymene methyl-monooxygenase
Reaction: *p*-cymene + O₂ + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ = 4-isopropylbenzyl alcohol + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
Other name(s): *cymAa* (gene name); *cymA* (gene name); *p*-cymene methyl hydroxylase

Systematic name: *p*-cymene,ferredoxin:oxygen oxidoreductase (methyl-hydroxylating)
Comments: The enzyme, characterized from several *Pseudomonas* strains, initiates *p*-cymene catabolism through hydroxylation of the methyl group. The enzyme has a distinct preference for substrates containing at least an alkyl or heteroatom substituent at the *para*-position of toluene. The electrons are provided by a reductase (EC 1.18.1.3, ferredoxin—NAD⁺ reductase) that transfers electrons from NADH via FAD and an [2Fe-2S] cluster. In *Pseudomonas chlororaphis* the presence of a third component of unknown function greatly increases the activity. *cf.* EC 1.14.15.26, toluene methyl-monooxygenase.
References: [910, 895, 2799, 894]

[EC 1.14.15.25 created 2018]

EC 1.14.15.26

Accepted name: toluene methyl-monooxygenase
Reaction: (1) toluene + O₂ + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ = benzyl alcohol + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(2) *p*-xylene + O₂ + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ = 4-methylbenzyl alcohol + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(3) *m*-xylene + O₂ + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ = 3-methylbenzyl alcohol + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
Other name(s): *xylM* (gene names); *ntmM* (gene names)
Systematic name: methylbenzene,ferredoxin:oxygen oxidoreductase (methyl-hydroxylating)
Comments: The enzyme, characterized from several *Pseudomonas* strains, catalyses the first step in the degradation of toluenes and xylenes. It has a broad substrate specificity and is also active with substituted compounds, such as chlorotoluenes. The electrons are provided by a reductase (EC 1.18.1.3, ferredoxin—NAD⁺ reductase) that transfers electrons from NADH via FAD and an [2Fe-2S] cluster. The enzyme can also act on its products, producing gem-diols that spontaneously dehydrate to form aldehydes.
References: [3754, 3467, 402, 1716]

[EC 1.14.15.26 created 2018]

EC 1.14.15.27

Accepted name: β-dihydromenaquinone-9 ω-hydroxylase
Reaction: β-dihydromenaquinone-9 + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ = ω-hydroxy-β-dihydromenaquinone-9 + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
Other name(s): *cyp128* (gene name)
Systematic name: β-dihydromenaquinone-9,reduced ferredoxin:oxygen oxidoreductase (ω-hydroxylating)
Comments: The bacterial cytochrome *P*-450 enzyme is involved in the biosynthesis of ω-sulfo-β-dihydromenaquinone-9 by members of the *Mycobacterium tuberculosis* complex.
References: [1550, 3570]

[EC 1.14.15.27 created 2018]

EC 1.14.15.28

Accepted name: cholest-4-en-3-one 26-monooxygenase [(25*R*)-3-oxocholest-4-en-26-oate forming]
Reaction: cholest-4-en-3-one + 6 reduced [2Fe-2S] ferredoxin + 3 O₂ = (25*R*)-3-oxocholest-4-en-26-oate + 6 oxidized [2Fe-2S] ferredoxin + 4 H₂O (overall reaction)
(1a) cholest-4-en-3-one + 2 reduced [2Fe-2S] ferredoxin + O₂ = (25*R*)-26-hydroxycholest-4-en-3-one + 2 oxidized [2Fe-2S] ferredoxin + H₂O
(1b) (25*R*)-26-hydroxycholest-4-en-3-one + 2 reduced [2Fe-2S] ferredoxin + O₂ = (25*R*)-26-oxocholest-4-en-3-one + 2 oxidized [2Fe-2S] ferredoxin + 2 H₂O
(1c) (25*R*)-26-oxocholest-4-en-3-one + 2 reduced [2Fe-2S] ferredoxin + O₂ = (25*R*)-3-oxocholest-4-en-26-oate + 2 oxidized [2Fe-2S] ferredoxin + H₂O
Other name(s): CYP142

Systematic name: cholest-4-en-3-one, reduced [2Fe-2S] ferredoxin:oxygen oxidoreductase [(25*R*)-3-oxocholest-4-en-26-oate forming]

Comments: This cytochrome *P*-450 (heme-thiolate) enzyme, found in several bacterial pathogens, is involved in degradation of the host cholesterol. It catalyses the hydroxylation of the C-26 carbon, followed by oxidation of the alcohol to the carboxylic acid via the aldehyde intermediate, initiating the degradation of the alkyl side-chain of cholesterol. The products are exclusively in the (25*R*) conformation. The enzyme also accepts cholesterol as a substrate. *cf.* EC 1.14.15.29, cholest-4-en-3-one 26-monooxygenase [(25*S*)-3-oxocholest-4-en-26-oate forming]. The enzyme can receive electrons from ferredoxin reductase *in vitro*, its natural electron donor is not known yet.

References: [872, 1766]

[EC 1.14.15.28 created 2016 as EC 1.14.13.221, transferred 2018 to EC 1.14.15.28]

EC 1.14.15.29

Accepted name: cholest-4-en-3-one 26-monooxygenase [(25*S*)-3-oxocholest-4-en-26-oate forming]

Reaction: cholest-4-en-3-one + 6 reduced ferredoxin [iron-sulfur] cluster + 6 H⁺ + 3 O₂ = (25*S*)-3-oxocholest-4-en-26-oate + 6 oxidized ferredoxin [iron-sulfur] cluster + 4 H₂O (overall reaction)
(1a) cholest-4-en-3-one + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = (25*S*)-26-hydroxycholest-4-en-3-one + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(1b) (25*S*)-26-hydroxycholest-4-en-3-one + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = (25*S*)-26-oxocholest-4-en-3-one + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
(1c) (25*S*)-26-oxocholest-4-en-3-one + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = (25*S*)-3-oxocholest-4-en-26-oate + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O

Other name(s): CYP125; CYP125A1; cholest-4-en-3-one 27-monooxygenase (misleading); cholest-4-en-3-one, NADH:oxygen oxidoreductase (26-hydroxylating); cholest-4-en-3-one 26-monooxygenase (ambiguous)

Systematic name: cholest-4-en-3-one, [reduced ferredoxin]:oxygen oxidoreductase [(25*S*)-3-oxocholest-4-en-26-oate forming]

Comments: A cytochrome *P*-450 (heme-thiolate) protein found in several bacterial pathogens. The enzyme is involved in degradation of the host's cholesterol. It catalyses the hydroxylation of the C-26 carbon, followed by oxidation of the alcohol to the carboxylic acid via the aldehyde intermediate, initiating the degradation of the alkyl side-chain of cholesterol [2917]. The products are exclusively in the (25*S*) configuration. The enzyme is part of a two-component system that also includes a ferredoxin reductase (most likely KshB, which also interacts with EC 1.14.15.30, 3-ketosteroid 9α-monooxygenase). The enzyme also accepts cholesterol as a substrate. *cf.* EC 1.14.15.28, cholest-4-en-3-one 27-monooxygenase.

References: [3237, 2489, 499, 2917]

[EC 1.14.15.29 created 2012 as EC 1.14.13.141, modified 2016, transferred 2018 to EC 1.14.15.29]

EC 1.14.15.30

Accepted name: 3-ketosteroid 9α-monooxygenase

Reaction: androsta-1,4-diene-3,17-dione + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = 9α-hydroxyandrosta-1,4-diene-3,17-dione + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O

Other name(s): KshA; 3-ketosteroid 9α-hydroxylase

Systematic name: androsta-1,4-diene-3,17-dione, [reduced ferredoxin]:oxygen oxidoreductase (9α-hydroxylating)

Comments: The enzyme is involved in the cholesterol degradation pathway of several bacterial pathogens, such as *Mycobacterium tuberculosis*. It forms a two-component system with a ferredoxin reductase (KshB). The enzyme contains a Rieske-type iron-sulfur center and non-heme iron. The product of the enzyme is unstable, and spontaneously converts to 3-hydroxy-9,10-seconandrost-1,3,5(10)-triene-9,17-dione.

References: [2994, 498, 497]

[EC 1.14.15.30 created 2012 as EC 1.14.13.142, transferred 2018 to EC 1.14.15.30]

EC 1.14.15.31

Accepted name: 2-hydroxy-5-methyl-1-naphthoate 7-hydroxylase
Reaction: 2-hydroxy-5-methyl-1-naphthoate + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = 2,7-dihydroxy-5-methyl-1-naphthoate + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
Other name(s): NcsB3
Systematic name: 2-hydroxy-5-methyl-1-naphthoate, reduced ferredoxin:oxygen oxidoreductase (7-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein involved in the synthesis of neocarzinostatin in the bacterium *Streptomyces carzinostaticus*.
References: [1368]

[EC 1.14.15.31 created 2014 as EC 1.14.99.49, transferred 2018 to EC 1.14.15.31]

EC 1.14.15.32

Accepted name: pentalenene oxygenase
Reaction: pentalenene + 4 reduced ferredoxin [iron-sulfur] cluster + 4 H⁺ + 2 O₂ = pentalen-13-al + 4 oxidized ferredoxin [iron-sulfur] cluster + 3 H₂O (overall reaction)
(1a) pentalenene + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = pentalen-13-ol + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(1b) pentalen-13-ol + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = pentalen-13-al + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): PtlI
Systematic name: pentalenene, reduced ferredoxin:oxygen 13-oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in the bacterium *Streptomyces avermitilis*. The enzyme is involved in the biosynthesis of pentalenolactone and related antibiotics.
References: [3088]

[EC 1.14.15.32 created 2011 as EC 1.14.13.133, transferred 2018 to EC 1.14.15.32]

EC 1.14.15.33

Accepted name: pikromycin synthase
Reaction: (1) narbomycin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = pikromycin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(2) narbomycin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = neopikromycin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(3) narbomycin + 4 reduced ferredoxin [iron-sulfur] cluster + 4 H⁺ + 2 O₂ = novapikromycin + 4 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
(4) 10-deoxymethymycin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = methymycin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(5) 10-deoxymethymycin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = neomethymycin + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
(6) 10-deoxymethymycin + 4 reduced ferredoxin [iron-sulfur] cluster + 4 H⁺ + 2 O₂ = novamethymycin + 4 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): PikC; CYP107L1
Systematic name: narbomycin, reduced ferredoxin:oxygen oxidoreductase (pikromycin-forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Involved in the biosynthesis of a number of bacterial macrolide antibiotics containing a desosamine glycoside unit. With narbomycin it hydroxylates at either C-12 to give pikromycin or C-14 to give neopikromycin or both positions to give narvopikromycin. With 10-deoxymethymycin it hydroxylates at either C-10 to give methymycin or C-12 to give neomethymycin or both positions to give novamethymycin.
References: [4289, 3480, 2232]

[EC 1.14.15.33 created 2014 as EC 1.14.13.185, transferred 2018 to EC 1.14.15.33]

EC 1.14.15.34

Accepted name: 20-oxo-5-*O*-mycaminosyltylactone 23-monooxygenase
Reaction: 20-oxo-5-*O*- β -mycaminosyltylactone + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = 5-*O*- β -mycaminosyltylonolide + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
Other name(s): *tylH1* (gene name)
Systematic name: 20-oxo-5-*O*- β -mycaminosyltylactone, reduced ferredoxin:oxygen oxidoreductase (23-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Involved in the biosynthetic pathway of the macrolide antibiotic tylosin, which is produced by several species of *Streptomyces* bacteria.
References: [183, 3155]

[EC 1.14.15.34 created 2014 as EC 1.14.13.186, transferred 2018 to EC 1.14.15.34]

EC 1.14.15.35

Accepted name: 6-deoxyerythronolide B hydroxylase
Reaction: 6-deoxyerythronolide B + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = erythronolide B + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O
Other name(s): DEB hydroxylase; *eryF* (gene name); P450(*eryF*); CYP107A1
Systematic name: 6-deoxyerythronolide-B, reduced ferredoxin:oxygen oxidoreductase
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the bacterium *Saccharopolyspora erythraea*. The enzyme is involved in the biosynthesis of the antibiotic erythromycin.
References: [4153, 3456, 710, 2685]

[EC 1.14.15.35 created 2014 as EC 1.14.13.188, transferred 2018 to EC 1.14.15.35]

EC 1.14.16 With reduced pteridine as one donor, and incorporation of one atom of oxygen into the other donor

EC 1.14.16.1

Accepted name: phenylalanine 4-monooxygenase
Reaction: L-phenylalanine + tetrahydrobiopterin + O₂ = L-tyrosine + 4a-hydroxytetrahydrobiopterin
Other name(s): phenylalaninase; phenylalanine 4-hydroxylase; phenylalanine hydroxylase
Systematic name: L-phenylalanine, tetrahydrobiopterin:oxygen oxidoreductase (4-hydroxylating)
Comments: The active centre contains mononuclear iron(II). The reaction involves an arene oxide that rearranges to give the phenolic hydroxy group. This results in the hydrogen at C-4 migrating to C-3 and in part being retained. This process is known as the NIH-shift. The 4a-hydroxytetrahydrobiopterin formed can dehydrate to 6,7-dihydrobiopterin, both spontaneously and by the action of EC 4.2.1.96, 4a-hydroxytetrahydrobiopterin dehydratase. The 6,7-dihydrobiopterin can be enzymically reduced back to tetrahydrobiopterin, by EC 1.5.1.34, 6,7-dihydropteridine reductase, or slowly rearranges into the more stable compound 7,8-dihydrobiopterin.
References: [1320, 1851, 2562, 3958, 511, 81, 964]

[EC 1.14.16.1 created 1961 as EC 1.99.1.2, transferred 1965 to EC 1.14.3.1, transferred 1972 to EC 1.14.16.1, modified 2002, modified 2003]

EC 1.14.16.2

Accepted name: tyrosine 3-monooxygenase
Reaction: L-tyrosine + tetrahydrobiopterin + O₂ = L-dopa + 4a-hydroxytetrahydrobiopterin
Other name(s): L-tyrosine hydroxylase; tyrosine 3-hydroxylase; tyrosine hydroxylase
Systematic name: L-tyrosine, tetrahydrobiopterin:oxygen oxidoreductase (3-hydroxylating)
Comments: The active centre contains mononuclear iron(II). The enzyme is activated by phosphorylation, catalysed by EC 2.7.11.27, [acetyl-CoA carboxylase] kinase. The 4a-hydroxytetrahydrobiopterin formed can dehydrate to 6,7-dihydrobiopterin, both spontaneously and by the action of EC 4.2.1.96, 4a-hydroxytetrahydrobiopterin dehydratase. The 6,7-dihydrobiopterin can be enzymically reduced back to tetrahydrobiopterin, by EC 1.5.1.34 (6,7-dihydropteridine reductase), or slowly rearranges into the more stable compound 7,8-dihydrobiopterin.

References: [2512, 1632, 2688, 3009, 1244]

[EC 1.14.16.2 created 1972, modified 2003]

EC 1.14.16.3

Accepted name: anthranilate 3-monooxygenase
Reaction: anthranilate + tetrahydrobiopterin + O₂ = 3-hydroxyanthranilate + dihydrobiopterin + H₂O
Other name(s): anthranilate 3-hydroxylase; anthranilate hydroxylase; anthranilic hydroxylase; anthranilic acid hydroxylase
Systematic name: anthranilate,tetrahydrobiopterin:oxygen oxidoreductase (3-hydroxylating)
Comments: Requires Fe²⁺.
References: [1734, 2694]

[EC 1.14.16.3 created 1972]

EC 1.14.16.4

Accepted name: tryptophan 5-monooxygenase
Reaction: L-tryptophan + tetrahydrobiopterin + O₂ = 5-hydroxy-L-tryptophan + 4a-hydroxytetrahydrobiopterin
Other name(s): L-tryptophan hydroxylase; indoleacetic acid-5-hydroxylase; tryptophan 5-hydroxylase; tryptophan hydroxylase
Systematic name: L-tryptophan,tetrahydrobiopterin:oxygen oxidoreductase (5-hydroxylating)
Comments: The active centre contains mononuclear iron(II). The enzyme is activated by phosphorylation, catalysed by a Ca²⁺-activated protein kinase. The 4a-hydroxytetrahydrobiopterin formed can dehydrate to 6,7-dihydrobiopterin, both spontaneously and by the action of EC 4.2.1.96, 4a-hydroxytetrahydrobiopterin dehydratase. The 6,7-dihydrobiopterin can be enzymically reduced back to tetrahydrobiopterin, by EC 1.5.1.34 (6,7-dihydropteridine reductase), or slowly rearranges into the more stable compound 7,8-dihydrobiopterin.
References: [1071, 1357, 1628, 1734, 4109]

[EC 1.14.16.4 created 1972, modified 2003]

EC 1.14.16.5

Accepted name: alkylglycerol monooxygenase
Reaction: 1-*O*-alkyl-*sn*-glycerol + tetrahydrobiopterin + O₂ = 1-*O*-(1-hydroxyalkyl)-*sn*-glycerol + dihydrobiopterin + H₂O
Other name(s): glyceryl-ether monooxygenase; glyceryl-ether cleaving enzyme; glyceryl ether oxygenase; glyceryl etherase; *O*-alkylglycerol monooxygenase
Systematic name: 1-alkyl-*sn*-glycerol,tetrahydrobiopterin:oxygen oxidoreductase
Comments: The enzyme cleaves alkylglycerols, but does not cleave alkenylglycerols (plasmalogens). Requires non-heme iron [4150], reduced glutathione and phospholipids for full activity. The product spontaneously breaks down to form a fatty aldehyde and glycerol.
References: [1665, 2999, 3568, 3585, 3891, 3775, 4150, 4178]

[EC 1.14.16.5 created 1972 as EC 1.14.99.17, transferred 1976 to EC 1.14.16.5, modified 2010]

EC 1.14.16.6

Accepted name: mandelate 4-monooxygenase
Reaction: (*S*)-2-hydroxy-2-phenylacetate + tetrahydrobiopterin + O₂ = (*S*)-4-hydroxymandelate + dihydrobiopterin + H₂O
Other name(s): L-mandelate 4-hydroxylase; mandelic acid 4-hydroxylase
Systematic name: (*S*)-2-hydroxy-2-phenylacetate,tetrahydrobiopterin:oxygen oxidoreductase (4-hydroxylating)
Comments: Requires Fe²⁺.
References: [291]

[EC 1.14.16.6 created 1984]

EC 1.14.16.7

Accepted name: phenylalanine 3-monooxygenase
Reaction: L-phenylalanine + tetrahydrobiopterin + O₂ = 3-hydroxy-L-phenylalanine + 4a-hydroxytetrahydrobiopterin
Other name(s): PacX; phenylalanine 3-hydroxylase
Systematic name: L-phenylalanine,tetrahydrobiopterin:oxygen oxidoreductase (3-hydroxylating)
Comments: The enzyme from the bacterium *Streptomyces coeruleorubidus* forms 3-hydroxy-L-phenylalanine (i.e. *m*-L-tyrosine), which is one of the building blocks in the biosynthesis of the uridyl peptide antibiotics pacidamycins.
References: [4445]

[EC 1.14.16.7 created 2014]

EC 1.14.17 With reduced ascorbate as one donor, and incorporation of one atom of oxygen into the other donor

EC 1.14.17.1

Accepted name: dopamine β-monooxygenase
Reaction: dopamine + ascorbate + O₂ = noradrenaline + dehydroascorbate + H₂O
Other name(s): dopamine β-hydroxylase; MDBH (membrane-associated dopamine β-monooxygenase); SDBH (soluble dopamine β-monooxygenase); dopamine-B-hydroxylase; 3,4-dihydroxyphenethylamine β-oxidase; 4-(2-aminoethyl)pyrocatechol β-oxidase; dopa β-hydroxylase; dopamine β-oxidase; dopamine hydroxylase; phenylamine β-hydroxylase; (3,4-dihydroxyphenethylamine)β-monooxygenase; DβM (gene name)
Systematic name: dopamine,ascorbate:oxygen oxidoreductase (β-hydroxylating)
Comments: A copper protein. Stimulated by fumarate.
References: [1072, 2211]

[EC 1.14.17.1 created 1965 as EC 1.14.2.1, transferred 1972 to EC 1.14.17.1]

[1.14.17.2 Deleted entry. 4-coumarate 3-monooxygenase. Now included with EC 1.14.18.1 monophenol monooxygenase]

[EC 1.14.17.2 created 1972, deleted 1984]

EC 1.14.17.3

Accepted name: peptidylglycine monooxygenase
Reaction: peptidylglycine + ascorbate + O₂ = peptidyl(2-hydroxyglycine) + dehydroascorbate + H₂O
Other name(s): peptidylglycine 2-hydroxylase; peptidyl α-amidating enzyme; peptide-α-amide synthetase; synthase, peptide α-amide; peptide α-amidating enzyme; peptide α-amide synthase; peptidylglycine α-hydroxylase; peptidylglycine α-amidating monooxygenase; PAM-A; PAM-B; PAM
Systematic name: peptidylglycine,ascorbate:oxygen oxidoreductase (2-hydroxylating)
Comments: A copper protein. Peptidylglycines with a neutral amino acid residue in the penultimate position are the best substrates for the enzyme. The product is unstable and dismutates to glyoxylate and the corresponding desglycine peptide amide, a reaction catalysed by EC 4.3.2.5 peptidylamidoglycolate lyase. Involved in the final step of biosynthesis of α-melanotropin and related biologically active peptides.
References: [379, 380, 1221, 1845, 2673, 2674]

[EC 1.14.17.3 created 1989]

EC 1.14.17.4

Accepted name: aminocyclopropanecarboxylate oxidase

Reaction: 1-aminocyclopropane-1-carboxylate + ascorbate + O₂ = ethene + cyanide + dehydroascorbate + CO₂ + 2 H₂O
Other name(s): ACC oxidase; ethylene-forming enzyme; 1-aminocyclopropane-1-carboxylate oxygenase (ethylene-forming)
Systematic name: 1-aminocyclopropane-1-carboxylate oxygenase (ethene-forming)
Comments: A nonheme iron enzyme. Requires CO₂ for activity. In the enzyme from plants, the ethene has signalling functions such as stimulation of fruit-ripening.
References: [4453, 4451, 3016, 549, 3881]

[EC 1.14.17.4 created 2003]

EC 1.14.18 With another compound as one donor, and incorporation of one atom of oxygen into the other donor

EC 1.14.18.1

Accepted name: tyrosinase
Reaction: (1) L-tyrosine + O₂ = dopaquinone + H₂O (overall reaction)
(1a) L-tyrosine + $\frac{1}{2}$ O₂ = L-dopa
(1b) L-dopa + $\frac{1}{2}$ O₂ = dopaquinone + H₂O
(2) 2 L-dopa + O₂ = 2 dopaquinone + 2 H₂O
Other name(s): monophenol monooxygenase; phenolase; monophenol oxidase; cresolase; monophenolase; tyrosine-dopa oxidase; monophenol monooxidase; monophenol dihydroxyphenylalanine:oxygen oxidoreductase; *N*-acetyl-6-hydroxytryptophan oxidase; monophenol, dihydroxy-L-phenylalanine oxygen oxidoreductase; *o*-diphenol:O₂ oxidoreductase; phenol oxidase
Systematic name: L-tyrosine,L-dopa:oxygen oxidoreductase
Comments: A type III copper protein found in a broad variety of bacteria, fungi, plants, insects, crustaceans, and mammals, which is involved in the synthesis of betalains and melanin. The enzyme, which is activated upon binding molecular oxygen, can catalyse both a monophenolase reaction cycle (reaction 1) or a diphenolase reaction cycle (reaction 2). During the monophenolase cycle, one of the bound oxygen atoms is transferred to a monophenol (such as L-tyrosine), generating an *o*-diphenol intermediate, which is subsequently oxidized to an *o*-quinone and released, along with a water molecule. The enzyme remains in an inactive deoxy state, and is restored to the active oxy state by the binding of a new oxygen molecule. During the diphenolase cycle the enzyme binds an external diphenol molecule (such as L-dopa) and oxidizes it to an *o*-quinone that is released along with a water molecule, leaving the enzyme in the intermediate met state. The enzyme then binds a second diphenol molecule and repeats the process, ending in a deoxy state [3223]. The second reaction is identical to that catalysed by the related enzyme catechol oxidase (EC 1.10.3.1). However, the latter can not catalyse the hydroxylation or monooxygenation of monophenols.
References: [757, 2961, 3034, 3200, 3304, 3636, 3223]

[EC 1.14.18.1 created 1972, modified 1976, modified 1980 (EC 1.14.17.2 created 1972, incorporated 1984), modified 2012]

EC 1.14.18.2

Accepted name: CMP-*N*-acetylneuraminate monooxygenase
Reaction: CMP-*N*-acetylneuraminate + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = CMP-*N*-glycoloylneuraminate + 2 ferricytochrome *b*₅ + H₂O
Other name(s): CMP-*N*-acetylneuraminic acid hydroxylase; CMP-Neu5Ac hydroxylase; cytidine monophosphoacetylneuraminate monooxygenase; *N*-acetylneuraminic monooxygenase; cytidine-5'-monophosphate-*N*-acetylneuraminic acid hydroxylase
Systematic name: CMP-*N*-acetylneuraminate,ferrocyclochrome-*b*₅:oxygen oxidoreductase (*N*-acetyl-hydroxylating)
Comments: This enzyme contains both a Rieske-type [2Fe-2S] cluster and a second iron site. The ferrocyclochrome *b*₅ produced is reduced by NADH and cytochrome-*b*₅ reductase (EC 1.6.2.2). The enzyme can be activated by Fe²⁺ or Fe³⁺.
References: [3469, 2050, 3378, 1861, 3370]

[EC 1.14.18.2 created 1992 as EC 1.14.13.45, transferred 2003 to EC 1.14.18.2]

EC 1.14.18.3

Accepted name: methane monooxygenase (particulate)
Reaction: methane + quinol + O₂ = methanol + quinone + H₂O
Systematic name: methane,quinol:oxygen oxidoreductase
Comments: Contains copper. It is membrane-bound, in contrast to the soluble methane monooxygenase (EC 1.14.13.25).
References: [3486, 210, 1949, 179]

[EC 1.14.18.3 created 2011]

EC 1.14.18.4

Accepted name: phosphatidylcholine 12-monooxygenase
Reaction: a 1-acyl-2-oleoyl-*sn*-glycero-3-phosphocholine + 2 ferrocycytochrome *b*₅ + O₂ + 2 H⁺ = a 1-acyl-2-[(12*R*)-12-hydroxyoleoyl]-*sn*-glycero-3-phosphocholine + 2 ferricytochrome *b*₅ + H₂O
Other name(s): ricinoleic acid synthase; oleate Δ¹²-hydroxylase; oleate Δ¹²-monooxygenase
Systematic name: 1-acyl-2-oleoyl-*sn*-glycero-3-phosphocholine,ferrocycytochrome-*b*₅:oxygen oxidoreductase (12-hydroxylating)
Comments: The enzyme, characterized from the plant *Ricinus communis* (castor bean), is involved in production of the 12-hydroxylated fatty acid ricinoleate. The enzyme, which shares sequence similarity with fatty-acyl desaturases, requires a cytochrome *b*₅ as the electron donor.
References: [1144, 2614, 3561, 2254, 413]

[EC 1.14.18.4 created 1984 as EC 1.14.13.26, transferred 2015 to EC 1.14.18.4]

EC 1.14.18.5

Accepted name: sphingolipid C4-monooxygenase
Reaction: a dihydroceramide + 2 ferrocycytochrome *b*₅ + O₂ + 2 H⁺ = a (4*R*)-4-hydroxysphinganine ceramide + 2 ferricytochrome *b*₅ + H₂O
Other name(s): sphinganine C4-monooxygenase; sphingolipid C4-hydroxylase; SUR2 (gene name); SBH1 (gene name); SBH₂ (gene name); DEGS2 (gene name)
Systematic name: dihydroceramide,ferrocycytochrome *b*₅:oxygen oxidoreductase (C4-hydroxylating)
Comments: The enzyme, which belongs to the family of endoplasmic reticular cytochrome *b*₅-dependent enzymes, is involved in the biosynthesis of sphingolipids in eukaryotes. Some enzymes are bifunctional and also catalyse EC 1.14.19.17, sphingolipid 4-desaturase [3849].
References: [1329, 1286, 3600, 3849, 2583]

[EC 1.14.18.5 created 2012 as EC 1.14.13.169, transferred 2015 to EC 1.14.18.5]

EC 1.14.18.6

Accepted name: 4-hydroxysphinganine ceramide fatty acyl 2-hydroxylase
Reaction: a phytoceramide + 2 ferrocycytochrome *b*₅ + O₂ + 2 H⁺ = a (2'*R*)-2'-hydroxyphytoceramide + 2 ferricytochrome *b*₅ + H₂O
Other name(s): FA2H (gene name); SCS7 (gene name)
Systematic name: (4*R*)-4-hydroxysphinganine ceramide,ferrocycytochrome-*b*₅:oxygen oxidoreductase (fatty acyl 2-hydroxylating)
Comments: The enzyme, characterized from yeast and mammals, catalyses the hydroxylation of carbon 2 of long- or very-long-chain fatty acids attached to (4*R*)-4-hydroxysphinganine during *de novo* ceramide synthesis. The enzymes from yeast and from mammals contain an N-terminal cytochrome *b*₅ domain that acts as the direct electron donor to the desaturase active site. The newly introduced 2-hydroxyl group has R-configuration. *cf.* EC 1.14.18.7, dihydroceramide fatty acyl 2-hydroxylase.
References: [2561, 890, 58, 913, 1318]

[EC 1.14.18.6 created 2015]

EC 1.14.18.7

- Accepted name:** dihydroceramide fatty acyl 2-hydroxylase
Reaction: a dihydroceramide + 2 ferrocytochrome b_5 + O_2 + 2 H^+ = a (2'*R*)-2'-hydroxydihydroceramide + 2 ferricytochrome b_5 + H_2O
Other name(s): FAH1 (gene name); FAH₂ (gene name); plant sphingolipid fatty acid 2-hydroxylase
Systematic name: dihydroceramide,ferrocytochrome- b_5 :oxygen oxidoreductase (fatty acyl 2-hydroxylating)
Comments: The enzyme, characterized from plants, catalyses the hydroxylation of carbon 2 of long- or very-long-chain fatty acids attached to sphinganine during *de novo* ceramide synthesis. The enzyme requires an external cytochrome b_5 as the electron donor. The newly introduced 2-hydroxyl group has R-configuration. *cf.* EC 1.14.18.6, 4-hydroxysphinganine ceramide fatty acyl 2-hydroxylase.
References: [2682, 2683, 2684]

[EC 1.14.18.7 created 2015]

EC 1.14.18.8

- Accepted name:** 7 α -hydroxycholest-4-en-3-one 12 α -hydroxylase
Reaction: 7 α -hydroxycholest-4-en-3-one + 2 ferrocytochrome b_5 + 2 H^+ + O_2 = 7 α ,12 α -dihydroxycholest-4-en-3-one + 2 ferricytochrome b_5 + H_2O
Other name(s): 7 α -hydroxy-4-cholesten-3-one 12 α -monooxygenase; CYP12; sterol 12 α -hydroxylase (ambiguous); HCO 12 α -hydroxylase
Systematic name: 7 α -hydroxycholest-4-en-3-one,ferrocytochrome- b_5 :oxygen oxidoreductase (12 α -hydroxylating)
Comments: A P-450 heme-thiolate protein. Requires EC 1.6.2.4, NADPH—hemoprotein reductase and cytochrome b_5 for maximal activity. This enzyme is important in bile acid biosynthesis, being responsible for the balance between the formation of cholic acid and chenodeoxycholic acid [925].
References: [1666, 925, 3263]

[EC 1.14.18.8 created 2005 as EC 1.14.13.95, transferred 2015 to EC 1.14.18.8]

EC 1.14.18.9

- Accepted name:** methylsterol monooxygenase
Reaction: 4,4-dimethyl-5 α -cholest-7-en-3 β -ol + 6 ferrocytochrome b_5 + 3 O_2 + 6 H^+ = 3 β -hydroxy-4 β -methyl-5 α -cholest-7-ene-4 α -carboxylate + 6 ferricytochrome b_5 + 4 H_2O (overall reaction)
(1a) 4,4-dimethyl-5 α -cholest-7-en-3 β -ol + 2 ferrocytochrome b_5 + O_2 + 2 H^+ = 4 β -hydroxymethyl-4 α -methyl-5 α -cholest-7-en-3 β -ol + 2 ferricytochrome b_5 + H_2O
(1b) 4 β -hydroxymethyl-4 α -methyl-5 α -cholest-7-en-3 β -ol + 2 ferrocytochrome b_5 + O_2 + 2 H^+ = 3 β -hydroxy-4 β -methyl-5 α -cholest-7-ene-4 α -carbaldehyde + 2 ferricytochrome b_5 + 2 H_2O
(1c) 3 β -hydroxy-4 β -methyl-5 α -cholest-7-ene-4 α -carbaldehyde + 2 ferrocytochrome b_5 + O_2 + 2 H^+ = 3 β -hydroxy-4 β -methyl-5 α -cholest-7-ene-4 α -carboxylate + 2 ferricytochrome b_5 + H_2O
Other name(s): methylsterol hydroxylase; 4-methylsterol oxidase; 4,4-dimethyl-5 α -cholest-7-en-3 β -ol,hydrogen-donor:oxygen oxidoreductase (hydroxylating)
Systematic name: 4,4-dimethyl-5 α -cholest-7-en-3 β -ol,ferrocytochrome- b_5 :oxygen oxidoreductase (hydroxylating)
Comments: Also acts on 4 α -methyl-5 α -cholest-7-en-3 β -ol. The sterol can be based on cycloartenol as well as lanosterol.
References: [2548, 1172, 381, 1112, 1863, 2951, 3103]

[EC 1.14.18.9 created 1972 as EC 1.14.99.16, transferred 2002 to EC 1.14.13.72, transferred 2017 to EC 1.14.18.9]

EC 1.14.19 With oxidation of a pair of donors resulting in the reduction of O_2 to two molecules of water

EC 1.14.19.1

- Accepted name:** stearyl-CoA 9-desaturase
Reaction: stearyl-CoA + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = oleoyl-CoA + 2 ferricytochrome b_5 + 2 H₂O
Other name(s): Δ⁹-desaturase; acyl-CoA desaturase; fatty acid desaturase; stearyl-CoA, hydrogen-donor:oxygen oxidoreductase
Systematic name: stearyl-CoA,ferrocytochrome- b_5 :oxygen oxidoreductase (9,10-dehydrogenating)
Comments: An iron protein. The rat liver enzyme is an enzyme system involving cytochrome b_5 and EC 1.6.2.2, cytochrome- b_5 reductase. The ferricytochrome b_5 produced is reduced by NADH and cytochrome- b_5 reductase (EC 1.6.2.2).
References: [1113, 2901, 2902, 3684]

[EC 1.14.19.1 created 1972 as EC 1.14.99.5, modified 1986, modified 2000, transferred 2000 to EC 1.14.19.1, modified 2003]

EC 1.14.19.2

- Accepted name:** stearyl-[acyl-carrier-protein] 9-desaturase
Reaction: stearyl-[acyl-carrier protein] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = oleoyl-[acyl-carrier protein] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): stearyl acyl carrier protein desaturase; stearyl-ACP desaturase; acyl-[acyl-carrier-protein] desaturase; acyl-[acyl-carrier protein],hydrogen-donor:oxygen oxidoreductase
Systematic name: stearyl-[acyl-carrier protein],reduced ferredoxin:oxygen oxidoreductase (9,10 *cis*-dehydrogenating)
Comments: The enzyme is found in the lumen of plastids, where *de novo* biosynthesis of fatty acids occurs, and acts on freshly synthesized saturated fatty acids that are still linked to acyl-carrier protein. The enzyme determines the position of the double bond by its distance from the carboxylic acid end of the fatty acid. It also acts on palmitoyl-[acyl-carrier-protein] [470, 495].
References: [1726, 2680, 3459, 470, 495]

[EC 1.14.19.2 created 1972 as EC 1.14.99.6, modified 2000, transferred 2000 to EC 1.14.19.2, modified 2015]

EC 1.14.19.3

- Accepted name:** acyl-CoA 6-desaturase
Reaction: (1) linoleoyl-CoA + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = γ-linolenoyl-CoA + 2 ferricytochrome b_5 + 2 H₂O
(2) α-linolenoyl-CoA + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = stearidonoyl-CoA + 2 ferricytochrome b_5 + 2 H₂O
Other name(s): Δ⁶-desaturase; Δ⁶-fatty acyl-CoA desaturase; Δ⁶-acyl CoA desaturase; fatty acid Δ⁶-desaturase; fatty acid 6-desaturase; linoleate desaturase; linoleic desaturase; linoleic acid desaturase; linoleoyl CoA desaturase; linoleoyl-coenzyme A desaturase; long-chain fatty acid Δ⁶-desaturase; linoleoyl-CoA,hydrogen-donor:oxygen oxidoreductase; linoleoyl-CoA desaturase; FADS2 (gene name)
Systematic name: acyl-CoA,ferrocytochrome b_5 :oxygen oxidoreductase (6,7 *cis*-dehydrogenating)
Comments: An iron protein. The enzyme introduces a *cis* double bond at carbon 6 of acyl-CoAs. It is a front-end desaturase, introducing the new double bond between a pre-existing double bond and the carboxyl-end of the fatty acid. The human enzyme has a broad substrate range. It also acts on palmitoyl-CoA, generating sapienoyl-CoA [1174], and on (9Z,12Z,15Z,18Z,21Z)-tetracos-9,12,15,18,21-pentaenoyl-CoA, converting it to (6Z,9Z,12Z,15Z,18Z,21Z)-tetracos-6,9,12,15,18,21-hexaenoyl-CoA as part of a pathway that produces docosahexaenoate [3608]. The enzyme contains a cytochrome b_5 domain that is assumed to act *in vivo* as the electron donor to the active site of the desaturase.
References: [2865, 602, 3608, 1174, 852]

[EC 1.14.19.3 created 1986 as EC 1.14.99.25, transferred 2000 to EC 1.14.19.3, modified 2015]

EC 1.14.19.4

- Accepted name:** acyl-lipid (11-3)-desaturase
Reaction: (1) an (11Z,14Z)-icosa-11,14-dienoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = an (8Z,11Z,14Z)-icosa-8,11,14-trienoyl-[glycerolipid] + 2 ferricytochrome b_5 + 2 H₂O

(2) an (11Z,14Z,17Z)-icosa-11,14,17-trienoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = an (8Z,11Z,14Z,17Z)-icosa-8,11,14,17-tetraenoyl-[glycerolipid] + 2 ferricytochrome b_5 + 2 H₂O
Other name(s): acyl-lipid 8-desaturase; Δ⁸ fatty acid desaturase; Δ⁸-desaturase; Δ⁸-fatty-acid desaturase; efd1 (gene name); D8Des (gene name); phytosphinganine,hydrogen donor:oxygen Δ⁸-oxidoreductase (incorrect); SLD

Systematic name: acyl-lipid,ferrocytochrome b_5 :oxygen oxidoreductase [(11-3),(11-2)-*cis*-dehydrogenating]

Comments: The enzyme, characterized from the protist *Euglena gracilis* [4094] and the microalga *Rebecca salina* [4475], introduces a *cis* double bond at the 8-position in 20-carbon fatty acids that are incorporated into a glycerolipid and have an existing Δ¹¹ desaturation. The enzyme is a front-end desaturase, introducing the new double bond between the pre-existing double bond and the carboxyl-end of the fatty acid. It contains a cytochrome b_5 domain that acts as the direct electron donor to the active site of the desaturase, and does not require an external cytochrome. Involved in alternative pathways for the biosynthesis of the polyunsaturated fatty acids arachidonate and icosapentaenoate.

References: [4094, 4475]

[EC 1.14.19.4 created 2008, modified 2015]

EC 1.14.19.5

Accepted name: acyl-CoA 11-(Z)-desaturase

Reaction: an acyl-CoA + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = an (11Z)-enoyl-CoA + 2 ferricytochrome b_5 + 2 H₂O

Other name(s): Δ¹¹ desaturase; fatty acid Δ¹¹-desaturase; TpDES_N; Cro-PG; Δ¹¹ fatty acid desaturase; Z/E11-desaturase; Δ¹¹-palmitoyl-CoA desaturase; acyl-CoA,hydrogen donor:oxygen Δ¹¹-oxidoreductase; Δ¹¹-fatty-acid desaturase

Systematic name: acyl-CoA,ferrocytochrome b_5 :oxygen oxidoreductase (11,12 *cis*-dehydrogenating)

Comments: The enzyme introduces a *cis* double bond at position C-11 of saturated fatty acyl-CoAs. In moths the enzyme participates in the biosynthesis of their sex pheromones. The enzyme from the marine microalga *Thalassiosira pseudonana* is specific for palmitoyl-CoA (16:0) [3910], that from the leafroller moth *Choristoneura rosaceana* desaturates myristoyl-CoA (14:0) [1385], while that from the moth *Spodoptera littoralis* accepts both substrates [2420]. The enzyme contains three histidine boxes that are conserved in all desaturases [3211]. It is membrane-bound, and contains a cytochrome b_5 -like domain at the N-terminus that serves as the electron donor for the active site of the desaturase.

References: [2420, 3211, 2748, 3910, 1385]

[EC 1.14.19.5 created 2008 (EC 1.14.99.32 created 2000, incorporated 2015), modified 2015]

EC 1.14.19.6

Accepted name: acyl-CoA (9+3)-desaturase

Reaction: (1) oleoyl-CoA + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = linoleoyl-CoA + 2 ferricytochrome b_5 + 2 H₂O

(2) palmitoleoyl-CoA + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = (9Z,12Z)-hexadeca-9,12-dienoyl-CoA + 2 ferricytochrome b_5 + 2 H₂O

Other name(s): oleoyl-CoA 12-desaturase; Δ¹² fatty acid desaturase; Δ¹²(ω⁶)-desaturase; oleoyl-CoA Δ¹² desaturase; Δ¹² desaturase; Δ¹²-desaturase; Δ¹²-fatty-acid desaturase; acyl-CoA,hydrogen donor:oxygen Δ¹²-oxidoreductase

Systematic name: acyl-CoA,ferrocytochrome b_5 :oxygen oxidoreductase (12,13 *cis*-dehydrogenating)

Comments: This microsomal enzyme introduces a *cis* double bond at position 12 of fatty-acyl-CoAs that contain a *cis* double bond at position 9. When acting on 19:1Δ¹⁰ fatty acyl-CoA the enzyme from the pathogenic protozoan *Trypanosoma brucei* introduces the new double bond at position 13, indicating that the new double bond is introduced three carbons from the existing *cis* double bond, towards the methyl-end of the fatty acid. Requires cytochrome b_5 as the electron donor [2993].

References: [352, 2292, 3899, 2993]

[EC 1.14.19.6 created 2008, modified 2015]

[1.14.19.7 Transferred entry. (S)-2-hydroxypropylphosphonic acid epoxidase. Now EC 1.11.1.23, (S)-2-hydroxypropylphosphonic acid epoxidase.]

[EC 1.14.19.7 created 2011, deleted 2014]

EC 1.14.19.8

Accepted name: pentalenolactone synthase
Reaction: pentalenolactone F + O₂ + 2 reduced ferredoxin + 2 H⁺ = pentalenolactone + 2 oxidized ferredoxin + 2 H₂O
Other name(s): *penM* (gene name); *pntM* (gene name)
Systematic name: pentalenolactone-reduced-ferredoxin:oxygen oxidoreductase (pentalenolactone forming)
Comments: A heme-thiolate protein (P-450). Isolated from the bacteria *Streptomyces exfoliatus* and *Streptomyces arenae*.
References: [4477]

[EC 1.14.19.8 created 2012 as EC 1.3.7.10, transferred 2013 to EC 1.14.19.8]

EC 1.14.19.9

Accepted name: tryptophan 7-halogenase
Reaction: tryptophan + FADH₂ + chloride + O₂ + H⁺ = 7-chloro-L-tryptophan + FAD + 2 H₂O
Other name(s): *prnA* (gene name); *rebH* (gene name); *ktzQ* (gene name)
Systematic name: L-tryptophan:FADH₂ oxidoreductase (7-halogenating)
Comments: A flavin-dependent halogenase. The enzyme from the bacterium *Lechevalieria aerocolonigenes* catalyses the initial step in the biosynthesis of rebeccamycin [4356]. It utilizes molecular oxygen to oxidize the FADH₂ cofactor, giving C4a-hydroperoxyflavin, which then reacts with chloride to produce a hypochlorite ion. The latter reacts with an active site lysine to generate a chloramine, which chlorinates the substrate. Also acts on bromide ion. *cf.* EC 1.14.19.58, tryptophan 5-halogenase, and EC 1.14.19.59, tryptophan 6-halogenase.
References: [854, 4356, 303, 1454]

[EC 1.14.19.9 created 2009 as EC 1.14.14.7, transferred 2014 to EC 1.14.19.9, modified 2018]

EC 1.14.19.10

Accepted name: icosanoyl-CoA 5-desaturase
Reaction: icosanoyl-CoA + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = (Z)-icos-5-enoyl-CoA + 2 ferricytochrome *b*₅ + 2 H₂O
Other name(s): acyl-CoA Δ⁵-desaturase (ambiguous)
Systematic name: icosanoyl-CoA,ferrocyclochrome *b*₅:oxygen oxidoreductase (5,6 *cis*-dehydrogenating)
Comments: The enzyme, characterized from the plant *Limnanthes douglasii* (meadowfoam), is involved in the biosynthesis of (5Z)-icos-5-enoate, an unusual monounsaturated fatty acid that makes up to 60% of the total fatty acids in *Limnanthes* sp. seed oil. The enzyme only acts on saturated fatty acids.
References: [471]

[EC 1.14.19.10 created 2015]

EC 1.14.19.11

Accepted name: acyl-[acyl-carrier-protein] 4-desaturase
Reaction: palmitoyl-[acyl-carrier protein] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = (4Z)-hexadec-4-enoyl-[acyl-carrier protein] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): Δ⁴-palmitoyl-[acyl carrier protein] desaturase
Systematic name: palmitoyl-[acyl-carrier protein],reduced acceptor:oxygen oxidoreductase (4,5 *cis*-dehydrogenating)

Comments: The enzymes from the plants *Coriandrum sativum* (coriander) and *Hedera helix* (English ivy) are involved in biosynthesis of petroselinate [(6Z)-octadec-6-enoate], which is formed by elongation of (4Z)-hexadec-4-enoate. The ivy enzyme can also act on oleoyl-[acyl-carrier protein] and palmitoleoyl-[acyl-carrier protein], generating the corresponding 4,9-diene.

References: [474, 472, 4200]

[EC 1.14.19.11 created 2015]

EC 1.14.19.12

Accepted name: acyl-lipid ω -(9-4) desaturase

Reaction: (1) linoleoyl-[glycerolipid] + 2 ferrocycytochrome b_5 + O₂ + 2 H⁺ = pinolenoyl-[glycerolipid] + 2 ferrocycytochrome b_5 + 2 H₂O
(2) α -linolenoyl-[glycerolipid] + 2 ferrocycytochrome b_5 + O₂ + 2 H⁺ = coniferonoyl-[glycerolipid] + 2 ferrocycytochrome b_5 + 2 H₂O

Other name(s): acyl-lipid ω -13 desaturase; acyl-lipid 7-desaturase (ambiguous)

Systematic name: acyl-[glycerolipid],ferrocycytochrome b_5 :oxygen oxidoreductase [ω (9-4), ω (9-5) *cis*-dehydrogenating]

Comments: The enzyme, characterized from the green alga *Chlamydomonas reinhardtii*, is a front-end desaturase that introduces a *cis* double bond in ω^9 unsaturated C₁₈ or C₂₀ fatty acids incorporated into lipids, at a position 4 carbon atoms from the existing ω^9 bond, towards the carboxy end of the fatty acid (at the ω^{13} position). When acting on 20:2 Δ (11,14) and 20:3 Δ (11,14,17) substrates it introduces the new double bond between carbons 7 and 8. The enzyme contains a cytochrome b_5 domain that acts as the direct electron donor for the active site of the desaturase.

References: [1802]

[EC 1.14.19.12 created 2015]

EC 1.14.19.13

Accepted name: acyl-CoA 15-desaturase

Reaction: (9Z,12Z)-hexadeca-9,12-dienoyl-CoA + reduced acceptor + O₂ = (9Z,12Z,15Z)-hexadeca-9,12,15-trienoyl-CoA + acceptor + 2 H₂O

Other name(s): DES3 (gene name)

Systematic name: acyl-CoA,reduced acceptor:oxygen oxidoreductase (15,16 *cis*-dehydrogenating)

Comments: The enzyme, characterized from the the plant *Sorghum bicolor*, is involved in the biosynthesis of sorgoleone, an allelopathic compound produced in root hair cells. The enzyme inserts a *cis* double bond at carbon 15. When acting on its natural substrate, (9Z,12Z)-hexadeca-9,12-dienoyl-CoA, it produces a product with a terminal double bond.

References: [2930]

[EC 1.14.19.13 created 2015]

EC 1.14.19.14

Accepted name: linoleoyl-lipid Δ^9 conjugase

Reaction: a linoleoyl-[glycerolipid] + reduced acceptor + O₂ = an (8E,10E,12Z)-octadeca-8,10,12-trienoyl-[glycerolipid] + acceptor + 2 H₂O

Systematic name: linoleoyl-lipid,reduced acceptor:oxygen 8,11-allylic oxidase (8E,10E-forming)

Comments: The enzyme, characterized from the plant *Calendula officinalis*, converts a single *cis* double bond at position 9 of fatty acids incorporated into glycerolipids into two conjugated *trans* double bonds at positions 8 and 10.

References: [3084, 473]

[EC 1.14.19.14 created 2015]

EC 1.14.19.15

- Accepted name:** (11Z)-hexadec-11-enoyl-CoA conjugase
Reaction: (11Z)-hexadec-11-enoyl-CoA + reduced acceptor + O₂ = (10E,12Z)-hexadeca-10,12-dienoyl-CoA + acceptor + 2 H₂O
Other name(s): Bmpgdesat1 (gene name)
Systematic name: (11Z)-hexadec-11-enoyl-CoA, reduced acceptor: oxygen 10,13-allylic oxidase (10E,12E-forming)
Comments: The enzyme, characterized from the silk moth *Bombyx mori*, catalyses a step in the pathway for the biosynthesis of bombykol, a sex pheromone produced by the moth. The enzyme converts a single *cis* double bond at position 11 of (11Z)-hexadec-11-enoyl-CoA into conjugated 10 *trans* and 12 *cis* double bonds. Prior to catalysing this reaction, the enzyme catalyses the introduction of the *cis* bond in position 11 (*cf.* EC 1.14.19.5, acyl-CoA 11-desaturase).
References: [2640]

[EC 1.14.19.15 created 2015]

EC 1.14.19.16

- Accepted name:** linoleoyl-lipid Δ^{12} conjugase (11E,13Z-forming)
Reaction: a linoleoyl-[glycerolipid] + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = a (9Z,11E,13Z)-octadeca-9,11,13-trienoyl-[glycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O
Other name(s): Fac (gene name)
Systematic name: linoleoyl-lipid, ferrocytochrome-*b*₅: oxygen 11,14 allylic oxidase (11E,13Z-forming)
Comments: The enzyme, characterized from the plants *Punica granatum* (pomegranate) and *Trichosanthes kirilowii* (Mongolian snake-gourd), converts a single *cis* double bond at position 12 of linoleate incorporated into phosphatidylcholine into conjugated 11-*trans* and 13-*cis* double bonds. *cf.* EC 1.14.19.33, Δ^{12} acyl-lipid conjugase (11E,13E-forming).
References: [1574, 1691]

[EC 1.14.19.16 created 2015]

EC 1.14.19.17

- Accepted name:** sphingolipid 4-desaturase
Reaction: a dihydroceramide + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = a (4E)-sphing-4-enine ceramide + 2 ferrocytochrome *b*₅ + 2 H₂O
Other name(s): dehydroceramide desaturase
Systematic name: dihydroceramide, ferrocytochrome *b*₅: oxygen oxidoreductase (4,5-dehydrogenating)
Comments: The enzyme, which has been characterized from plants, fungi, and mammals, generates a *trans* double bond at position 4 of sphinganine bases in sphingolipids [3653]. The preferred substrate is dihydroceramide, but the enzyme is also active with dihydroglucosylceramide [2526]. Unlike EC 1.14.19.29, sphingolipid 8-desaturase, this enzyme does not contain an integral cytochrome *b*₅ domain [3849] and requires an external cytochrome *b*₅ [522]. The product serves as an important signalling molecules in mammals and is required for spermatide differentiation [2523].
References: [3653, 2526, 522, 3849, 2523]

[EC 1.14.19.17 created 2015]

EC 1.14.19.18

- Accepted name:** sphingolipid 8-(E)-desaturase
Reaction: a (4E)-sphing-4-enine ceramide + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = a (4E,8E)-sphing-4,8-dienine ceramide + 2 ferricytochrome *b*₅ + 2 H₂O
Other name(s): 8-sphingolipid desaturase (ambiguous); 8 fatty acid desaturase (ambiguous); DELTA8-sphingolipid desaturase (ambiguous)
Systematic name: (4E)-sphing-4-enine ceramide, ferrocytochrome *b*₅: oxygen oxidoreductase (8,9-*trans* dehydrogenating)

Comments: The enzyme, characterized from the yeasts *Kluyveromyces lactis* and *Candida albicans* [3785] and from the diatom *Thalassiosira pseudonana* [3911], introduces a *trans* double bond at the 8-position of sphingoid bases in sphingolipids. The enzyme determines the position of the double bond by its distance from the alcohol end of the sphingoid base, and contains a cytochrome *b*₅ domain that acts as the direct electron donor to the active site of the desaturase [2919]. The homologous enzymes from higher plants, EC 1.14.19.29, sphingolipid 8-(*E/Z*)-desaturase, act on phytosphinganine (4-hydroxysphinganine) and produces a mixture of *trans* and *cis* isomers.

References: [3785, 3911, 2919]

[EC 1.14.19.18 created 2015]

EC 1.14.19.19

Accepted name: sphingolipid 10-desaturase
Reaction: a (4*E*,8*E*)-sphinga-4,8-dienine ceramide + 2 ferrocycytochrome *b*₅ + O₂ + 2 H⁺ = a (4*E*,8*E*,10*E*)-sphinga-4,8,10-trienine ceramide + 2 ferricytochrome *b*₅ + 2 H₂O
Other name(s): *desA* (gene name)
Systematic name: a (4*E*,8*E*)-sphinga-4,8-dienine ceramide,ferrocycytochrome *b*₅:oxygen oxidoreductase (10,11 *trans*-dehydrogenating)
Comments: The enzyme, characterized from the marine diatom *Thalassiosira pseudonana*, produces an *all-trans* product. Similar triunsaturated sphingoid bases are found in some marine invertebrates. The enzyme determines the position of the double bond by its distance from the alcohol end of the sphingoid base, and contains a cytochrome *b*₅ domain that acts as the direct electron donor to the active site of the desaturase.
References: [2522]

[EC 1.14.19.19 created 2015]

EC 1.14.19.20

Accepted name: Δ⁷-sterol 5(6)-desaturase
Reaction: a Δ⁷-sterol + 2 ferrocycytochrome *b*₅ + O₂ + 2 H⁺ = a Δ^{5,7}-sterol + 2 ferricytochrome *b*₅ + 2 H₂O
Other name(s): lathosterol oxidase; Δ⁷-sterol Δ⁵-dehydrogenase; Δ⁷-sterol 5-desaturase; Δ⁷-sterol-C5(6)-desaturase; 5-DES; SC5DL (gene name); ERG3 (gene name)
Systematic name: Δ⁷-sterol,ferrocycytochrome *b*₅:oxygen oxidoreductase 5,6-dehydrogenating
Comments: This enzyme, found in eukaryotic organisms, catalyses the introduction of a double bond between the C₅ and C₆ carbons of the B ring of Δ⁷-sterols, to yield the corresponding Δ^{5,7}-sterols. The enzymes from yeast, plants and vertebrates act on avenasterol, episterol, and lathosterol, respectively. The enzyme is located at the endoplasmic reticulum and is membrane bound.
References: [791, 1554, 125, 3824, 2797, 3823, 3029]

[EC 1.14.19.20 created 1972 as EC 1.3.3.2, transferred 2005 to EC 1.14.21.6, transferred 2015 to EC 1.14.19.20]

EC 1.14.19.21

Accepted name: cholesterol 7-desaturase
Reaction: cholesterol + O₂ + NAD(P)H + H⁺ = cholesta-5,7-dien-3β-ol + NAD(P)⁺ + 2 H₂O
Other name(s): *nvd* (gene name); *daf-36* (gene name)
Systematic name: cholesterol,NAD(P)H:oxygen oxidoreductase (7,8 dehydrogenating)
Comments: The enzyme, characterized from several organisms including the worm *Caenorhabditis elegans*, the fly *Drosophila melanogaster*, and the ciliate *Tetrahymena thermophila*, is a Rieske oxygenase. In insects it participates in the biosynthesis of ecdysteroid hormones. The electrons are transferred from NAD(P)H via an electron transfer chain likely to include ferredoxin reductase and ferredoxin. The enzyme differs from regular desaturases, such as EC 1.14.19.20, 7-sterol 5(6)-desaturase, which are cytochrome *b*₅-dependent and contain the three His-boxes that are typical to most desaturases.
References: [4387, 4243, 2698, 207]

[EC 1.14.19.21 created 2015]

EC 1.14.19.22

- Accepted name:** acyl-lipid ω -6 desaturase (cytochrome b_5)
Reaction: an oleoyl-[glycerolipid] + 2 ferrocycytochrome b_5 + O₂ + 2 H⁺ = a linoleoyl-[glycerolipid] + 2 ferricytochrome b_5 + 2 H₂O
Other name(s): oleate desaturase (ambiguous); linoleate synthase (ambiguous); oleoyl-CoA desaturase (incorrect); oleoylphosphatidylcholine desaturase (ambiguous); phosphatidylcholine desaturase (ambiguous); n -6 desaturase (ambiguous); FAD2 (gene name)
Systematic name: 1-acyl-2-oleoyl-*sn*-glycero-3-phosphocholine,ferrocycytochrome- b_5 :oxygen oxidoreductase (12,13 *cis*-dehydrogenating)
Comments: This microsomal enzyme introduces a *cis* double bond in fatty acids attached to lipid molecules at a location 6 carbons away from the methyl end of the fatty acid. The distance from the carboxylic acid end of the molecule does not affect the location of the new double bond. The most common substrates are oleoyl groups attached to either the *sn*-1 or *sn*-2 position of the glycerol backbone in phosphatidylcholine. *cf.* EC 1.14.19.23, acyl-lipid ω -6 desaturase (ferredoxin).
References: [3073, 3549, 3697, 3559, 1865, 2553]

[EC 1.14.19.22 created 1984 as EC 1.3.1.35, transferred 2015 to EC 1.14.19.22]

EC 1.14.19.23

- Accepted name:** acyl-lipid (n+3)-(Z)-desaturase (ferredoxin)
Reaction: an oleoyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = a linoleoyl-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): acyl-lipid ω^6 -desaturase (ferredoxin); oleate desaturase (ambiguous); linoleate synthase (ambiguous); oleoyl-CoA desaturase (ambiguous); oleoylphosphatidylcholine desaturase (ambiguous); phosphatidylcholine desaturase (ambiguous); FAD6 (gene name)
Systematic name: oleoyl-[glycerolipid],ferredoxin:oxygen oxidoreductase (12,13 *cis*-dehydrogenating)
Comments: This plastidial enzyme is able to insert a *cis* double bond in monounsaturated fatty acids incorporated into glycerolipids. The enzyme introduces the new bond at a position 3 carbons away from the existing double bond, towards the methyl end of the fatty acid. The native substrates are oleoyl (18:1 Δ^9) and (Z)-hexadec-7-enoyl (16:1 Δ^7) groups attached to either position of the glycerol backbone in glycerolipids, resulting in the introduction of the second double bond at positions 12 and 10, respectively. This prompted the suggestion that this is an ω^6 desaturase. However, when acting on palmitoleoyl groups (16:1 Δ^9), the enzyme introduces the second double bond at position 12 (ω^4), indicating it is an (n+3) desaturase [1522]. *cf.* EC 1.14.19.34, acyl-lipid (9+3)-(E)-desaturase.
References: [3374, 3375, 1522, 979, 3373]

[EC 1.14.19.23 created 2015]

EC 1.14.19.24

- Accepted name:** acyl-CoA 11-(E)-desaturase
Reaction: an acyl-CoA + 2 ferrocycytochrome b_5 + O₂ + 2 H⁺ = an (11E)-enoyl-CoA + 2 ferricytochrome b_5 + 2 H₂O
Systematic name: acyl-CoA,ferrocycytochrome b_5 :oxygen oxidoreductase (11,12 *trans*-dehydrogenating)
Comments: Involved in sex pheromone synthesis in the Lepidoptera (moths). The enzyme from the moth *Spodoptera littoralis* prefers 13:0 and 14:0 substrates. The product is formed by the stereospecific removal of the *pro-R* H at C-11 and the *pro-S* H at C-12. *cf.* EC 1.14.19.5, acyl-CoA 11-(Z)-desaturase.
References: [1041, 2420, 2748, 3013]

[EC 1.14.19.24 created 2000 as EC 1.14.99.31, transferred 2015 to EC 1.14.19.24]

EC 1.14.19.25

Accepted name: acyl-lipid ω -3 desaturase (cytochrome b_5)
Reaction: a linoleoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = an α -linolenoyl-[glycerolipid] + ferrocytochrome b_5 + 2 H₂O
Other name(s): FAD3
Systematic name: (9Z,12Z)-octadeca-9,12-dienoyl-[glycerolipid],ferrocytochrome b_5 :oxygen oxidoreductase (15,16 *cis*-dehydrogenating)
Comments: This microsomal enzyme introduces a *cis* double bond three carbons away from the methyl end of a fatty acid incorporated into a glycerolipid. The distance from the carboxylic acid end of the molecule does not have an effect. The plant enzyme acts on carbon 15 of linoleoyl groups incorporated into both the *sn*-1 and *sn*-2 positions of the glycerol backbone of phosphatidylcholine and other phospholipids, converting them into α -linolenoyl groups. The enzyme from the fungus *Mortierella alpina* acts on γ -linolenoyl and arachidonoyl groups, converting them into stearidonoyl and icosapentaenoyl groups, respectively [3297]. *cf.* EC 1.14.19.35, acyl-lipid ω -3 desaturase (ferredoxin).
References: [420, 123, 3297]

[EC 1.14.19.25 created 2015]

EC 1.14.19.26

Accepted name: acyl-[acyl-carrier-protein] 6-desaturase
Reaction: palmitoyl-[acyl-carrier protein] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = (6Z)-hexadec-6-enoyl-[acyl-carrier protein] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): DELTA6 palmitoyl-ACP desaturase; DELTA6 16:0-ACP desaturase
Systematic name: palmitoyl-[acyl-carrier protein],reduced ferredoxin:oxygen oxidoreductase (6,7 *cis*-dehydrogenating)
Comments: The enzyme, characterized from the endosperm of the plant *Thunbergia alata* (black-eyed Susan vine), introduces a *cis* double bond at carbon 6 of several saturated acyl-[acp]s. It is most active with palmitoyl-[acp] (16:0), but can also act on myristoyl-[acp] (14:0) and stearoyl-[acp] (18:0). The position of the double bond is determined by its distance from the carboxyl end of the fatty acid.
References: [468, 470]

[EC 1.14.19.26 created 2015]

EC 1.14.19.27

Accepted name: *sn*-2 palmitoyl-lipid 9-desaturase
Reaction: a 1-acyl-2-palmitoyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = a 1-acyl-2-palmitoleoyl-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): DesC2
Systematic name: 1-acyl-2-palmitoyl-[glycerolipid],ferredoxin:oxygen oxidoreductase (9,10 *cis*-dehydrogenating)
Comments: The enzyme, characterized from the cyanobacterium *Nostoc* sp. 36, introduces a *cis* double bond at carbon 9 of palmitoyl groups (16:0) attached to the *sn*-2 position of glycerolipids.
References: [594]

[EC 1.14.19.27 created 2015]

EC 1.14.19.28

Accepted name: *sn*-1 stearoyl-lipid 9-desaturase
Reaction: a 1-stearoyl-2-acyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = a 1-oleoyl-2-acyl-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): *desC* (gene name)
Systematic name: 1-stearoyl-2-acyl-[glycerolipid],ferredoxin:oxygen oxidoreductase (9,10 *cis*-dehydrogenating)
Comments: The enzyme, characterized from cyanobacteria, introduces a *cis* double bond at carbon 9 of stearoyl groups (18:0) attached to the *sn*-1 position of glycerolipids. The enzyme is nonspecific with respect to the polar head group of the glycerolipid.
References: [4074, 1494, 3294]

[EC 1.14.19.28 created 2015]

EC 1.14.19.29

- Accepted name:** sphingolipid 8-(*E/Z*)-desaturase
- Reaction:** (1) a (4*R*)-4-hydroxysphinganine ceramide + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = a (4*R*,8*E*)-4-hydroxysphing-8-enine ceramide + 2 ferricytochrome *b*₅ + 2 H₂O
(2) a (4*R*)-4-hydroxysphinganine ceramide + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = a (4*R*,8*Z*)-4-hydroxysphing-8-enine ceramide + 2 ferricytochrome *b*₅ + 2 H₂O
- Other name(s):** 8-sphingolipid desaturase (ambiguous); 8 fatty acid desaturase (ambiguous); DELTA8-sphingolipid desaturase (ambiguous)
- Systematic name:** (4*R*)-4-hydroxysphinganine ceramide,ferrocytochrome *b*₅:oxygen oxidoreductase (8,9 *cis/trans*-dehydrogenating)
- Comments:** The enzymes from higher plants convert sphinganine, 4*E*-sphing-4-enine and phytosphinganine into *E/Z*-mixtures of Δ⁸-desaturated products displaying different proportions of geometrical isomers depending on plant species. The nature of the actual desaturase substrate has not yet been studied experimentally. The enzymes contain an N-terminal cytochrome *b*₅ domain that acts as the direct electron donor to the active site of the desaturase [3601]. The homologous enzymes from some yeasts and diatoms, EC 1.14.19.18, sphingolipid 8-(*E*)-desaturase, act on sphing-4-enine ceramides and produce only the *trans* isomer.
- References:** [3601, 3597, 3599, 238, 3268, 573]

[EC 1.14.19.29 created 2015]

EC 1.14.19.30

- Accepted name:** acyl-lipid (8-3)-desaturase
- Reaction:** (1) an (8*Z*,11*Z*,14*Z*)-icosa-8,11,14-trienoyl-[glycerolipid] + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = a (5*Z*,8*Z*,11*Z*,14*Z*)-icosatetra-5,8,11,14-tetraenoyl-[glycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O
(2) an (8*Z*,11*Z*,14*Z*,17*Z*)-icosa-8,11,14,17-tetraenoyl-[glycerolipid] + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = a (5*Z*,8*Z*,11*Z*,14*Z*,17*Z*)-icosa-5,8,11,14,17-pentaenoyl-[glycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O
- Other name(s):** acyl-lipid 5-desaturase; Δ⁵-fatty-acid desaturase; DES5 (gene name); D5des (gene name); FADS1
- Systematic name:** Δ⁸ acyl-lipid,ferrocytochrome *b*₅:oxygen oxidoreductase (5,6 *cis*-dehydrogenating)
- Comments:** The enzyme, which has been characterized from multiple organisms including the moss *Physcomitrella patens*, the marine microalga *Rebecca salina*, and the filamentous fungus *Mortierella alpina*, introduces a *cis* double bond at the 5-position in 20-carbon polyunsaturated fatty acids incorporated in a glycerolipid that contain a Δ⁸ double bond. The enzyme contains a cytochrome *b*₅ domain that acts as the direct electron donor to the active site of the desaturase, and does not require an external cytochrome.
- References:** [2521, 1794, 4475]

[EC 1.14.19.30 created 2015]

EC 1.14.19.31

- Accepted name:** acyl-lipid (7-3)-desaturase
- Reaction:** (1) a (7*Z*,10*Z*,13*Z*,16*Z*,19*Z*)-docosa-7,10,13,16,19-pentaenoyl-[glycerolipid] + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = a (4*Z*,7*Z*,10*Z*,13*Z*,16*Z*,19*Z*)-docosa-4,7,10,13,16,19-hexaenoyl-[glycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O
(2) a (7*Z*,10*Z*,13*Z*,16*Z*)-docosa-7,10,13,16-tetraenoyl-[glycerolipid] + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = a (4*Z*,7*Z*,10*Z*,13*Z*,16*Z*)-docosa-4,7,10,13,16-pentaenoyl-[glycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O
- Other name(s):** D4Des (gene name); des1 (gene name); CrΔ⁴FAD (gene name); acyl-lipid 4-desaturase
- Systematic name:** Δ⁷ acyl-lipid,ferrocytochrome *b*₅:oxygen oxidoreductase (4,5 *cis*-dehydrogenating)

Comments: The enzymes from several algae introduce a *cis* double bond at the 4-position in 22-carbon polyunsaturated fatty acids that contain a Δ^7 double bond. The enzyme from the fresh water alga *Chlamydomonas reinhardtii* acts on the 16 carbon fatty acid (7Z,10Z,13Z)-hexadeca-7,10,13-trienoate [4427]. The enzyme contains an N-terminal cytochrome *b*₅ domain that acts as the direct electron donor to the active site of the desaturase, and does not require an external cytochrome.

References: [3083, 3909, 2517, 4475, 4427]

[EC 1.14.19.31 created 2015]

EC 1.14.19.32

Accepted name: palmitoyl-CoA 14-(*E/Z*)-desaturase

Reaction: (1) palmitoyl-CoA + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = (14*E*)-hexadec-14-enoyl-CoA + 2 ferricytochrome *b*₅ + 2 H₂O
(2) palmitoyl-CoA + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = (14*Z*)-hexadec-14-enoyl-CoA + 2 ferricytochrome *b*₅ + 2 H₂O

Systematic name: palmitoyl-CoA,ferrocyclochrome *b*₅:oxygen oxidoreductase (14,15 *cis/trans*-dehydrogenating)

Comments: The enzyme, found in the moth *Ostrinia furnacalis* (Asian corn borer), produces a mixture of (*E*)- and (*Z*)- isomers. The products are subsequently truncated by partial β -oxidation to a blend of 12(*E/Z*)-tetradec-12-enoyl-CoA, which are converted to the species-specific sex pheromones (*E*)- and (*Z*)-tetradec-12-enoyl acetates.

References: [3216, 4288, 3290]

[EC 1.14.19.32 created 2015]

EC 1.14.19.33

Accepted name: Δ^{12} acyl-lipid conjugase (11*E*,13*E*-forming)

Reaction: (1) a linoleoyl-[glycerolipid] + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = an α -eleostearoyl-[glycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O
(2) a γ -linolenoyl-[glycerolipid] + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = an α -parinaroyl-[glycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O

Other name(s): fatty acid Δ^{12} -conjugase (ambiguous); FADX (gene name)

Systematic name: Δ^{12} acyl-lipid,ferrocyclochrome-*b*₅:oxygen 11,14 allylic oxidase (11*E*,13*E*-forming)

Comments: The enzyme, characterized from the plants *Impatiens balsamina*, *Momordica charantia* (bitter gourd) and *Vernicia fordii* (tung tree), converts a single *cis* double bond at carbon 12 to two conjugated *trans* bonds at positions 11 and 13. The enzyme from *Vernicia fordii* can also act as a 12(*E*) desaturase when acting on the monounsaturated fatty acids oleate and palmitoleate. *cf.* EC 1.14.19.16, linoleoyl-lipid Δ^{12} conjugase (11*E*,13*Z*-forming).

References: [467, 898]

[EC 1.14.19.33 created 2015]

EC 1.14.19.34

Accepted name: acyl-lipid (9+3)-(*E*)-desaturase

Reaction: (1) an oleoyl-[glycerolipid] + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = a (9*Z*,12*E*)-octadeca-9,12-dienoyl-[glycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O
(2) a palmitoleoyl-[glycerolipid] + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = a (9*Z*,12*E*)-hexadeca-9,12-dienoyl-[glycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O

Other name(s): acyl-lipid 12-(*E*)-desaturase; DsFAD2-1; FADX

Systematic name: Δ^9 acyl-lipid,ferrocyclochrome *b*₅:oxygen oxidoreductase (12,13 *trans*-dehydrogenating)

Comments: The enzymes from the plants *Dimorphotheca sinuata* (African daisy) and *Vernicia fordii* (tung oil tree) insert a *trans* double bond in position C-12 of oleate and palmitoleate incorporated into glycerolipids. The enzyme introduces the new double bond at a position three carbons away from an existing double bond at position 9, towards the methyl end of the fatty acid. The enzyme from tung oil tree also possesses the activity of EC 1.14.19.33, Δ^{12} acyl-lipid conjugase.

References: [898, 469]

[EC 1.14.19.34 created 2015]

EC 1.14.19.35

Accepted name: *sn*-2 acyl-lipid ω -3 desaturase (ferredoxin)
Reaction: (1) a (7Z,10Z)-hexadeca-7,10-dienoyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = a (7Z,10Z,13Z)-hexadeca-7,10,13-trienoyl-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
(2) a linoleoyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = an α -linolenoyl-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): FAD7; FAD8
Systematic name: (7Z,10Z)-hexadeca-7,10-dienoyl-[glycerolipid],ferredoxin:oxygen oxidoreductase (13,14 *cis*-dehydrogenating)
Comments: This plastidial enzyme desaturates 16:2 fatty acids attached to the *sn*-2 position of glycerolipids to 16:3 fatty acids, and converts 18:2 to 18:3 in both the *sn*-1 and *sn*-2 positions. It acts on all 16:2- or 18:2-containing chloroplast membrane lipids, including phosphatidylglycerol, monogalactosyldiacylglycerol, digalactosyldiacylglycerol, and sulfoquinovosyldiacylglycerol. The enzyme introduces a *cis* double bond at a location 3 carbons away from the methyl end of the fatty acid. The distance from the carboxylic acid end of the molecule does not affect the location of the new double bond. *cf.* EC 1.14.19.25, acyl-lipid ω -3 desaturase (cytochrome *b*₅) and EC 1.14.19.36, *sn*-1 acyl-lipid ω -3 desaturase (ferredoxin).
References: [1622, 2478, 4030]

[EC 1.14.19.35 created 2015]

EC 1.14.19.36

Accepted name: *sn*-1 acyl-lipid ω -3 desaturase (ferredoxin)
Reaction: (1) a 1- γ -linolenoyl-2-acyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = a 1-stearidonoyl-2-acyl-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
(2) a 1-linoleoyl-2-acyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = a 1- α -linolenoyl-2-acyl-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): *desB* (gene name)
Systematic name: 1- γ -linolenoyl-2-acyl-[glycerolipid],ferredoxin:oxygen oxidoreductase (15,16 *cis*-dehydrogenating)
Comments: The enzyme, characterized from cyanobacteria, introduces a *cis* double bond at carbon 15 of linoleoyl and γ -linolenoyl groups attached to the *sn*-1 position of glycerolipids. The enzyme is an ω desaturase, and determines the location of the double bond by counting three carbons from the methyl end of the fatty acid. It is nonspecific with respect to the polar head group of the glycerolipid. *cf.* EC 1.14.19.35, *sn*-2 acyl-lipid ω -3 desaturase (ferredoxin).
References: [3293]

[EC 1.14.19.36 created 2015]

EC 1.14.19.37

Accepted name: acyl-CoA 5-desaturase
Reaction: (1) (11Z,14Z)-icosa-11,14-dienoyl-CoA + reduced acceptor + O₂ = (5Z,11Z,14Z)-icosa-5,11,14-trienoyl-CoA + acceptor + 2 H₂O
(2) (11Z,14Z,17Z)-icosa-11,14,17-trienoyl-CoA + reduced acceptor + O₂ = (5Z,11Z,14Z,17Z)-icosa-5,11,14,17-tetraenoyl-CoA + acceptor + 2 H₂O
Other name(s): acyl-CoA 5-desaturase (non-methylene-interrupted)
Systematic name: acyl-CoA,acceptor:oxygen oxidoreductase (5,6 *cis*-dehydrogenating)

Comments: The enzyme, characterized from the plant *Anemone leveillei*, introduces a *cis* double bond at carbon 5 of acyl-CoAs that do not contain a double bond at position 8. *In vivo* it forms non-methylene-interrupted polyunsaturated fatty acids such as sciadonate and juniperonate. When expressed in *Arabidopsis thaliana* the enzyme could also act on unsaturated substrates such as palmitoyl-CoA. *cf.* EC 1.14.19.44, acyl-CoA (8-3)-desaturase.

References: [3336]

[EC 1.14.19.37 created 2015]

EC 1.14.19.38

Accepted name: acyl-lipid Δ^6 -acetylenase

Reaction: (1) a γ -linolenoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = a (9Z,12Z)-octadeca-9,12-dien-6-ynoyl-[glycerolipid] + 2 ferricytochrome b_5 + 2 H₂O
(2) a stearidonoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = a (9Z,12Z,15Z)-octadeca-9,12,15-trien-6-ynoyl-[glycerolipid] + 2 ferricytochrome b_5 + 2 H₂O

Systematic name: Δ^6 acyl-lipid,ferrocytochrome- b_5 :oxygen oxidoreductase (6,7-dehydrogenating)

Comments: The enzyme, characterized from the moss *Ceratodon purpureus*, converts the double bond at position 6 of γ -linolenate and stearidonate into a triple bond. The product of the latter, dicranin, is the main fatty acid found in *C. purpureus*. The enzyme contains a cytochrome b_5 domain that acts as the direct electron donor to the desaturase active site. The enzyme also has the activity of EC 1.14.19.47, acyl-lipid (9-3)-desaturase.

References: [3598]

[EC 1.14.19.38 created 2015]

EC 1.14.19.39

Accepted name: acyl-lipid Δ^{12} -acetylenase

Reaction: linoleoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = crepenynyl-[glycerolipid] + 2 ferricytochrome b_5 + 2 H₂O

Systematic name: Δ^{12} acyl-lipid,ferrocytochrome- b_5 :oxygen oxidoreductase (12,13-dehydrogenating)

Comments: The enzyme, characterized from the plant *Crepis alpina*, converts the double bond at position 12 of linoleate into a triple bond. The product is the main fatty acid found in triacylglycerols in the seed oil of *Crepis alpina*.

References: [187, 2172, 2725]

[EC 1.14.19.39 created 2000 as EC 1.14.99.33, transferred 2015 to EC 1.14.19.39]

EC 1.14.19.40

Accepted name: hex-5-enoyl-[acyl-carrier protein] acetylenase

Reaction: hex-5-enoyl-[acyl-carrier protein] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = hex-5-ynoyl-[acyl-carrier protein] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O

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

Systematic name: hex-5-enoyl-[acyl-carrier protein],reduced ferredoxin:oxygen oxidoreductase (5,6-dehydrogenating)

Comments: The enzyme, characterized from the marine cyanobacterium *Moorea producens*, is involved in production of the ion channel blocker jamaicamide A. It is specific for hexanoate or hex-5-enoate loaded onto a dedicated acyl-carrier protein (JamC), which is encoded by a gene in the same operon.

References: [4483]

[EC 1.14.19.40 created 2015]

EC 1.14.19.41

Accepted name: sterol 22-desaturase

Reaction: ergosta-5,7,24(28)-trien-3 β -ol + NADPH + H⁺ + O₂ = ergosta-5,7,22,24(28)-tetraen-3 β -ol + NADP⁺ + 2 H₂O

Other name(s): ERG5 (gene name); CYP710A (gene name)
Systematic name: ergosta-5,7,24(28)-trien-3 β -ol,NADPH:oxygen oxidoreductase (22,23-dehydrogenating)
Comments: A heme-thiolate protein (*P*-450). The enzyme, found in yeast and plants, catalyses the introduction of a double bond between the C-22 and C-23 carbons of certain sterols. In yeast the enzyme acts on ergosta-5,7,24(28)-trien-3 β -ol, a step in the biosynthesis of ergosterol. The enzyme from the plant *Arabidopsis thaliana* acts on sitosterol and 24-*epi*-campesterol, producing stigmasterol and brassicasterol, respectively.
References: [1878, 3547, 2622]

[EC 1.14.19.41 created 2015]

EC 1.14.19.42

Accepted name: palmitoyl-[glycerolipid] 7-desaturase
Reaction: a 1-acyl-2-palmitoyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = a 1-acyl-2-[(7*Z*)-hexadec-7-enoyl]-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): FAD5
Systematic name: 1-acyl-2-palmitoyl-[glycerolipid],ferredoxin:oxygen oxidoreductase (7,8-*cis*-dehydrogenating)
Comments: The enzyme introduces a *cis* double bond at carbon 7 of a palmitoyl group attached to the *sn*-2 position of glycerolipids. The enzyme from the plant *Arabidopsis thaliana* is specific for palmitate in monogalactosyldiacylglycerol.
References: [2083, 1461]

[EC 1.14.19.42 created 2015]

EC 1.14.19.43

Accepted name: palmitoyl-[glycerolipid] 3-(*E*)-desaturase
Reaction: a 1-acyl-2-palmitoyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = a 1-acyl-2-[(3*E*)-hexadec-3-enoyl]-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): FAD4
Systematic name: 1-acyl-2-palmitoyl-[glycerolipid],ferredoxin:oxygen oxidoreductase (3,4-*trans*-dehydrogenating)
Comments: The enzyme introduces an unusual *trans* double bond at carbon 3 of a palmitoyl group attached to the *sn*-2 position of glycerolipids. The enzyme from the plant *Arabidopsis thaliana* is specific for palmitate in phosphatidylglycerol. The enzyme from tobacco can also accept oleate and α -linolenate if present at the *sn*-2 position of phosphatidylglycerol [1079].
References: [1079, 1152]

[EC 1.14.19.43 created 2015]

EC 1.14.19.44

Accepted name: acyl-CoA (8-3)-desaturase
Reaction: (1) (8*Z*,11*Z*,14*Z*)-icosa-8,11,14-trienoyl-CoA + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = arachidonoyl-CoA + 2 ferrocytochrome *b*₅ + 2 H₂O
(2) (8*Z*,11*Z*,14*Z*,17*Z*)-icosa-8,11,14,17-tetraenoyl-CoA + 2 ferrocytochrome *b*₅ + O₂ + 2 H⁺ = (5*Z*,8*Z*,11*Z*,14*Z*,17*Z*)-icosa-5,8,11,14,17-pentaenoyl-CoA + 2 ferrocytochrome *b*₅ + 2 H₂O
Other name(s): FADS1 (gene name); acyl-CoA 5-desaturase (methylene-interrupted)
Systematic name: Δ^8 -acyl-CoA,ferrocytochrome *b*₅:oxygen oxidoreductase (5,6-*cis*-dehydrogenating)
Comments: The enzyme introduces a *cis* double bond at carbon 5 of acyl-CoAs that contain a double bond at position 8. The enzymes from algae, mosses, mammals and the protozoan *Leishmania major* catalyse the desaturation of dihomogamma-linoleate [(8*Z*,11*Z*,14*Z*)-icosa-8,11,14-trienoate] and (8*Z*,11*Z*,14*Z*,17*Z*)-icosa-8,11,14,17-tetraenoate to generate arachidonate and (5*Z*,8*Z*,11*Z*,14*Z*,17*Z*)-icosa-5,8,11,14,17-pentaenoate, respectively. The enzyme contains a cytochrome *b*₅ domain that acts as the direct electron donor to the desaturase active site and does not require an external cytochrome. *cf.* EC 1.14.19.37, acyl-CoA 5-desaturase.
References: [601, 2200, 3929, 3829]

[EC 1.14.19.44 created 2015]

EC 1.14.19.45

- Accepted name:** *sn*-1 oleoyl-lipid 12-desaturase
Reaction: a 1-oleoyl-2-acyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = a 1-linoleoyl-2-acyl-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): *desA* (gene name)
Systematic name: 1-oleoyl-2-acyl-[glycerolipid],ferredoxin:oxygen oxidoreductase (12,13-*cis*-dehydrogenating)
Comments: The enzyme, characterized from cyanobacteria, introduces a *cis* double bond at carbon 12 of oleoyl groups (18:1) attached to the *sn*-1 position of glycerolipids. The enzyme is a methyl-end desaturase, introducing the new double bond between a pre-existing double bond and the methyl-end of the fatty acid. It is nonspecific with respect to the polar head group of the glycerolipid.
References: [4073, 1494, 77]

[EC 1.14.19.45 created 2015]

EC 1.14.19.46

- Accepted name:** *sn*-1 linoleoyl-lipid 6-desaturase
Reaction: a 1-linoleoyl-2-acyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = a 1- γ -linolenoyl-2-acyl-[glycerolipid] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): *desD* (gene name)
Systematic name: 1-linoleoyl-2-acyl-[glycerolipid],ferredoxin:oxygen oxidoreductase (6,7-*cis*-dehydrogenating)
Comments: The enzyme, characterized from cyanobacteria, introduces a *cis* double bond at carbon 6 of linoleoyl groups (18:2) attached to the *sn*-1 position of glycerolipids. The enzyme is a front-end desaturase, introducing the new double bond between a pre-existing double bond and the carboxyl-end of the fatty acid. It is nonspecific with respect to the polar head group of the glycerolipid.
References: [1494, 3145, 2088]

[EC 1.14.19.46 created 2015]

EC 1.14.19.47

- Accepted name:** acyl-lipid (9-3)-desaturase
Reaction: (1) an α -linolenoyl-[glycerolipid] + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = a stearidonoyl-[glycerolipid] + ferricytochrome *b*₅ + 2 H₂O
(2) a linoleoyl-[glycerolipid] + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = a γ -linolenoyl-[glycerolipid] + ferricytochrome *b*₅ + 2 H₂O
Other name(s): acyl-lipid 6-desaturase; Δ^6 -desaturase; DES6 (gene name)
Systematic name: Δ^9 acyl-[glycerolipid],ferrocyclochrome *b*₅:oxygen oxidoreductase (6,7-*cis*-dehydrogenating)
Comments: The enzyme, characterized from the moss *Physcomitrella patens* and the plant *Borago officinalis* (borage), introduces a *cis* double bond at carbon 6 of several acyl-lipids that contain an existing Δ^9 *cis* double bond. The enzyme contains a cytochrome *b*₅ domain that acts as the electron donor for the active site of the desaturase.
References: [3337, 1208]

[EC 1.14.19.47 created 2015]

EC 1.14.19.48

- Accepted name:** *tert*-amyl alcohol desaturase
Reaction: *tert*-amyl alcohol + NADPH + H⁺ + O₂ = isoprenyl alcohol + NADP⁺ + 2 H₂O
Other name(s): *mdpJK* (gene names)
Systematic name: *tert*-amyl alcohol,NADPH:oxygen oxidoreductase (1,2-dehydrogenating)

Comments: The enzyme, characterized from the bacterium *Aquicola tertiaricarbonis*, is a Rieske nonheme mononuclear iron oxygenase. It can also act, with lower efficiency, on butan-2-ol, converting it to but-1-en-3-ol. Depending on the substrate, the enzyme also catalyses EC 1.14.13.229, *tert*-butanol monooxygenase.

References: [3348, 3406]

[EC 1.14.19.48 created 2016]

EC 1.14.19.49

Accepted name: tetracycline 7-halogenase

Reaction: tetracycline + FADH₂ + chloride + O₂ + H⁺ = 7-chlorotetracycline + FAD + 2 H₂O

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

Systematic name: tetracycline:FADH₂ oxidoreductase (7-halogenating)

Comments: The enzyme, characterized from the bacterium *Streptomyces aureofaciens*, is a member of the flavin-dependent halogenase family. The enzyme forms a lysine chloramine intermediate on an internal lysine residue before transferring the chlorine to the substrate. It is stereo-selective for the 4*S* (natural) isomer of tetracycline. FADH₂ is provided by a dedicated EC 1.5.1.36, flavin reductase (NADH).

References: [731, 4481]

[EC 1.14.19.49 created 2016]

EC 1.14.19.50

Accepted name: noroxomaritidine synthase

Reaction: (1) 4'-*O*-methylnorbelladine + [reduced NADPH—hemoprotein reductase] + O₂ = (4a*R*,10b*S*)-noroxomaritidine + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(2) 4'-*O*-methylnorbelladine + [reduced NADPH—hemoprotein reductase] + O₂ = (4a*S*,10b*R*)-noroxomaritidine + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

Other name(s): CYP96T1 (gene name)

Systematic name: 4'-*O*-methylnorbelladine,NADPH—hemoprotein reductase:oxygen oxidoreductase (noroxomaritidine-forming)

Comments: A *P*-450 (heme-thiolate) enzyme. The enzyme, characterized from *Narcissus pseudonarcissus* (daffodil), forms the two enantiomers of the *Amaryllidacea* alkaloid noroxomaritidine by catalysing intramolecular oxidative *para-para'* phenol coupling. The oxidation involves molecular oxygen without its incorporation into the product.

References: [1904]

[EC 1.14.19.50 created 2016]

EC 1.14.19.51

Accepted name: (*S*)-corytuberine synthase

Reaction: (*S*)-reticuline + [reduced NADPH—hemoprotein reductase] + O₂ = (*S*)-corytuberine + [oxidized NADPH—hemoprotein reductase] + 2 H₂O.

Other name(s): CYP80G2

Systematic name: (*S*)-reticuline,NADPH:oxygen oxidoreductase (C-C phenol-coupling; (*S*)-corytuberine-forming)

Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme is involved in the biosynthesis of the quaternary benzyloquinoline alkaloid magnoflorine in the plant *Coptis japonica*. It is specific for (*S*)-reticuline.

References: [1638]

[EC 1.14.19.51 created 2017]

EC 1.14.19.52

Accepted name: camalexin synthase

Reaction: 2-(L-cystein-*S*-yl)-2-(1*H*-indol-3-yl)acetonitrile + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = camalexin + hydrogen cyanide + CO₂ + 2 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)

(1a) 2-(L-cystein-*S*-yl)-2-(1*H*-indol-3-yl)acetonitrile + [reduced NADPH—hemoprotein reductase] + O₂ = (*R*)-dihydrocamalexate + hydrogen cyanide + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1b) (*R*)-dihydrocamalexate + [reduced NADPH—hemoprotein reductase] + O₂ = camalexin + CO₂ + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

Other name(s): CYP71B15 (gene name); bifunctional dihydrocamalexate synthase/camalexin synthase

Systematic name: 2-(cystein-*S*-yl)-2-(1*H*-indol-3-yl)-acetonitrile, [reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (camalexin-forming)

Comments: This cytochrome *P*-450 (heme thiolate) enzyme, which has been characterized from the plant *Arabidopsis thaliana*, catalyses the last two steps in the biosynthesis of camalexin, the main phytoalexin in that plant. The enzyme catalyses two successive oxidation events. During the first oxidation the enzyme introduces a C-N double bond, liberating hydrogen cyanide, and during the second oxidation it catalyses a decarboxylation.

References: [3396, 364]

[EC 1.14.19.52 created 2017]

EC 1.14.19.53

Accepted name: *all-trans*-retinol 3,4-desaturase

Reaction: *all-trans*-retinol + 2 reduced adrenodoxin + 2 H⁺ + O₂ = *all-trans*-3,4-didehydroretinol + 2 oxidized adrenodoxin + 2 H₂O

Other name(s): CYP27C1 (gene name)

Systematic name: *all-trans*-retinol, reduced adrenodoxin:oxygen 3,4-oxidoreductase

Comments: A cytochrome *P*-450 (heme thiolate) enzyme found in vertebrates. The enzyme is also active with retinal and retinoic acid.

References: [955, 2054]

[EC 1.14.19.53 created 2018]

EC 1.14.19.54

Accepted name: 1,2-dehydroreticuline synthase

Reaction: (*S*)-reticuline + [reduced NADPH—hemoprotein reductase] + O₂ = 1,2-dehydroreticuline + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

Other name(s): STORR; CYP82Y2 (gene name); DRS (gene name)

Systematic name: (*S*)-reticuline, [reduced NADPH—hemoprotein reductase]:oxygen 1,2-oxidoreductase

Comments: A *P*-450 (heme-thiolate) cytochrome. The enzyme from *Papaver rhoeas* (field poppy) is specific for (*S*)-reticuline and does not act on the (*R*)-form. The enzyme from *Papaver somniferum* (opium poppy), which is involved in the biosynthesis of morphine and related alkaloids, forms a fusion protein with EC 1.5.1.27, 1,2-dehydroreticulinium reductase (NADPH), which catalyses the reduction of 1,2-dehydroreticuline to (*R*)-reticuline, thus forming an epimerase system that converts (*S*)-reticuline to (*R*)-reticuline.

References: [1517, 4227, 991]

[EC 1.14.19.54 created 2018]

EC 1.14.19.55

Accepted name: 4-hydroxybenzoate brominase (decarboxylating)

Reaction: (1) 4-hydroxybenzoate + 2 NADPH + 2 bromide + 2 O₂ + 2 H⁺ = 2,4-dibromophenol + 2 NADP⁺ + CO₂ + 4 H₂O (overall reaction)

(1a) 4-hydroxybenzoate + NADPH + bromide + O₂ + H⁺ = 3-bromo-4-hydroxybenzoate + NADP⁺ + 2 H₂O

(1b) 3-bromo-4-hydroxybenzoate + NADPH + bromide + O₂ + H⁺ = 2,4-dibromophenol + NADP⁺ + CO₂ + 2 H₂O

(2) 3,4-dihydroxybenzoate + 2 NADPH + 2 bromide + 2 O₂ + 2 H⁺ = 3,5-dibromobenzene-1,2-diol + 2 NADP⁺ + CO₂ + 4 H₂O (overall reaction)

(2a) 3,4-dihydroxybenzoate + NADPH + bromide + O₂ + H⁺ = 3-bromo-4,5-dihydroxybenzoate + NADP⁺ + 2 H₂O

(2b) 3-bromo-4,5-dihydroxybenzoate + NADPH + bromide + O₂ + H⁺ = 3,5-dibromobenzene-1,2-diol + NADP⁺ + CO₂ + 2 H₂O

Other name(s): bmp5 (gene name)
Systematic name: 4-hydroxybenzoate:NADPH oxidoreductase (brominating, decarboxylating)
Comments: Contains FAD. The enzyme, described from epiphytic marine bacteria of the genera *Pseudoal-teromonas* and *Marinomonas*, is an unusual single-component FAD-dependent halogenase that contains a distinct NAD(P)H binding domain and does not require an additional flavin reductase for activity. The enzyme catalyses a bromination of its substrate, followed by a second bromination concurrent with decarboxylation.
References: [30, 31]

[EC 1.14.19.55 created 2018]

EC 1.14.19.56

Accepted name: 1H-pyrrole-2-carbonyl-[peptidyl-carrier protein] chlorinase
Reaction: 1H-pyrrole-2-carbonyl-[PtlL peptidyl-carrier protein] + 2 FADH₂ + 2 chloride + 2 O₂ = 4,5-dichloro-1H-pyrrole-2-carbonyl-[PtlL peptidyl-carrier protein] + 2 FAD + 4 H₂O (overall reaction)
(1a) 1H-pyrrole-2-carbonyl-[PtlL peptidyl-carrier protein] + FADH₂ + chloride + O₂ = 5-chloro-1H-pyrrole-2-carbonyl-[PtlL peptidyl-carrier protein] + FAD + 2 H₂O
(1b) 5-chloro-1H-pyrrole-2-carbonyl-[PtlL peptidyl-carrier protein] + FADH₂ + chloride + O₂ = 4,5-dichloro-1H-pyrrole-2-carbonyl-[PtlL peptidyl-carrier protein] + FAD + H₂O
Other name(s): *pltA* (gene name)
Systematic name: 1H-pyrrole-2-carbonyl-[peptidyl-carrier protein]:FADH₂ oxidoreductase (chlorinating)
Comments: The enzyme, characterized from the bacterium *Pseudomonas protegens* Pf-5, is a flavin-dependent chlorinase that participates in the biosynthesis of the antibacterial and antifungal compound pyolute-orin.
References: [2823, 859, 2932]

[EC 1.14.19.56 created 2018]

EC 1.14.19.57

Accepted name: 1H-pyrrole-2-carbonyl-[peptidyl-carrier protein] brominase
Reaction: 1H-pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + 3 FADH₂ + 3 bromide + 3 O₂ = 3,4,5-tribromo-1H-pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + 3 FAD + 6 H₂O (overall reaction)
(1a) 1H-pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + FADH₂ + bromide + O₂ = 5-bromo-1H-pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + FAD + 2 H₂O
(1b) 5-bromo-1H-pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + FADH₂ + bromide + O₂ = 4,5-dibromo-1H-pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + FAD + 2 H₂O
(1c) 4,5-dibromo-1H-pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + FADH₂ + bromide + O₂ = 3,4,5-tribromo-1H-pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + FAD + 2 H₂O
Other name(s): bmp2 (gene name)
Systematic name: 1H-pyrrole-2-carbonyl-[peptidyl-carrier protein]:FADH₂ oxidoreductase (brominating)

Comments: The enzyme, characterized from marine bacteria of the *Pseudoalteromonas* genus, belongs to a family of FAD-dependent halogenases that act on acyl-carrier protein-tethered substrates. It catalyses three successive rounds of bromination. While the order has not been verified, it is believed to resemble that of EC 1.14.19.56, *S*-(1*H*-pyrrole-2-carbonyl)-[peptidyl-carrier protein] chlorinase, due to significant sequence homology. Reduced FAD is provided in situ by a dedicated reductase and diffuses into the active site, where it reacts with the oxygen and bromide ion, resulting in formation of a bromoamine intermediate on a catalytic lysine side chain, and the eventual transfer of the bromide to the substrate. The enzyme from *Pseudoalteromonas luteoviolacea* 2ta16 is specific for bromide and does not accept chloride.

References: [30]

[EC 1.14.19.57 created 2018]

EC 1.14.19.58

Accepted name: tryptophan 5-halogenase
Reaction: L-tryptophan + FADH₂ + chloride + O₂ + H⁺ = 5-chloro-L-tryptophan + FAD + 2 H₂O
Other name(s): *pyrH* (gene name)
Systematic name: L-tryptophan:FADH₂ oxidoreductase (5-halogenating)
Comments: A flavin-dependent halogenase. The enzyme from the bacterium *Streptomyces rugosporus* catalyses halogenation of the C-5 position of tryptophan during the biosynthesis of the antibiotic compound pyrroindomycin B. It utilizes molecular oxygen to oxidize the FADH₂ cofactor, giving C4a-hydroperoxyflavin, which then reacts with chloride to produce a hypochlorite ion. The latter reacts with an active site lysine to generate a chloramine, which chlorinates the substrate. *cf.* EC 1.14.19.59, tryptophan 6-halogenase and EC 1.14.19.9, tryptophan 7-halogenase.

References: [4430, 4482]

[EC 1.14.19.58 created 2018]

EC 1.14.19.59

Accepted name: tryptophan 6-halogenase
Reaction: (1) L-tryptophan + FADH₂ + chloride + O₂ + H⁺ = 6-chloro-L-tryptophan + FAD + 2 H₂O
(2) D-tryptophan + FADH₂ + chloride + O₂ + H⁺ = 6-chloro-D-tryptophan + FAD + 2 H₂O
Other name(s): *sttH* (gene name); *thdH* (gene name)
Systematic name: L-tryptophan:FADH₂ oxidoreductase (6-halogenating)
Comments: The enzyme is a flavin-dependent halogenase that has been described from several bacterial species. It utilizes molecular oxygen to oxidize the FADH₂ cofactor, giving C4a-hydroperoxyflavin, which then reacts with chloride to produce a hypochlorite ion. The latter reacts with an active site lysine to generate a chloramine, which chlorinates the substrate. *cf.* EC 1.14.19.58, tryptophan 5-halogenase, and EC 1.14.19.9, tryptophan 7-halogenase.

References: [4434, 2539, 3478]

[EC 1.14.19.59 created 2018]

EC 1.14.19.60

Accepted name: 7-chloro-L-tryptophan 6-halogenase
Reaction: 7-chloro-L-tryptophan + FADH₂ + chloride + O₂ + H⁺ = 6,7-dichloro-L-tryptophan + FAD + 2 H₂O
Other name(s): *ktzR* (gene name)
Systematic name: 7-chloro-L-tryptophan:FADH₂ oxidoreductase (6-halogenating)
Comments: An FAD-dependent halogenase. The enzyme, characterized from the bacterium *Kutzneria* sp. 744, works in tandem with EC 1.14.19.9, tryptophan 7-halogenase, (*ktzQ*) to generate 6,7-dichloro-L-tryptophan, which is incorporated as a pyrroloindoline in the kutznerides family of natural products. It has a 120-fold preference for 7-chloro-L-tryptophan over L-tryptophan as substrate.

References: [1454]

[EC 1.14.19.60 created 2018]

EC 1.14.19.61

- Accepted name:** dihydrorhizobitoxine desaturase
Reaction: dihydrorhizobitoxine + 2 reduced ferredoxin [iron-sulfur] cluster + O₂ + 2 H⁺ = rhizobitoxine + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
Other name(s): *rtxC* (gene name)
Systematic name: dihydrorhizobitoxine,ferredoxin:oxygen oxidoreductase (3,4 *trans*-dehydrogenating)
Comments: The enzyme, characterized from the bacterium *Bradyrhizobium elkanii*, catalyses the final step in the biosynthesis of the nodulation enhancer compound rhizobitoxine.
References: [4352, 2866]

[EC 1.14.19.61 created 2018]

EC 1.14.19.62

- Accepted name:** secologanin synthase
Reaction: loganin + [reduced NADPH—hemoprotein reductase] + O₂ = secologanin + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Systematic name: loganin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (ring-cleaving)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Secologanin is the precursor of the monoterpene indole alkaloids and ipecac alkaloids.
References: [4313, 4312, 1661]

[EC 1.14.19.62 created 2002 as EC 1.3.3.9, transferred 2018 to EC 1.14.19.62]

EC 1.14.19.63

- Accepted name:** pseudobaptigenin synthase
Reaction: (1) calycosin + [reduced NADPH—hemoprotein reductase] + O₂ = pseudobaptigenin + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
(2) pratensein + [reduced NADPH—hemoprotein reductase] + O₂ = 5-hydroxypseudobaptigenin + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Systematic name: calycosin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (methylenedioxy-bridge-forming)
Comments: A cytochrome *P*-450 (heme-thiolate) enzyme catalysing an oxidative reaction that does not incorporate oxygen into the product. Catalyses a step in the biosynthesis of (–)-maackiain, the main pterocarpan phytoalexin in chickpea (*Cicer arietinum*).
References: [3270]

[EC 1.14.19.63 created 2011 as EC 1.14.21.8, transferred 2018 to EC 1.14.19.63]

EC 1.14.19.64

- Accepted name:** (*S*)-stylopine synthase
Reaction: (*S*)-cheilanthifoline + [reduced NADPH—hemoprotein reductase] + O₂ = (*S*)-stylopine + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): (*S*)-cheilanthifoline oxidase (methylenedioxy-bridge-forming)
Systematic name: (*S*)-cheilanthifoline,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (methylenedioxy-bridge-forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein catalysing an oxidative reaction that does not incorporate oxygen into the product. Forms the second methylenedioxy bridge of the protoberberine alkaloid stylopine from oxidative ring closure of adjacent phenolic and methoxy groups of cheilanthifoline.
References: [220]

[EC 1.14.19.64 created 1999 as EC 1.1.3.32, transferred 2002 to EC 1.14.21.1, transferred 2018 to EC 1.14.19.64]

EC 1.14.19.65

- Accepted name:** (*S*)-cheilanthifoline synthase
Reaction: (*S*)-scoulerine + [reduced NADPH—hemoprotein reductase] + O₂ = (*S*)-cheilanthifoline + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): CYP719A14 (gene name); (*S*)-scoulerine oxidase (methylenedioxy-bridge-forming) (ambiguous)
Systematic name: (*S*)-scoulerine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase [(*S*)-cheilanthifoline-forming]
Comments: A cytochrome *P*-450 (heme-thiolate) protein catalysing an oxidative reaction that does not incorporate oxygen into the product. Forms the methylenedioxy bridge of the protoberberine alkaloid cheilanthifoline by the oxidative ring closure of adjacent phenolic and methoxy groups of scoulerine. *cf.* EC 1.14.19.73, (*S*)-nandinine synthase, which catalyses a similar reaction at the other side of the (*S*)-scoulerine molecule, forming (*S*)-nandinine.
References: [220, 560]

[EC 1.14.19.65 created 1999 as EC 1.1.3.33, transferred 2002 to EC 1.14.21.2, modified 2016, transferred 2018 to EC 1.14.19.65]

EC 1.14.19.66

- Accepted name:** berbamunine synthase
Reaction: (*S*)-*N*-methylcoclaurine + (*R*)-*N*-methylcoclaurine + [reduced NADPH—hemoprotein reductase] + O₂ = berbamunine + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): (*S*)-*N*-methylcoclaurine oxidase (C-O phenol-coupling)
Systematic name: (*S*)-*N*-methylcoclaurine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (C-O phenol-coupling)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. Forms the bisbenzylisoquinoline alkaloid berbamunine by phenol oxidation of *N*-methylcoclaurine without the incorporation of oxygen into the product. Reaction of two molecules of (*R*)-*N*-methylcoclaurine gives the dimer guattagaumerine.
References: [3613]

[EC 1.14.19.66 created 1999 as EC 1.1.3.34, transferred 2002 to EC 1.14.21.3, transferred 2018 to EC 1.14.19.66]

EC 1.14.19.67

- Accepted name:** salutaridine synthase
Reaction: (*R*)-reticuline + [reduced NADPH—hemoprotein reductase] + O₂ = salutaridine + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): (*R*)-reticuline oxidase (C-C phenol-coupling)
Systematic name: (*R*)-reticuline,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (C-C phenol-coupling)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. Forms the morphinan alkaloid salutaridine by intramolecular phenol oxidation of reticuline without the incorporation of oxygen into the product.
References: [1181]

[EC 1.14.19.67 created 1999 as EC 1.1.3.35, transferred 2002 to EC 1.14.21.4, transferred 2018 to EC 1.14.19.67]

EC 1.14.19.68

- Accepted name:** (*S*)-canadine synthase
Reaction: (*S*)-tetrahydrocolumbamine + [reduced NADPH—hemoprotein reductase] + O₂ = (*S*)-canadine + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): (*S*)-tetrahydroberberine synthase; (*S*)-tetrahydrocolumbamine oxidase (methylenedioxy-bridge-forming); CYP719A (gene name)
Systematic name: (*S*)-tetrahydrocolumbamine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (methylenedioxy-bridge-forming)

Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. The enzyme catalyses an oxidative reaction that does not incorporate oxygen into the product. Oxidation of the methoxyphenol group of the alkaloid tetrahydrocolumbamine results in the formation of the methylenedioxy bridge of canadine.

References: [3255, 1639, 738]

[EC 1.14.19.68 created 1999 as EC 1.1.3.36, transferred 2002 to EC 1.14.21.5, transferred 2018 to EC 1.14.19.68]

EC 1.14.19.69

Accepted name: biflaviolin synthase

Reaction: (1) 2 flaviolin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = 3,3'-biflaviolin + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O
(2) 2 flaviolin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = 3,8'-biflaviolin + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O

Other name(s): CYP158A2 (gene name); cytochrome P450 158A2

Systematic name: flaviolin, reduced ferredoxin: oxygen oxidoreductase

Comments: This cytochrome-*P*-450 (heme-thiolate) enzyme, from the soil-dwelling bacterium *Streptomyces coelicolor* A3(2), catalyses a phenol oxidation C-C coupling reaction, which results in the polymerization of flaviolin to form biflaviolin or triflaviolin without the incorporation of oxygen into the product [4454, 4456]. The products are highly conjugated pigments that protect the bacterium from the deleterious effects of UV irradiation [4454].

References: [4454, 4455, 4456]

[EC 1.14.19.69 created 2008 as EC 1.14.21.7, transferred 2018 to EC 1.14.19.69]

EC 1.14.19.70

Accepted name: mycocyclosin synthase

Reaction: cyclo(L-tyrosyl-L-tyrosyl) + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = mycocyclosin + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O

Other name(s): CYP121; rv2276 (locus name)

Systematic name: cyclo(L-tyrosyl-L-tyrosyl), reduced ferredoxin: oxygen oxidoreductase (diarylbridge-forming)

Comments: A cytochrome *P*-450 (heme-thiolate) protein from the bacterium *Mycobacterium tuberculosis* catalysing an oxidative reaction that does not incorporate oxygen into the product.

References: [251]

[EC 1.14.19.70 created 2013 as EC 1.14.21.9, transferred 2018 to EC 1.14.19.70]

EC 1.14.19.71

Accepted name: fumitremorgin C synthase

Reaction: tryprostatin A + [reduced NADPH—hemoprotein reductase] + O₂ = fumitremorgin C + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

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

Systematic name: tryprostatin A, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase

Comments: A cytochrome *P*-450 (heme-thiolate) protein. The protein from the fungus *Aspergillus fumigatus* also has activity with tryprostatin B forming demethoxyfumitremorgin C. Involved in the biosynthetic pathways of several indole alkaloids such as fumitremorgins and verruculogen.

References: [1838]

[EC 1.14.19.71 created 2013 as EC 1.14.21.10, transferred 2018 to EC 1.14.19.71]

EC 1.14.19.72

Accepted name: (-)-pluviatolide synthase

Reaction: (-)-matairesinol + [reduced NADPH—hemoprotein reductase] + O₂ = (-)-pluviatolide + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

Other name(s): CYP719A23 (gene name)
Systematic name: (–)-matairesinol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (methylenedioxy-bridge-forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme from the plants *Sinopodophyllum hexandrum* and *Podophyllum peltatum* catalyses the formation of a methylenedioxy-bridge. It is involved in the biosynthesis of podophyllotoxin, a non-alkaloid toxin lignan whose derivatives are important anticancer drugs.
References: [2404]

[EC 1.14.19.72 created 2016 as EC 1.14.21.11, transferred 2018 to EC 1.14.19.72]

EC 1.14.19.73

Accepted name: (*S*)-nandinine synthase
Reaction: (*S*)-scoulerine + [reduced NADPH—hemoprotein reductase] + O₂ = (*S*)-nandinine + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): CYP719A3
Systematic name: (*S*)-scoulerine,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase [(*S*)-nandinine-forming]
Comments: A cytochrome *P*-450 (heme-thiolate) enzyme found in plants. The enzyme catalyses an oxidative reaction that does not incorporate oxygen into the product. Forms the methylenedioxy bridge of the protoberberine alkaloid (*S*)-nandinine by the oxidative ring closure of adjacent phenolic and methoxy groups of (*S*)-scoulerine. *cf.* EC 1.14.19.65, (*S*)-cheilanthifoline synthase, which catalyses a similar reaction at the other side of the (*S*)-scoulerine molecule, forming (*S*)-cheilanthifoline.
References: [1637, 560]

[EC 1.14.19.73 created 2016 as EC 1.14.21.12, transferred 2018 to EC 1.14.19.73]

EC 1.14.19.74

Accepted name: (+)-piperitol/(+)-sesamin synthase
Reaction: (1) (+)-pinoresinol + [reduced NADPH-hemoprotein reductase]_I + O₂ = (+)-piperitol + [oxidized NADPH-hemoprotein reductase] + 2 H₂O
(2) (+)-piperitol + [reduced NADPH-hemoprotein reductase] + O₂ = (+)-sesamin + [oxidized NADPH-hemoprotein reductase] + 2 H₂O
Other name(s): CYP81Q1; CYP81Q2; PS; PSS; SS; piperitol synthase; sesamin synthase
Systematic name: (+)-pinoresinol,[reduced NADPH-hemoprotein reductase]:oxygen oxidoreductase (cyclizing)
Comments: A cytochrome *P*-450 (heme-thiolate) protein. Isolated from *Sesamum indicum* (sesame) and *S. radiatum* (black sesame).
References: [2889]

[EC 1.14.19.74 created 2018]

EC 1.14.19.75

Accepted name: very-long-chain acyl-lipid ω-9 desaturase
Reaction: (1) 1-hexacosanoyl-2-acyl-[phosphoglycerolipid] + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = 1-[(17*Z*)-hexacos-17-enoyl]-2-acyl-[phosphoglycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O
(2) 1-tetracosanoyl-2-acyl-[phosphoglycerolipid] + 2 ferrocyclochrome *b*₅ + O₂ + 2 H⁺ = 1-[(15*Z*)-tetracos-15-enoyl]-2-acyl-[phosphoglycerolipid] + 2 ferricytochrome *b*₅ + 2 H₂O
Other name(s): ADS2 (gene name)
Systematic name: very-long-chain acyl-[glycerolipid],ferrocyclochrome *b*₅:oxygen oxidoreductase (ω⁹,ω⁸-*cis*-dehydrogenating)
Comments: The enzyme, characterized from the plant *Arabidopsis thaliana*, acts on both 24:0 and 26:0 fatty acids, introducing a *cis* double bond at a position 9 carbons from the methyl end. These very-long-chain fatty acids are found as a minor component of seed lipids, but also in the membrane phosphatidylethanolamine and phosphatidylserine, in sphingolipids, as precursors and components of cuticular and epicuticular waxes, and in suberin.

References: [1103, 3560]

[EC 1.14.19.75 created 2018]

EC 1.14.19.76

Accepted name: flavone synthase II
Reaction: a flavanone + [reduced NADPH—hemoprotein reductase] + O₂ = a flavone + [oxidized NADPH—hemoprotein reductase] + 2 H₂O
Other name(s): CYP93B16 (gene name); CYP93G1 (gene name); FNS II
Systematic name: flavanone,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (flavone-forming)
Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. The rice enzyme channels flavanones to the biosynthesis of tricin O-linked conjugates. *cf.* EC 1.14.20.5, flavone synthase I.
References: [2408, 1025, 2117]

[EC 1.14.19.76 created 2018]

EC 1.14.20 With 2-oxoglutarate as one donor, and the other dehydrogenated

EC 1.14.20.1

Accepted name: deacetoxycephalosporin-C synthase
Reaction: penicillin N + 2-oxoglutarate + O₂ = deacetoxycephalosporin C + succinate + CO₂ + H₂O
Other name(s): DAOCS; penicillin N expandase; DAOC synthase
Systematic name: penicillin-N,2-oxoglutarate:oxygen oxidoreductase (ring-expanding)
Comments: Forms part of the penicillin biosynthesis pathway (for pathway, click here).
References: [494, 2168, 4357, 3986, 863]

[EC 1.14.20.1 created 2002]

[1.14.20.2 *Transferred entry. 2,4-dihydroxy-1,4-benzoxazin-3-one-glucoside dioxygenase. Now EC 1.14.11.59, 2,4-dihydroxy-1,4-benzoxazin-3-one-glucoside dioxygenase*]

[EC 1.14.20.2 created 2012, deleted 2018]

EC 1.14.20.3

Accepted name: (5*R*)-carbapenem-3-carboxylate synthase
Reaction: (3*S*,5*S*)-carbapenam-3-carboxylate + 2-oxoglutarate + O₂ = (5*R*)-carbapen-2-em-3-carboxylate + succinate + CO₂ + H₂O
Other name(s): *carC* (gene name)
Systematic name: (3*S*,5*S*)-carbapenam-3-carboxylate,2-oxoglutarate:oxygen oxidoreductase (dehydrating)
Comments: Requires Fe²⁺. 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*. It catalyses a stereoinversion at C-5 and introduces a double bond between C-2 and C-3.
References: [633, 3622, 3551]

[EC 1.14.20.3 created 2013]

EC 1.14.20.4

Accepted name: anthocyanidin synthase
Reaction: a (2*R*,3*S*,4*S*)-leucoanthocyanidin + 2-oxoglutarate + O₂ = an anthocyanidin + succinate + CO₂ + 2 H₂O (overall reaction)
(1a) a (2*R*,3*S*,4*S*)-leucoanthocyanidin + 2-oxoglutarate + O₂ = a (4*S*)- 2,3-dehydroflavan-3,4-diol + succinate + CO₂ + H₂O
(1b) a (4*S*)- 2,3-dehydroflavan-3,4-diol = an anthocyanidin + H₂O

Other name(s): leucocyanidin oxygenase; leucocyanidin,2-oxoglutarate:oxygen oxidoreductase; ANS (gene name)
Systematic name: (2*R*,3*S*,4*S*)-leucoanthocyanidin,2-oxoglutarate:oxygen oxidoreductase
Comments: The enzyme requires Fe(II) and ascorbate. It is involved in the pathway by which many flowering plants make anthocyanin flower pigments (glycosylated anthocyanidins). The enzyme hydroxylates the C-3 carbon, followed by a *trans* diaxial elimination, forming a C-2,C-3 enol. The product loses a second water molecule to form anthocyanidins. When assayed *in vitro*, non-enzymic epimerization of the product can lead to formation of dihydroflavanols. Thus when the substrate is leucocyanidin, a mixture of (+)-taxifolin and (+)-epitaxifolin are formed. The enzyme can also oxidize the formed (+)-taxifolin to quercetin (*cf.* EC 1.14.20.6, flavonol synthase) [3948, 4225].
References: [3282, 3948, 4225, 3946, 4170]

[EC 1.14.20.4 created 2001 as EC 1.14.11.19, transferred 2018 to EC 1.14.20.4]

EC 1.14.20.5

Accepted name: flavone synthase I
Reaction: a flavanone + 2-oxoglutarate + O₂ = a flavone + succinate + CO₂ + H₂O
Other name(s): FNSI (gene name)
Systematic name: flavanone,2-oxoglutarate:oxygen oxidoreductase (dehydrating)
Comments: The enzyme, which has been found in rice and in members of the Apiaceae (a plant family), is a member of the 2-oxoglutarate-dependent dioxygenases, and requires ascorbate and Fe²⁺ for full activity.
References: [2410, 2315, 2409]

[EC 1.14.20.5 created 2004 as EC 1.14.11.22, transferred 2018 to EC 1.14.20.5]

EC 1.14.20.6

Accepted name: flavonol synthase
Reaction: a dihydroflavonol + 2-oxoglutarate + O₂ = a flavonol + succinate + CO₂ + H₂O
Other name(s): FLS (gene name)
Systematic name: dihydroflavonol,2-oxoglutarate:oxygen oxidoreductase
Comments: In addition to the desaturation of (2*R*,3*R*)-dihydroflavonols to flavonols, the enzyme from *Citrus unshiu* (satsuma mandarin) also has a non-specific activity that *trans*-hydroxylates the flavanones (2*S*)-naringenin and the unnatural (2*R*)-naringenin at C-3 to kaempferol and (2*R*,3*R*)-dihydrokaempferol, respectively [2316]. Requires Fe²⁺.
References: [4171, 2316, 2409, 3947]

[EC 1.14.20.6 created 2004 as EC 1.14.11.23, transferred 2018 to EC 1.14.20.6]

EC 1.14.20.7

Accepted name: 2-oxoglutarate/L-arginine monooxygenase/decarboxylase (succinate-forming)
Reaction: L-arginine + 2-oxoglutarate + O₂ = succinate + CO₂ + guanidine + (S)-1-pyrroline-5-carboxylate + H₂O (overall reaction)
(1a) L-arginine + 2-oxoglutarate + O₂ = succinate + CO₂ + 5-hydroxy-L-arginine
(1b) 5-hydroxy-L-arginine = guanidine + (S)-1-pyrroline-5-carboxylate + H₂O
Other name(s): ethene-forming enzyme; ethylene-forming enzyme; EFE
Systematic name: L-arginine,2-oxoglutarate:oxygen oxidoreductase (succinate-forming)
Comments: This is one of two simultaneous reactions catalysed by the enzyme, which is responsible for ethylene production in bacteria of the *Pseudomonas syringae* group. In the other reaction [EC 1.13.12.19, 2-oxoglutarate dioxygenase (ethene-forming)] the enzyme catalyses the dioxygenation of 2-oxoglutarate forming ethene and three molecules of carbon dioxide. The enzyme catalyses two cycles of the ethene-forming reaction for each cycle of the succinate-forming reaction, so that the stoichiometry of the products ethene and succinate is 2:1.
References: [2679, 1107, 1106, 2419]

[EC 1.14.20.7 created 2011 as EC 1.14.11.34, transferred 2018 to EC 1.14.20.7]

EC 1.14.20.8

- Accepted name:** (–)-deoxypodophyllotoxin synthase
Reaction: (–)-yatein + 2-oxoglutarate + O₂ = (–)-deoxypodophyllotoxin + succinate + CO₂ + H₂O
Other name(s): 2-ODD (gene name)
Systematic name: (–)-yatein,2-oxoglutarate:oxygen oxidoreductase (ring-forming)
Comments: The enzyme, characterized from the plant *Sinopodophyllum hexandrum* (mayapple), is involved in the biosynthetic pathway of podophyllotoxin, a non-alkaloid toxin lignan whose derivatives are important anticancer drugs. It catalyses the closure of the central six-membered ring in the aryltetralin scaffold.
References: [2151]

[EC 1.14.20.8 created 2016 as EC 1.14.11.50, transferred 2018 to EC 1.14.20.8]

EC 1.14.20.9

- Accepted name:** L-tyrosine isonitrile desaturase
Reaction: (2*S*)-3-(4-hydroxyphenyl)-2-isocyanopropanoate + 2-oxoglutarate + O₂ = (2*E*)-3-(4-hydroxyphenyl)-2-isocyanoprop-2-enoate + succinate + CO₂ + H₂O
Other name(s): *pvcB* (gene name)
Systematic name: (2*S*)-3-(4-hydroxyphenyl)-2-isocyanopropanoate,2-oxoglutarate:oxygen oxidoreductase
Comments: The enzyme is a member of the Fe²⁺, 2-oxoglutarate-dependent oxygenases and requires Fe²⁺. It has been characterized from bacteria that form the isonitrile-functionalized compound paerucumarin. *cf.* EC 1.14.20.10, L-tyrosine isonitrile desaturase/decarboxylase.
References: [629, 869, 4479]

[EC 1.14.20.9 created 2018]

EC 1.14.20.10

- Accepted name:** L-tyrosine isonitrile desaturase/decarboxylase
Reaction: (2*S*)-3-(4-hydroxyphenyl)-2-isocyanopropanoate + 2-oxoglutarate + O₂ = 4-[(*E*)-2-isocyanoethenyl]phenol + succinate + 2 CO₂ + H₂O
Other name(s): *pvcB* (gene name)
Systematic name: (2*S*)-3-(4-hydroxyphenyl)-2-isocyanopropanoate,2-oxoglutarate:oxygen oxidoreductase (decarboxylating)
Comments: The enzyme, characterized from the bacterium *Xenorhabdus nematophila*, is involved in rhabduscin biosynthesis. The enzyme is a member of the Fe²⁺, 2-oxoglutarate-dependent oxygenases. It is similar to EC 1.14.20.9, L-tyrosine isonitrile desaturase. However, the latter does not catalyse a decarboxylation of the substrate.
References: [693, 4479]

[EC 1.14.20.10 created 2018]

EC 1.14.20.11

- Accepted name:** 3-[(*Z*)-2-isocyanoethenyl]-1*H*-indole synthase
Reaction: (2*S*)-3-(1*H*-indol-3-yl)-2-isocyanopropanoate + 2-oxoglutarate + O₂ = 3-[(*Z*)-2-isocyanoethenyl]-1*H*-indole + succinate + 2 CO₂ + H₂O
Other name(s): *ambI3* (gene name); *famH3* (gene name)
Systematic name: (2*S*)-3-(1*H*-indol-3-yl)-2-isocyanopropanoate,2-oxoglutarate:oxygen oxidoreductase (decarboxylating, 3-[(*Z*)-2-isocyanoethenyl]-1*H*-indole-forming)
Comments: The enzyme, characterized from the cyanobacterium *Fischerella ambigua* UTEX 1903, participates in the biosynthesis of hapalindole-type alkaloids. The enzyme catalyses an Fe²⁺, 2-oxoglutarate-dependent monooxygenation at C-3, which is followed by decarboxylation and dehydration, resulting in the generation of a *cis* C-C double bond. *cf.* EC 1.14.20.12, L-tryptophan isonitrile desaturase/decarboxylase (3-[(*E*)-2-isocyanoethenyl]-1*H*-indole-forming).

References: [1507, 544]

[EC 1.14.20.11 created 2018]

EC 1.14.20.12

Accepted name: 3-[(*E*)-2-isocyanoethenyl]-1*H*-indole synthase
Reaction: (2*S*)-3-(1*H*-indol-3-yl)-2-isocyanopropanoate + 2-oxoglutarate + O₂ = 3-[(*E*)-2-isocyanoethenyl]-1*H*-indole + succinate + 2 CO₂ + H₂O
Other name(s): *isnB* (gene name)
Systematic name: (2*S*)-3-(1*H*-indol-3-yl)-2-isocyanopropanoate,2-oxoglutarate:oxygen oxidoreductase (decarboxylating, 3-[(*E*)-2-isocyanoethenyl]-1*H*-indole-forming)
Comments: The enzyme has been characterized from an unidentified soil bacterium. It catalyses an Fe²⁺, 2-oxoglutarate-dependent monooxygenation at C-3, which is followed by decarboxylation and dehydration, resulting in the generation of a *trans* C-C double bond. *cf.* EC 1.14.20.11, L-tryptophan isonitrile desaturase/decarboxylase (3-[(*Z*)-2-isocyanoethenyl]-1*H*-indole-forming).
References: [382, 544]

[EC 1.14.20.12 created 2018]

EC 1.14.20.13

Accepted name: 6β-hydroxyhyoscyamine epoxidase
Reaction: (6*S*)-6β-hydroxyhyoscyamine + 2-oxoglutarate + O₂ = scopolamine + succinate + CO₂ + H₂O
Other name(s): hydroxyhyoscyamine dioxygenase; (6*S*)-6-hydroxyhyoscyamine,2-oxoglutarate oxidoreductase (epoxide-forming)
Systematic name: (6*S*)-6β-hydroxyhyoscyamine,2-oxoglutarate:oxygen oxidoreductase (epoxide-forming)
Comments: Requires Fe²⁺ and ascorbate.
References: [1410]

[EC 1.14.20.13 created 1992 as EC 1.14.11.14, transferred 2018 to EC 1.14.20.13]

EC 1.14.20.14

Accepted name: hapalindole-type alkaloid chlorinase
Reaction: (1) hapalindole U + 2-oxoglutarate + O₂ + chloride = hapalindole G + succinate + CO₂ + H₂O
(2) 12-*epi*-fischerindole U + 2-oxoglutarate + O₂ + chloride = 12-*epi*-fischerindole G + succinate + CO₂ + H₂O
Other name(s): *ambO5* (gene name); *welO5* (gene name)
Systematic name: 12-*epi*-fischerindole U,2-oxoglutarate:oxygen oxidoreductase (13-halogenating)
Comments: The enzyme, characterized from hapalindole-type alkaloids-producing cyanobacteria, is a specialized iron(II)/2-oxoglutarate-dependent oxygenase that catalyses the chlorination of its substrates in a reaction that requires oxygen, chloride ions, iron(II) and 2-oxoglutarate.
References: [1505, 4480, 1506]

[EC 1.14.20.14 created 2018]

EC 1.14.20.15

Accepted name: L-threonyl-[L-threonyl-carrier protein] 4-chlorinase
Reaction: an L-threonyl-[L-threonyl-carrier protein] + 2-oxoglutarate + O₂ + Cl⁻ = a 4-chloro-L-threonyl-[L-threonyl-carrier protein] + succinate + CO₂ + H₂O
Other name(s): *syrB2* (gene name)
Systematic name: L-threonyl-[L-threonyl-carrier protein],2-oxoglutarate:oxygen oxidoreductase (4-halogenating)
Comments: The enzyme, characterized from the bacterium *Pseudomonas syringae*, participates in syringomycin E biosynthesis. The enzyme is a specialized iron(II)/2-oxoglutarate-dependent oxygenase that catalyses the chlorination of its substrate in a reaction that requires oxygen, chloride ions, ferrous iron and 2-oxoglutarate.

References: [\[3984\]](#)

[EC 1.14.20.15 created 2018]

EC 1.14.21 With NADH or NADPH as one donor, and the other dehydrogenated

- [1.14.21.1] *Transferred entry. (S)-stylopine synthase. Now EC 1.14.19.64, (S)-stylopine synthase*
[EC 1.14.21.1 created 2002, deleted 2018]
- [1.14.21.2] *Transferred entry. (S)-cheilanthifoline synthase. Now EC 1.14.19.65, (S)-cheilanthifoline synthase*
[EC 1.14.21.2 created 2002, modified 2016, deleted 2018]
- [1.14.21.3] *Transferred entry. berbamunine synthase. Now EC 1.14.19.66, berbamunine synthase*
[EC 1.14.21.3 created 2002, deleted 2018]
- [1.14.21.4] *Transferred entry. salutaridine synthase. Now EC 1.14.19.67, salutaridine synthase*
[EC 1.14.21.4 created 2002, deleted 2018]
- [1.14.21.5] *Transferred entry. (S)-canadine synthase. Now EC 1.14.19.68, (S)-canadine synthase*
[EC 1.14.21.5 created 2002, deleted 2018]
- [1.14.21.6] *Transferred entry. lathosterol oxidase. Now EC 1.14.19.20, Δ^7 -sterol 5(6)-desaturase*
[EC 1.14.21.6 created 1972 as EC 1.3.3.2, transferred 2005 to EC 1.14.21.6, deleted 2015]
- [1.14.21.7] *Transferred entry. biflaviolin synthase. Now EC 1.14.19.69, biflaviolin synthase*
[EC 1.14.21.7 created 2008, deleted 2018]
- [1.14.21.8] *Transferred entry. pseudobaptigenin synthase. Now EC 1.14.19.63, pseudobaptigenin synthase.]*
[EC 1.14.21.8 created 2011, deleted 2018]
- [1.14.21.9] *Transferred entry. mycocyclosin synthase. Now EC 1.14.19.70, mycocyclosin synthase*
[EC 1.14.21.9 created 2013, deleted 2018]
- [1.14.21.10] *Transferred entry. fumitremorgin C synthase. Now EC 1.14.19.71, fumitremorgin C synthase*
[EC 1.14.21.10 created 2013, deleted 2018]
- [1.14.21.11] *Transferred entry. (-)-pluviatolide synthase. Now EC 1.14.19.72, (-)-pluviatolide synthase*
[EC 1.14.21.11 created 2016, deleted 2018]
- [1.14.21.12] *Transferred entry. (S)-nandinine synthase. Now EC 1.14.19.73, (S)-nandinine synthase*
[EC 1.14.21.12 created 2016, deleted 2018]

EC 1.14.99 Miscellaneous

EC 1.14.99.1

- Accepted name:** prostaglandin-endoperoxide synthase
Reaction: arachidonate + reduced acceptor + 2 O₂ = prostaglandin H₂ + acceptor + H₂O
Other name(s): prostaglandin synthase; prostaglandin G/H synthase; (PG)H synthase; PG synthetase; prostaglandin synthetase; fatty acid cyclooxygenase; prostaglandin endoperoxide synthetase
Systematic name: (5Z,8Z,11Z,14Z)-icosa-5,8,11,14-tetraenoate,hydrogen-donor:oxygen oxidoreductase
Comments: This enzyme acts both as a dioxygenase and as a peroxidase.
References: [\[809, 2848\]](#) 464

[EC 1.14.99.1 created 1972, modified 1990]

EC 1.14.99.2

Accepted name: kynurenine 7,8-hydroxylase
Reaction: kynurenate + reduced acceptor + O₂ = 7,8-dihydro-7,8-dihydroxykynurenate + acceptor
Other name(s): kynurenic acid hydroxylase; kynurenic hydroxylase; kynurenate 7,8-hydroxylase
Systematic name: kynurenate,hydrogen-donor:oxygen oxidoreductase (hydroxylating)
References: [3816]

[EC 1.14.99.2 created 1965 as EC 1.14.1.4, transferred 1972 to EC 1.14.99.2]

[1.14.99.3 *Transferred entry. heme oxygenase (biliverdin-producing). Now EC 1.14.14.18, heme oxygenase (biliverdin-producing)*]

[EC 1.14.99.3 created 1972, modified 2006, deleted 2015]

EC 1.14.99.4

Accepted name: progesterone monooxygenase
Reaction: progesterone + reduced acceptor + O₂ = testosterone acetate + acceptor + H₂O
Other name(s): progesterone hydroxylase
Systematic name: progesterone,hydrogen-donor:oxygen oxidoreductase (hydroxylating)
Comments: Has a wide specificity. A single enzyme from ascomycete the *Neonectria radicola* (EC 1.14.13.54 ketosteroid monooxygenase) catalyses both this reaction and that catalysed by EC 1.14.99.12 androst-4-ene-3,17-dione monooxygenase.
References: [3104]

[EC 1.14.99.4 created 1972, modified 1999]

[1.14.99.5 *Transferred entry. stearyl-CoA desaturase. Now EC 1.14.19.1, stearyl-CoA 9-desaturase*]

[EC 1.14.99.5 created 1972, modified 1986, modified 2000, deleted 2000]

[1.14.99.6 *Transferred entry. acyl-[acyl-carrier-protein] desaturase. Now EC 1.14.19.2, acyl-[acyl-carrier-protein] desaturase*]

[EC 1.14.99.6 created 1972, modified 2000, deleted 2000]

[1.14.99.7 *Transferred entry. squalene monooxygenase. Transferred to EC 1.14.13.132, squalene monooxygenase.*]

[EC 1.14.99.7 created 1961 as EC 1.99.1.13, transferred 1965 to EC 1.14.1.3, part transferred 1972 to EC 1.14.99.7 rest to EC 5.4.99.7, deleted 2011]

[1.14.99.8 *Deleted entry. arene monooxygenase (epoxidizing). Now included with EC 1.14.14.1 unspecific monooxygenase*]

[EC 1.14.99.8 created 1972, deleted 1984]

[1.14.99.9 *Transferred entry. steroid 17 α -monooxygenase, now classified as EC 1.14.14.19, steroid 17 α -monooxygenase*]

[EC 1.14.99.9 created 1961 as EC 1.99.1.9, transferred 1965 to EC 1.14.1.7, transferred 1972 to EC 1.14.99.9, modified 2013, deleted 2015]

[1.14.99.10 *Transferred entry. steroid 21-monooxygenase. Now EC 1.14.14.16, steroid 21-monooxygenase*]

[EC 1.14.99.10 created 1961 as EC 1.99.1.11, transferred 1965 to EC 1.14.1.8, transferred 1972 to EC 1.14.99.10, modified 2013, deleted 2015]

EC 1.14.99.11

Accepted name: estradiol 6 β -monooxygenase
Reaction: estradiol-17 β + reduced acceptor + O₂ = 6 β -hydroxyestradiol-17 β + acceptor + H₂O
Other name(s): estradiol 6 β -hydroxylase
Systematic name: estradiol-17 β ,hydrogen-donor:oxygen oxidoreductase (6 β -hydroxylating)
References: [1344, 2645]

[EC 1.14.99.11 created 1965 as EC 1.14.1.10, transferred 1972 to EC 1.14.99.11]

EC 1.14.99.12

Accepted name: androst-4-ene-3,17-dione monooxygenase
Reaction: androstenedione + reduced acceptor + O₂ = testolactone + acceptor + H₂O
Other name(s): androstene-3,17-dione hydroxylase; androst-4-ene-3,17-dione 17-oxidoreductase; androst-4-ene-3,17-dione hydroxylase; androstenedione monooxygenase; 4-androstene-3,17-dione monooxygenase
Systematic name: androst-4-ene-3,17-dione-hydrogen-donor:oxygen oxidoreductase (13-hydroxylating, lactonizing)
Comments: Has a wide specificity. A single enzyme from the ascomycete *Neonectria radicola* (EC 1.14.13.54, ketosteroid monooxygenase) catalyses both this reaction and that catalysed by EC 1.14.99.4, progesterone monooxygenase.
References: [3052]

[EC 1.14.99.12 created 1972, modified 1999]

[1.14.99.13 Transferred entry. 3-hydroxybenzoate 4-monooxygenase. Now EC 1.14.13.23, 3-hydroxybenzoate 4-monooxygenase]

[EC 1.14.99.13 created 1972, deleted 1984]

EC 1.14.99.14

Accepted name: progesterone 11 α -monooxygenase
Reaction: progesterone + reduced acceptor + O₂ = 11 α -hydroxyprogesterone + acceptor + H₂O
Other name(s): progesterone 11 α -hydroxylase
Systematic name: progesterone,hydrogen-donor:oxygen oxidoreductase (11 α -hydroxylating)
References: [3482]

[EC 1.14.99.14 created 1972]

EC 1.14.99.15

Accepted name: 4-methoxybenzoate monooxygenase (*O*-demethylating)
Reaction: 4-methoxybenzoate + reduced acceptor + O₂ = 4-hydroxybenzoate + formaldehyde + acceptor + H₂O
Other name(s): 4-methoxybenzoate 4-monooxygenase (*O*-demethylating); 4-methoxybenzoate *O*-demethylase; *p*-anisic *O*-demethylase; piperonylate-4-*O*-demethylase
Systematic name: 4-methoxybenzoate,hydrogen-donor:oxygen oxidoreductase (*O*-demethylating)
Comments: The bacterial enzyme consists of a ferredoxin-type protein and an iron-sulfur flavoprotein (FMN). Also acts on 4-ethoxybenzoate, *N*-methyl-4-aminobenzoate and toluate. The fungal enzyme acts best on veratrate.
References: [273, 2952, 3953]

[EC 1.14.99.15 created 1972]

[1.14.99.16 Transferred entry. methylsterol monooxygenase. Now EC 1.14.13.72, methylsterol monooxygenase]

[EC 1.14.99.16 created 1972, deleted 2002]

[1.14.99.17 Transferred entry. glyceryl-ether monooxygenase. Now EC 1.14.16.5, glyceryl-ether monooxygenase]

[EC 1.14.99.17 created 1972, deleted 1976]

[1.14.99.18 Deleted entry. CMP-*N*-acetylneuraminate monooxygenase]

[EC 1.14.99.18 created 1976, modified 1999, deleted 2003]

EC 1.14.99.19

Accepted name: plasmanyethanolamine desaturase
Reaction: *O*-1-alkyl-2-acyl-*sn*-glycero-3-phosphoethanolamine + reduced acceptor + O₂ = *O*-1-alk-1-enyl-2-acyl-*sn*-glycero-3-phosphoethanolamine + acceptor + 2 H₂O

Other name(s): alkylacylglycerophosphoethanolamine desaturase; alkylacylglycero-phosphorylethanolamine dehydrogenase; dehydrogenase, alkyl-acylglycerophosphorylethanolamine; 1-*O*-alkyl-2-acyl-*sn*-glycero-3-phosphorylethanolamine desaturase; 1-*O*-alkyl 2-acyl-*sn*-glycero-3-phosphorylethanolamine desaturase
Systematic name: *O*-1-alkyl-2-acyl-*sn*-glycero-3-phosphoethanolamine,hydrogen-donor:oxygen oxidoreductase
Comments: Requires NADPH or NADH. May involve cytochrome *b*₅. Requires Mg²⁺ and ATP.
References: [2928, 4272]

[EC 1.14.99.19 created 1976]

EC 1.14.99.20

Accepted name: phyloquinone monooxygenase (2,3-epoxidizing)
Reaction: phyloquinone + reduced acceptor + O₂ = 2,3-epoxyphyloquinone + acceptor + H₂O
Other name(s): phyloquinone epoxidase; vitamin K 2,3-epoxidase; vitamin K epoxidase; vitamin K₁ epoxidase
Systematic name: phyloquinone,hydrogen-donor:oxygen oxidoreductase (2,3-epoxidizing)
References: [4224]

[EC 1.14.99.20 created 1976]

EC 1.14.99.21

Accepted name: *Latia*-luciferin monooxygenase (demethylating)
Reaction: *Latia* luciferin + reduced acceptor + 2 O₂ = oxidized *Latia* luciferin + CO₂ + formate + acceptor + H₂O + *hν*
Other name(s): luciferase (*Latia* luciferin); *Latia* luciferin monooxygenase (demethylating)
Systematic name: *Latia*-luciferin,hydrogen-donor:oxygen oxidoreductase (demethylating)
Comments: A flavoprotein. *Latia* is a bioluminescent mollusc. The reaction possibly involves two enzymes, an oxygenase followed by a monooxygenase for the actual light-emitting step.
References: [3504, 3506]

[EC 1.14.99.21 created 1976, modified 1982]

EC 1.14.99.22

Accepted name: ecdysone 20-monooxygenase
Reaction: ecdysone + reduced acceptor + O₂ = 20-hydroxyecdysone + acceptor + H₂O
Other name(s): α-ecdysone C-20 hydroxylase; ecdysone 20-hydroxylase
Systematic name: Ecdysone,hydrogen-donor:oxygen oxidoreductase (20-hydroxylating)
Comments: An enzyme from insect fat body or malpighian tubules involving a heme-thiolate protein (*P*-450). NADPH can act as ultimate hydrogen donor.
References: [1761, 2789, 3564]

[EC 1.14.99.22 created 1978]

EC 1.14.99.23

Accepted name: 3-hydroxybenzoate 2-monooxygenase
Reaction: 3-hydroxybenzoate + reduced acceptor + O₂ = 2,3-dihydroxybenzoate + acceptor + H₂O
Other name(s): 3-hydroxybenzoate 2-hydroxylase; 3-HBA-2-hydroxylase
Systematic name: 3-hydroxybenzoate,hydrogen-donor:oxygen oxidoreductase (2-hydroxylating)
References: [751]

[EC 1.14.99.23 created 1984]

EC 1.14.99.24

Accepted name: steroid 9 α -monooxygenase
Reaction: pregna-4,9(11)-diene-3,20-dione + reduced acceptor + O₂ = 9,11 α -epoxypregn-4-ene-3,20-dione + acceptor + H₂O
Other name(s): steroid 9 α -hydroxylase
Systematic name: steroid,hydrogen-donor:oxygen oxidoreductase (9-epoxidizing)
Comments: An enzyme system involving a flavoprotein (FMN) and two iron-sulfur proteins.
References: [3682]

[EC 1.14.99.24 created 1986]

[1.14.99.25 *Transferred entry. linoleoyl-CoA desaturase. Now EC 1.14.19.3, linoleoyl-CoA desaturase*]

[EC 1.14.99.25 created 1986, deleted 2000]

EC 1.14.99.26

Accepted name: 2-hydroxypyridine 5-monooxygenase
Reaction: 2-hydroxypyridine + reduced acceptor + O₂ = 2,5-dihydroxypyridine + acceptor + H₂O
Other name(s): 2-hydroxypyridine oxygenase
Systematic name: 2-hydroxypyridine,hydrogen-donor:oxygen oxidoreductase (5-hydroxylating)
Comments: Also oxidizes 2,5-dihydroxypyridine, but does not act on 3-hydroxypyridine, 4-hydroxypyridine or 2,6-dihydroxypyridine.
References: [3463]

[EC 1.14.99.26 created 1989]

[1.14.99.27 *Transferred entry. juglone 3-monooxygenase, now classified as EC 1.17.3.4, juglone 3-monooxygenase*]

[EC 1.14.99.27 created 1989, deleted 2016]

[1.14.99.28 *Transferred entry. linalool 8-monooxygenase. Now EC 1.14.14.84, linalool 8-monooxygenase*]

[EC 1.14.99.28 created 1989, deleted 2012]

EC 1.14.99.29

Accepted name: deoxyhypusine monooxygenase
Reaction: [eIF5A]-deoxyhypusine + reduced acceptor + O₂ = [eIF5A]-hypusine + acceptor + H₂O
Other name(s): deoxyhypusine hydroxylase; deoxyhypusine dioxygenase
Systematic name: deoxyhypusine,hydrogen-donor:oxygen oxidoreductase (2-hydroxylating)
Comments: The enzyme catalyses the final step in the formation of the amino acid hypusine in the eukaryotic initiation factor 5A.
References: [1]

[EC 1.14.99.29 created 1989]

[1.14.99.30 *Transferred entry. carotene 7,8-desaturase. Now EC 1.3.5.6, 9,9'-dicis- ζ -carotene desaturase.*]

[EC 1.14.99.30 created 1999, deleted 2011]

[1.14.99.31 *Transferred entry. myristoyl-CoA 11-(E) desaturase. Now classified as EC 1.14.19.24, myristoyl-CoA 11-(E) desaturase*]

[EC 1.14.99.31 created 2000, deleted 2015]

[1.14.99.32 *Transferred entry. myristoyl-CoA 11-(Z) desaturase. Now classified as EC 1.14.19.5, acyl-CoA 11-(Z)-desaturase.*]

[EC 1.14.99.32 created 2000, deleted 2015]

[1.14.99.33 *Transferred entry. Δ^{12} -fatty acid dehydrogenase. Now EC 1.14.19.39, acyl-lipid Δ^{12} -acetylenase*]

[EC 1.14.99.33 created 2000, deleted 2015]

EC 1.14.99.34

- Accepted name:** monoprenyl isoflavone epoxidase
Reaction: 7-*O*-methylluteone + NADPH + H⁺ + O₂ = dihydrofurano derivatives + NADP⁺ + H₂O
Other name(s): monoprenyl isoflavone monooxygenase; 7-*O*-methylluteone:O₂ oxidoreductase; 7-*O*-methylluteone,NADPH:O₂ oxidoreductase
Systematic name: 7-*O*-methylluteone,NADPH:oxygen oxidoreductase
Comments: A flavoprotein (FAD) with high specificity for monoprenyl isoflavone. The product of the prenyl epoxidation reaction contains an oxygen atom derived from O₂, but not from H₂O. It is slowly and non-enzymically converted into the corresponding dihydrofurano derivative. The enzyme in the fungus *Botrytis cinerea* is induced by the substrate analogue, 6-prenylnaringenin.
References: [3803]

[EC 1.14.99.34 created 2000]

EC 1.14.99.35

- Accepted name:** thiophene-2-carbonyl-CoA monooxygenase
Reaction: thiophene-2-carbonyl-CoA + reduced acceptor + O₂ = 5-hydroxythiophene-2-carbonyl-CoA + acceptor + H₂O
Other name(s): thiophene-2-carboxyl-CoA dehydrogenase; thiophene-2-carboxyl-CoA hydroxylase; thiophene-2-carboxyl-CoA monooxygenase
Systematic name: thiophene-2-carbonyl-CoA, hydrogen-donor:oxygen oxidoreductase
Comments: A molybdenum enzyme. Highly specific for thiophene-2-carbonyl-CoA. Tetrazolium salts can act as electron acceptors.
References: [184]

[EC 1.14.99.35 created 2000]

[1.14.99.36 *Transferred entry. β-carotene 15,15-monooxygenase. Now classified as EC 1.13.11.63, β-carotene 15,15'-dioxygenase.*]

[EC 1.14.99.36 created 1972 as EC 1.13.11.21, transferred 2001 to EC 1.14.99.36, deleted 2015]

EC 1.14.99.37

- Accepted name:** taxadiene 5α-hydroxylase
Reaction: taxa-4,11-diene + reduced acceptor + O₂ = taxa-4(20),11-dien-5α-ol + acceptor + H₂O
Systematic name: taxa-4,11-diene,hydrogen-donor:oxygen oxidoreductase (5α-hydroxylating)
Comments: This microsomal cytochrome-*P*-450-dependent enzyme is involved in the biosynthesis of the diterpenoid antineoplastic drug Taxol (paclitaxel). The reaction includes rearrangement of the 4(5)-double bond to a 4(20)-double bond, possibly through allylic oxidation.
References: [1455]

[EC 1.14.99.37 created 2002]

EC 1.14.99.38

- Accepted name:** cholesterol 25-hydroxylase
Reaction: cholesterol + reduced acceptor + O₂ = 25-hydroxycholesterol + acceptor + H₂O
Other name(s): cholesterol 25-monooxygenase
Systematic name: cholesterol,hydrogen-donor:oxygen oxidoreductase (25-hydroxylating)
Comments: Unlike most other sterol hydroxylases, this enzyme is not a cytochrome *P*-450. Instead, it uses diiron cofactors to catalyse the hydroxylation of hydrophobic substrates [2319]. The diiron cofactor can be either Fe-O-Fe or Fe-OH-Fe and is bound to the enzyme through interactions with clustered histidine or glutamate residues [1042, 3263]. In cell cultures, this enzyme down-regulates cholesterol synthesis and the processing of sterol regulatory element binding proteins (SREBPs).
References: [2319, 570, 2317, 1042, 3263]

[EC 1.14.99.38 created 2005]

EC 1.14.99.39

Accepted name: ammonia monooxygenase
Reaction: $\text{NH}_3 + \text{a reduced acceptor} + \text{O}_2 = \text{NH}_2\text{OH} + \text{an acceptor} + \text{H}_2\text{O}$
Other name(s): AMO
Systematic name: ammonia,donor:oxygen oxidoreductase (hydroxylamine-producing)
Comments: The enzyme catalyses the first reaction in the pathway of ammonia oxidation to nitrite. It contains copper [957], iron [4420] and possibly zinc [1204]. The enzyme requires two electrons, which are derived indirectly from the quinone pool via a membrane-bound donor.
References: [957, 1617, 267, 1546, 4420, 2591, 4197, 124, 1204]

[EC 1.14.99.39 created 2010]

[1.14.99.40 Transferred entry. 5,6-dimethylbenzimidazole synthase. Now EC 1.13.11.79, 5,6-dimethylbenzimidazole synthase]

[EC 1.14.99.40 created 2010, deleted 2014]

[1.14.99.41 Transferred entry. all-trans-8'-apo- β -carotenal 15,15'-oxygenase. Now EC 1.13.11.75, all-trans-8'-apo- β -carotenal 15,15'-oxygenase]

[EC 1.14.99.41 created 2010, deleted 2013]

[1.14.99.42 Transferred entry. zeaxanthin 7,8-dioxygenase. Now EC 1.13.11.84, crocetin dialdehyde synthase]

[EC 1.14.99.42 created 2011, modified 2014, deleted 2017]

[1.14.99.43 Transferred entry. β -amyrin 24-hydroxylase. Now EC 1.14.14.134, β -amyrin 24-hydroxylase]

[EC 1.14.99.43 created 2011, deleted 2018]

EC 1.14.99.44

Accepted name: diapolycopene oxygenase
Reaction: $4,4'$ -diapolycopene + 4 reduced acceptor + 4 $\text{O}_2 = 4,4'$ -diapolycopenedial + 4 acceptor + 6 H_2O
Other name(s): *crtP* (ambiguous)
Systematic name: 4,4'-diapolycopene,AH₂:oxygen oxidoreductase (4,4'-hydroxylating)
Comments: Little activity with neurosporene or lycopene. Involved in the biosynthesis of C₃₀ carotenoids such as staphyloxanthin. The enzyme oxidizes each methyl group to the hydroxymethyl and then a dihydroxymethyl group, followed by the spontaneous loss of water to give an aldehyde group.
References: [2536, 3821]

[EC 1.14.99.44 created 2011]

[1.14.99.45 Transferred entry. carotene ϵ -monooxygenase. Now EC 1.14.14.158, carotene ϵ -monooxygenase]

[EC 1.14.99.45 created 2011, deleted 2018]

EC 1.14.99.46

Accepted name: pyrimidine oxygenase
Reaction: (1) uracil + FMNH₂ + O₂ = (Z)-3-ureidoacrylate peracid + FMN
(2) thymine + FMNH₂ + O₂ = (Z)-2-methylureidoacrylate peracid + FMN
Other name(s): RutA
Systematic name: uracil,FMNH₂:oxygen oxidoreductase (uracil hydroxylating, ring-opening)
Comments: *In vitro* the product (Z)-3-ureidoacrylate peracid is spontaneously reduced to ureidoacrylate [2648, 1915]. Part of the Rut pyrimidine catabolic pathway.
References: [2648, 1915]

[EC 1.14.99.46 created 2012]

EC 1.14.99.47

Accepted name: (+)-larreatricin hydroxylase
Reaction: (+)-larreatricin + reduced acceptor + O₂ = (+)-3'-hydroxylarreatricin + acceptor + H₂O
Systematic name: (+)-larreatricin:oxygen 3'-hydroxylase
Comments: Isolated from the plant *Larrea tridentata* (creosote bush). The enzyme has a strong preference for the 3' position of (+)-larreatricin.
References: [603]

[EC 1.14.99.47 created 2012]

EC 1.14.99.48

Accepted name: heme oxygenase (staphylobilin-producing)
Reaction: (1) protoheme + 5 reduced acceptor + 4 O₂ = β-staphylobilin + Fe²⁺ + formaldehyde + 5 acceptor + 4 H₂O
(2) protoheme + 5 reduced acceptor + 4 O₂ = δ-staphylobilin + Fe²⁺ + formaldehyde + 5 acceptor + 4 H₂O
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 some 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 % δ-staphylobilin, respectively.
References: [3169, 2445, 3676]

[EC 1.14.99.48 created 2013]

[1.14.99.49 Transferred entry. 2-hydroxy-5-methyl-1-naphthoate 7-hydroxylase. Now EC 1.14.15.31, 2-hydroxy-5-methyl-1-naphthoate 7-hydroxylase]

[EC 1.14.99.49 created 2014, deleted 2018]

EC 1.14.99.50

Accepted name: γ-glutamyl mercynylcysteine S-oxide synthase
Reaction: mercynine + γ-L-glutamyl-L-cysteine + O₂ = γ-L-glutamyl-S-(mercyn-2-yl)-L-cysteine S-oxide + H₂O
Other name(s): EgtB
Systematic name: mercynine,γ-L-glutamyl-L-cysteine:oxygen oxidoreductase [γ-L-glutamyl-S-(mercyn-2-yl)-L-cysteine S-oxide-forming]
Comments: Requires Fe²⁺ for activity. The enzyme, found in bacteria, is specific for both mercynine and γ-L-glutamyl-L-cysteine. It is part of the biosynthesis pathway of ergothioneine.
References: [3421, 3023]

[EC 1.14.99.50 created 2015]

EC 1.14.99.51

Accepted name: mercynylcysteine S-oxide synthase
Reaction: mercynine + L-cysteine + O₂ = S-(mercyn-2-yl)-L-cysteine S-oxide + H₂O
Other name(s): Egt1; Egt-1
Systematic name: mercynine,L-cysteine:oxygen [S-(mercyn-2-yl)-L-cysteine S-oxide-forming]
Comments: Requires Fe²⁺ for activity. The enzyme, found in fungal species, is part of a fusion protein that also has the activity of EC 2.1.1.44, L-histidine N^α-methyltransferase. It is part of the biosynthesis pathway of ergothioneine. The enzyme can also use L-selenocysteine to produce mercynylselenocysteine, which can be converted to selenoneine.

References: [3023]

[EC 1.14.99.51 created 2015]

EC 1.14.99.52

Accepted name: L-cysteinyl-L-histidinylsulfoxide synthase
Reaction: L-histidine + L-cysteine + O₂ = S-(L-histidin-5-yl)-L-cysteine S-oxide + H₂O
Other name(s): OvoA
Systematic name: L-histidine,L-cysteine:oxygen [S-(L-histidin-5-yl)-L-cysteine S-oxide-forming]
Comments: Requires Fe²⁺ for activity. The enzyme participates in ovothiol biosynthesis. It also has some activity as EC 1.13.11.20, cysteine dioxygenase, and can perform the reaction of EC 1.14.99.50, γ-glutamyl mercynylcysteine sulfoxide synthase, albeit with low activity [3579].
References: [388, 3580, 2427, 3579]

[EC 1.14.99.52 created 2015]

EC 1.14.99.53

Accepted name: lytic chitin monooxygenase
Reaction: [(1→4)-N-acetyl-β-D-glucosaminyl](m+n) + reduced acceptor + O₂ = [(1→4)-N-acetyl-β-D-glucosaminyl](m-1)-(1→4)-2-(acetylamino)-2-deoxy-D-glucono-1,5-lactone + [(1→4)-N-acetyl-β-D-glucosaminyl]_n + acceptor + H₂O
Other name(s): LPMO (ambiguous); CBP21; chitin oxidohydrolase
Systematic name: chitin, hydrogen-donor:oxygen oxidoreductase (N-acetyl-β-D-glucosaminyl C1-hydroxylating/C4-dehydrogenating)
Comments: The enzyme cleaves chitin in an oxidative manner, releasing fragments of chitin with an N-acetylamino-D-glucono-1,5-lactone at the reducing end. The initially formed lactone at the reducing end of the shortened chitin chain quickly hydrolyses spontaneously to the aldonic acid. *In vitro* ascorbate can serve as reducing agent. The enzyme contains copper at the active site.
References: [3981, 3980, 1307, 4438]

[EC 1.14.99.53 created 2017]

EC 1.14.99.54

Accepted name: lytic cellulose monooxygenase (C1-hydroxylating)
Reaction: [(1→4)-β-D-glucosyl]_{n+m} + reduced acceptor + O₂ = [(1→4)-β-D-glucosyl]_{m-1}-(1→4)-D-glucono-1,5-lactone + [(1→4)-β-D-glucosyl]_n + acceptor + H₂O
Other name(s): lytic polysaccharide monooxygenase (ambiguous); LPMO (ambiguous); LPMO9A
Systematic name: cellulose, hydrogen-donor:oxygen oxidoreductase (D-glucosyl C1-hydroxylating)
Comments: This copper-containing enzyme, found in fungi and bacteria, cleaves cellulose in an oxidative manner. The cellulose fragments that are formed contain a D-glucono-1,5-lactone residue at the reducing end, which hydrolyses quickly and spontaneously to the aldonic acid. The electrons are provided *in vivo* by the cytochrome *b* domain of EC 1.1.99.18, cellobiose dehydrogenase (acceptor) [3000]. Ascorbate can serve as the electron donor *in vitro*.
References: [3000, 242, 2235, 288, 1081, 2954, 677]

[EC 1.14.99.54 created 2017]

EC 1.14.99.55

Accepted name: lytic starch monooxygenase
Reaction: starch + reduced acceptor + O₂ = D-glucono-1,5-lactone-terminated malto-oligosaccharides + short-chain malto-oligosaccharides + acceptor + H₂O
Other name(s): LPMO (ambiguous)
Systematic name: starch, hydrogen-donor:oxygen oxidoreductase (D-glucosyl C1-hydroxylating)

Comments: The enzyme cleaves starch in an oxidative manner. It releases fragments of starch with a D-glucono-1,5-lactone at the reducing end. The initially formed α -D-glucono-1,5-lactone at the reducing end of the shortend amylose chain quickly hydrolyses spontaneously to the aldonic acid. *In vitro* ascorbate has been found to be able to serve as reducing agent. The enzyme contains copper at the active site.

References: [4071, 1307, 2185]

[EC 1.14.99.55 created 2017]

EC 1.14.99.56

Accepted name: lytic cellulose monooxygenase (C4-dehydrogenating)

Reaction: [(1 \rightarrow 4)- β -D-glucosyl] $_{n+m}$ + reduced acceptor + O₂ = 4-dehydro- β -D-glucosyl-[(1 \rightarrow 4)- β -D-glucosyl] $_{n-1}$ + [(1 \rightarrow 4)- β -D-glucosyl] $_m$ + acceptor + H₂O

Systematic name: cellulose, hydrogen-donor:oxygen oxidoreductase (D-glucosyl 4-dehydrogenating)

Comments: This copper-containing enzyme, found in fungi and bacteria, cleaves cellulose in an oxidative manner. The cellulose fragments that are formed contain a 4-dehydro-D-glucose residue at the non-reducing end. Some enzymes also oxidize cellulose at the C-1 position of the reducing end forming a D-glucono-1,5-lactone residue [*cf.* EC 1.14.99.54, lytic cellulose monooxygenase (C1-hydroxylating)].

References: [242, 2235, 1038, 353, 2954]

[EC 1.14.99.56 created 2017]

EC 1.14.99.57

Accepted name: heme oxygenase (mycobilin-producing)

Reaction: (1) protoheme + 3 reduced acceptor + 3 O₂ = mycobilin a + Fe²⁺ + 3 acceptor + 3 H₂O

(2) protoheme + 3 reduced acceptor + 3 O₂ = mycobilin b + Fe²⁺ + 3 acceptor + 3 H₂O

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

Systematic name: protoheme,donor:oxygen oxidoreductase (mycobilin-producing)

Comments: The enzyme, characterized from the bacterium *Mycobacterium tuberculosis*, is involved in heme degradation and iron utilization. The enzyme binds two stacked protoheme molecules per monomer. Unlike the canonical heme oxygenases, the enzyme does not release carbon monoxide or formaldehyde. Instead, it forms unique products, named mycobilins, that retain the α -*meso*-carbon at the ring cleavage site as an aldehyde group. EC 1.6.2.4, NADPH-hemoprotein reductase, can act as electron donor *in vitro*.

References: [592, 2730, 1263]

[EC 1.14.99.57 created 2017]

EC 1.14.99.58

Accepted name: heme oxygenase (biliverdin-IX- β and δ -forming)

Reaction: (1) protoheme + 3 reduced acceptor + 3 O₂ = biliverdin-IX- δ + CO + Fe²⁺ + 3 acceptor + 3 H₂O

(2) protoheme + 3 reduced acceptor + 3 O₂ = biliverdin-IX- β + CO + Fe²⁺ + 3 acceptor + 3 H₂O

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

Systematic name: protoheme,donor:oxygen oxidoreductase (biliverdin-IX- β and δ -forming)

Comments: The enzyme, characterized from the bacterium *Pseudomonas aeruginosa*, differs from EC 1.14.15.20, heme oxygenase (biliverdin-producing, ferredoxin), in that the heme substrate is rotated by approximately 110 degrees within the active site, resulting in cleavage at a different part of the ring. It forms a mixture of about 70% biliverdin-IX- δ and 30% biliverdin-IX- β .

References: [3131, 476, 1069]

[EC 1.14.99.58 created 2017]

EC 1.14.99.59

Accepted name: tryptamine 4-monooxygenase

Reaction: tryptamine + reduced acceptor + O₂ = 4-hydroxytryptamine + acceptor + H₂O
Other name(s): PsiH
Systematic name: tryptamine,hydrogen-donor:oxygen oxidoreductase (4-hydroxylating)
Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the fungus *Psilocybe cubensis*. Involved in the biosynthesis of the psychoactive compound psilocybin.
References: [1067]

[EC 1.14.99.59 created 2017]

EC 1.14.99.60

Accepted name: 3-demethoxyubiquinol 3-hydroxylase
Reaction: 6-methoxy-3-methyl-2-(*all-trans*-polyprenyl)-1,4-benzoquinol + a reduced acceptor + O₂ = 3-demethylubiquinol + acceptor + H₂O
Other name(s): 6-methoxy-3-methyl-2-(*all-trans*-polyprenyl)-1,4-benzoquinol 5-hydroxylase; COQ7 (gene name); clk-1 (gene name); *ubiF* (gene name)
Systematic name: 6-methoxy-3-methyl-2-(*all-trans*-polyprenyl)-1,4-benzoquinol,acceptor:oxygen oxidoreductase (5-hydroxylating)
Comments: The enzyme catalyses the last hydroxylation reaction during the biosynthesis of ubiquinone.
References: [2392, 3985, 2107, 3639, 3922]

[EC 1.14.99.60 created 2018]

EC 1.14.99.61

Accepted name: cyclooctat-9-en-7-ol 5-monooxygenase
Reaction: cyclooctat-9-en-7-ol + reduced acceptor + O₂ = cyclooctat-9-ene-5,7-diol + acceptor + H₂O
Other name(s): CotB3
Systematic name: cyclooctat-9-en-7-ol,hydrogen-donor:oxygen oxidoreductase (5-hydroxylating)
Comments: Isolated from the bacterium *Streptomyces melanosporofaciens* M1614-43f2. Involved in the biosynthesis of cyclooctatin.
References: [1921, 1246]

[EC 1.14.99.61 created 2018]

EC 1.14.99.62

Accepted name: cyclooctatin synthase
Reaction: cyclooctat-9-ene-5,7-diol + reduced acceptor + O₂ = cyclooctatin + acceptor + H₂O
Other name(s): CotB4
Systematic name: cyclooctat-9-ene-5,7-diol,hydrogen-donor:oxygen oxidoreductase (18-hydroxylating)
Comments: Isolated from the bacterium *Streptomyces melanosporofaciens* M1614-43f2.
References: [1921, 1246]

[EC 1.14.99.62 created 2018]

EC 1.14.99.63

Accepted name: β-carotene 4-ketolase
Reaction: (1) β-carotene + 2 reduced acceptor + 2 O₂ = echinenone + 2 acceptor + 3 H₂O
(2) echinenone + 2 reduced acceptor + 2 O₂ = canthaxanthin + 2 acceptor + 3 H₂O
Other name(s): BKT (ambiguous); β-C-4 oxygenase; β-carotene ketolase; *crtS* (gene name); *crtW* (gene name)
Systematic name: β-carotene,donor:oxygen oxidoreductase (echinenone-forming)
Comments: The enzyme, studied from algae, plants, fungi, and bacteria, adds an oxo group at position 4 of a carotenoid β ring. It is involved in the biosynthesis of carotenoids such as astaxanthin and flexixanthin. The enzyme does not act on β rings that are hydroxylated at position 3, such as in zeaxanthin (*cf.* EC 1.14.99.64, zeaxanthin 4-ketolase). The enzyme from the yeast *Xanthophyllomyces dendrorhous* is bifunctional and also catalyses the activity of EC 1.14.15.24, β-carotene 3-hydroxylase.

References: [2300, 395, 3634, 2856, 3822, 1834]

[EC 1.14.99.63 created 2018]

EC 1.14.99.64

Accepted name: zeaxanthin 4-ketolase
Reaction: (1) zeaxanthin + 2 reduced acceptor + 2 O₂ = adonixanthin + 2 acceptor + 3 H₂O
(2) adonixanthin + 2 reduced acceptor + 2 O₂ = (3*S*,3'*S*)-astaxanthin + 2 acceptor + 3 H₂O
Other name(s): BKT (ambiguous); *crtW*148 (gene name)
Systematic name: zeaxanthin,donor:oxygen oxidoreductase (adonixanthin-forming)
Comments: The enzyme has a similar activity to that of EC 1.14.99.63, β-carotene 4-ketolase, but unlike that enzyme is able to also act on zeaxanthin.
References: [4469, 1595]

[EC 1.14.99.64 created 2018]

EC 1.15 Acting on superoxide as acceptor

This subclass contains enzymes that act on superoxide as acceptor in a single sub-subclass (EC 1.15.1).

EC 1.15.1 Acting on superoxide as acceptor (only sub-subclass identified to date)

EC 1.15.1.1

Accepted name: superoxide dismutase
Reaction: 2 superoxide + 2 H⁺ = O₂ + H₂O₂
Other name(s): superoxidase dismutase; copper-zinc superoxide dismutase; Cu-Zn superoxide dismutase; ferrisuperoxide dismutase; superoxide dismutase I; superoxide dismutase II; SOD; Cu,Zn-SOD; Mn-SOD; Fe-SOD; SODF; SODS; SOD-1; SOD-2; SOD-3; SOD-4; hemocuprein; erythrocuprein; cytocuprein; cuprein; hepatocuprein
Systematic name: superoxide:superoxide oxidoreductase
Comments: A metalloprotein; also known as erythrocuprein, hemocuprein or cytocuprein. Enzymes from most eukaryotes contain both copper and zinc; those from mitochondria and most prokaryotes contain manganese or iron.
References: [1868, 3335, 4014]

[EC 1.15.1.1 created 1972]

EC 1.15.1.2

Accepted name: superoxide reductase
Reaction: superoxide + reduced rubredoxin + 2 H⁺ = H₂O₂ + oxidized rubredoxin
Other name(s): neelaredoxin; desulfoferrodoxin
Systematic name: rubredoxin:superoxide oxidoreductase
Comments: The enzyme contains non-heme iron.
References: [1733, 4355, 2293, 6]

[EC 1.15.1.2 created 2001 as EC 1.18.96.1, transferred 2001 to EC 1.15.1.2]

EC 1.16 Oxidizing metal ions

This subclass contains enzymes that oxidize metal ions (donors) to a higher valency state. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.16.1), oxygen (EC 1.16.3) and flavin (EC 1.16.8).

EC 1.16.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.16.1.1

Accepted name: mercury(II) reductase
Reaction: $\text{Hg} + \text{NADP}^+ + \text{H}^+ = \text{Hg}^{2+} + \text{NADPH}$
Other name(s): mercuric reductase; mercurate(II) reductase; mercuric ion reductase; mercury reductase; reduced NADP:mercuric ion oxidoreductase; mer A
Systematic name: Hg:NADP⁺ oxidoreductase
Comments: A dithiol enzyme.
References: [1043, 1044]

[EC 1.16.1.1 created 1984]

EC 1.16.1.2

Accepted name: diferric-transferrin reductase
Reaction: $\text{transferrin}[\text{Fe}(\text{II})]_2 + \text{NAD}^+ + \text{H}^+ = \text{transferrin}[\text{Fe}(\text{III})]_2 + \text{NADH}$
Other name(s): diferric transferrin reductase; NADH diferric transferrin reductase; transferrin reductase
Systematic name: transferrin[Fe(II)]₂:NAD⁺ oxidoreductase
References: [2304]

[EC 1.16.1.2 created 1989]

EC 1.16.1.3

Accepted name: aquacobalamin reductase
Reaction: $2 \text{cob}(\text{II})\text{alamin} + \text{NAD}^+ + 2 \text{H}_2\text{O} = 2 \text{aquacob}(\text{III})\text{alamin} + \text{NADH} + \text{H}^+$
Other name(s): aquocobalamin reductase; vitamin B_{12a} reductase; NADH-linked aquacobalamin reductase; B_{12a} reductase; NADH₂:cob(III)alamin oxidoreductase
Systematic name: cob(II)alamin:NAD⁺ oxidoreductase
Comments: A flavoprotein.
References: [4088]

[EC 1.16.1.3 created 1972 as EC 1.6.99.8, transferred 2002 to EC 1.16.1.3]

EC 1.16.1.4

Accepted name: cob(II)alamin reductase
Reaction: $2 \text{cob}(\text{I})\text{alamin} + \text{NAD}^+ = 2 \text{cob}(\text{II})\text{alamin} + \text{NADH} + \text{H}^+$
Other name(s): vitamin B_{12r} reductase; B_{12r} reductase; NADH₂:cob(II)alamin oxidoreductase
Systematic name: cob(I)alamin:NAD⁺ oxidoreductase
Comments: A flavoprotein.
References: [4088]

[EC 1.16.1.4 created 1972 as EC 1.6.99.9, transferred 2002 to EC 1.16.1.4]

EC 1.16.1.5

Accepted name: aquacobalamin reductase (NADPH)
Reaction: $2 \text{cob}(\text{II})\text{alamin} + \text{NADP}^+ + 2 \text{H}_2\text{O} = 2 \text{aquacob}(\text{III})\text{alamin} + \text{NADPH} + \text{H}^+$

Other name(s): aquacobalamin (reduced nicotinamide adenine dinucleotide phosphate) reductase; NADPH-linked aquacobalamin reductase; NADPH₂:aquacob(III)alamin oxidoreductase
Systematic name: cob(II)alamin:NADP⁺ oxidoreductase
Comments: A flavoprotein. Acts on aquacob(III)alamin and hydroxycobalamin, but not on cyanocobalamin.
References: [4138, 4140]

[EC 1.16.1.5 created 1989 as EC 1.6.99.11, transferred 2002 to EC 1.16.1.5]

EC 1.16.1.6

Accepted name: cyanocobalamin reductase (cyanide-eliminating)
Reaction: 2 cob(II)alamin-[cyanocobalamin reductase] + 2 hydrogen cyanide + NADP⁺ = 2 cyanocob(III)alamin + 2 [cyanocobalamin reductase] + NADPH + H⁺
Other name(s): MMACHC (gene name); CblC; cyanocobalamin reductase; cyanocobalamin reductase (NADPH, cyanide-eliminating); cyanocobalamin reductase (NADPH, CN-eliminating); NADPH:cyanocob(III)alamin oxidoreductase (cyanide-eliminating); cob(I)alamin, cyanide:NADP⁺ oxidoreductase
Systematic name: cob(II)alamin, hydrogen cyanide:NADP⁺ oxidoreductase
Comments: The mammalian enzyme, which is cytosolic, can bind internalized cyanocobalamin and process it to cob(II)alamin by removing the upper axial ligand. The product remains bound to the protein, which, together with its interacting partner MMADHC, transfers it directly to downstream enzymes involved in adenosylcobalamin and methylcobalamin biosynthesis. In addition to its decyanase function, the mammalian enzyme also catalyses an entirely different chemical reaction with alkylcobalamins, using the thiolate of glutathione for nucleophilic displacement, generating cob(I)alamin and the corresponding glutathione thioether (*cf.* EC 2.5.1.151, alkylcobalamin dealkylase).
References: [4139, 1909, 2045, 2365]

[EC 1.16.1.6 created 1989 as EC 1.6.99.12, transferred 2002 to EC 1.16.1.6, modified 2018]

EC 1.16.1.7

Accepted name: ferric-chelate reductase (NADH)
Reaction: 2 Fe(II)-siderophore + NAD⁺ + H⁺ = 2 Fe(III)-siderophore + NADH
Other name(s): ferric chelate reductase (ambiguous); iron chelate reductase (ambiguous); NADH:Fe³⁺-EDTA reductase; NADH₂:Fe³⁺ oxidoreductase; *ferB* (gene name); Fe(II):NAD⁺ oxidoreductase
Systematic name: Fe(II)-siderophore:NAD⁺ oxidoreductase
Comments: Contains FAD. The enzyme catalyses the reduction of bound ferric iron in a variety of iron chelators (siderophores), resulting in the release of ferrous iron. The plant enzyme is involved in the transport of iron across plant plasma membranes. The enzyme from the bacterium *Paracoccus denitrificans* can also reduce chromate. *cf.* EC 1.16.1.9, ferric-chelate reductase (NADPH) and EC 1.16.1.10, ferric-chelate reductase [NAD(P)H].
References: [132, 423, 424, 440, 3305, 2475]

[EC 1.16.1.7 created 1992 as EC 1.6.99.13, transferred 2002 to EC 1.16.1.7, modified 2011, modified 2014]

EC 1.16.1.8

Accepted name: [methionine synthase] reductase
Reaction: 2 [methionine synthase]-methylcob(I)alamin + 2 *S*-adenosylhomocysteine + NADP⁺ = 2 [methionine synthase]-cob(II)alamin + NADPH + H⁺ + 2 *S*-adenosyl-L-methionine
Other name(s): methionine synthase cob(II)alamin reductase (methylating); methionine synthase reductase; [methionine synthase]-cobalamin methyltransferase (cob(II)alamin reducing)
Systematic name: [methionine synthase]-methylcob(I)alamin,*S*-adenosylhomocysteine:NADP⁺ oxidoreductase
Comments: In humans, the enzyme is a flavoprotein containing FAD and FMN. The substrate of the enzyme is the inactivated [Co(II)] form of EC 2.1.1.13, methionine synthase. Electrons are transferred from NADPH to FAD to FMN. Defects in this enzyme lead to hereditary hyperhomocysteinemia.
References: [2161, 2881, 2882]

[EC 1.16.1.8 created 1999 as EC 2.1.1.135, transferred 2003 to EC 1.16.1.8]

EC 1.16.1.9

- Accepted name:** ferric-chelate reductase (NADPH)
Reaction: $2 \text{ Fe(II)-siderophore} + \text{NADP}^+ + \text{H}^+ = 2 \text{ Fe(III)-siderophore} + \text{NADPH}$
Other name(s): ferric chelate reductase (ambiguous); iron chelate reductase (ambiguous); NADPH:Fe³⁺-EDTA reductase; NADPH-dependent ferric reductase; *yqjH* (gene name); Fe(II):NADP⁺ oxidoreductase
Systematic name: Fe(II)-siderophore:NADP⁺ oxidoreductase
Comments: Contains FAD. The enzyme, which is widespread among bacteria, catalyses the reduction of ferric iron bound to a variety of iron chelators (siderophores), including ferric triscatecholates and ferric dicitrate, resulting in the release of ferrous iron. The enzyme from the bacterium *Escherichia coli* has the highest efficiency with the hydrolysed ferric enterobactin complex ferric *N*-(2,3-dihydroxybenzoyl)-L-serine [2530]. *cf.* EC 1.16.1.7, ferric-chelate reductase (NADH) and EC 1.16.1.10, ferric-chelate reductase [NAD(P)H].
References: [185, 4121, 2530]

[EC 1.16.1.9 created 1992 as EC 1.6.99.13, transferred 2002 to EC 1.16.1.7, transferred 2011 to EC 1.16.1.9, modified 2012, modified 2014]

EC 1.16.1.10

- Accepted name:** ferric-chelate reductase [NAD(P)H]
Reaction: $2 \text{ Fe(II)-siderophore} + \text{NAD(P)}^+ + \text{H}^+ = 2 \text{ Fe(III)-siderophore} + \text{NAD(P)H}$
Other name(s): ferric reductase (ambiguous)
Systematic name: Fe(II)-siderophore:NAD(P)⁺ oxidoreductase
Comments: A flavoprotein. The enzyme catalyses the reduction of bound ferric iron in a variety of iron chelators (siderophores), resulting in the release of ferrous iron. The enzyme from the hyperthermophilic archaeon *Archaeoglobus fulgidus* is not active with uncomplexed Fe(III). *cf.* EC 1.16.1.7, ferric-chelate reductase (NADH) and EC 1.16.1.9, ferric-chelate reductase (NADPH).
References: [3983, 599]

[EC 1.16.1.10 created 2014]

EC 1.16.3 With oxygen as acceptor

EC 1.16.3.1

- Accepted name:** ferroxidase
Reaction: $4 \text{ Fe(II)} + 4 \text{ H}^+ + \text{O}_2 = 4 \text{ Fe(III)} + 2 \text{ H}_2\text{O}$
Other name(s): ceruloplasmin; caeruloplasmin; ferroxidase I; iron oxidase; iron(II):oxygen oxidoreductase; ferro:O₂ oxidoreductase; iron II:oxygen oxidoreductase; hephaestin; HEPH
Systematic name: Fe(II):oxygen oxidoreductase
Comments: The enzyme in blood plasma (ceruloplasmin) belongs to the family of multicopper oxidases. In humans it accounts for 95% of plasma copper. It oxidizes Fe(II) to Fe(III), which allows the subsequent incorporation of the latter into proteins such as apotransferrin and lactoferrin. An enzyme from iron oxidizing bacterium strain TI-1 contains heme *a*.
References: [2897, 2898, 2263, 3784, 568]

[EC 1.16.3.1 created 1972, modified 2011]

EC 1.16.3.2

- Accepted name:** bacterial non-heme ferritin
Reaction: $4 \text{ Fe(II)} + \text{O}_2 + 6 \text{ H}_2\text{O} = 4 [\text{FeO(OH)}] + 8 \text{ H}^+$ (overall reaction)
(1a) $2 \text{ Fe(II)} + \text{O}_2 + 4 \text{ H}_2\text{O} = 2 [\text{FeO(OH)}] + 4 \text{ H}^+ + \text{H}_2\text{O}_2$
(1b) $2 \text{ Fe(II)} + \text{H}_2\text{O}_2 + 2 \text{ H}_2\text{O} = 2 [\text{FeO(OH)}] + 4 \text{ H}^+$

Other name(s): FtnA; HuHF
Systematic name: Fe(II):oxygen oxidoreductase ([FeO(OH)]core-producing)
Comments: Ferritins are intracellular iron-storage and detoxification proteins found in all kingdoms of life. They are formed from two subunits that co-assemble in various ratios to form a spherical protein shell. Thousands of mineralized iron atoms are stored within the core of the structure. The product of dioxygen reduction by the bacterial non-heme ferritin is hydrogen peroxide, which is consumed in a subsequent reaction.
References: [1602, 3650, 366]

[EC 1.16.3.2 created 2014]

EC 1.16.3.3

Accepted name: manganese oxidase
Reaction: $4 \text{Mn}^{2+} + 2 \text{O}_2 + 4 \text{H}_2\text{O} = 4 \text{Mn}^{\text{IV}}\text{O}_2 + 8 \text{H}^+$ (overall reaction)
(1a) $4 \text{Mn}^{2+} + \text{O}_2 + 4 \text{H}^+ = 4 \text{Mn}^{3+} + 2 \text{H}_2\text{O}$
(1b) $4 \text{Mn}^{3+} + \text{O}_2 + 6 \text{H}_2\text{O} = 4 \text{Mn}^{\text{IV}}\text{O}_2 + 12 \text{H}^+$
Other name(s): *mnxG* (gene name); *mofA* (gene name); *moxA* (gene name); *cotA* (gene name)
Systematic name: manganese(II):oxygen oxidoreductase
Comments: The enzyme, which belongs to the multicopper oxidase family, is found in many bacterial strains. It oxidizes soluble manganese(II) to insoluble manganese(IV) oxides. Since the enzyme is localized to the outer surface of the cell, its activity usually results in encrustation of the cells by the oxides. The physiological function of bacterial manganese(II) oxidation remains unclear.
References: [666, 1051, 3185, 1190, 3700]

[EC 1.16.3.3 created 2017]

EC 1.16.5 With a quinone or similar compound as acceptor

[1.16.5.1 *Transferred entry. ascorbate ferrireductase (transmembrane). Now EC 7.2.1.3, ascorbate ferrireductase (transmembrane)*]

[EC 1.16.5.1 created 2011, deleted 2018]

EC 1.16.8 With a flavin as acceptor

EC 1.16.8.1

Accepted name: cob(II)yrinic acid *a,c*-diamide reductase
Reaction: $2 \text{cob(I)yrinic acid } a,c\text{-diamide} + \text{FMN} + 2 \text{H}^+ = 2 \text{cob(II)yrinic acid } a,c\text{-diamide} + \text{FMNH}_2$
Other name(s): cob(II)yrinic acid-*a,c*-diamide:FMN oxidoreductase (incorrect)
Systematic name: cob(I)yrinic acid-*a,c*-diamide:FMN oxidoreductase
Comments: This enzyme also catalyses the reduction of cob(II)yrinic acid, cob(II)inamide, cob(II)inamide phosphate, GDP-cob(II)inamide and cob(II)alamin although cob(II)yrinic acid *a,c*-diamide is thought to be the physiological substrate [317]. Also uses FAD and NADH but not NADPH.
References: [317, 4137]

[EC 1.16.8.1 created 2004]

EC 1.16.9 With a copper protein as acceptor

EC 1.16.9.1

Accepted name: iron:rusticyanin reductase

Reaction: Fe(II) + rusticyanin = Fe(III) + reduced rusticyanin
Other name(s): Cyc2
Systematic name: Fe(II):rusticyanin oxidoreductase
Comments: Contains *c*-type heme. The enzyme in *Acidithiobacillus ferrooxidans* is a component of an electron transfer chain from Fe(II), comprising this enzyme, the copper protein rusticyanin, cytochrome *c*₄, and cytochrome *c* oxidase (EC 1.9.3.1).
References: [312, 106, 4349, 4348, 3776, 519, 3089]

[EC 1.16.9.1 created 2011 as EC 1.16.98.1, transferred 2011 to EC 1.16.9.1]

EC 1.16.98 With other, known, physiological acceptors

[1.16.98.1 *Transferred entry. Now EC 1.16.9.1 iron:rusticyanin reductase*]

[EC 1.16.98.1 created 2011, deleted 2011]

EC 1.17 Acting on CH or CH₂ groups

This subclass contains enzymes that oxidize the -CH₂- group of donors to -CHOH- (or -CH- to -COH-) and the oxidative cleavage of HC- bonds (as in formate); in the reverse direction, those acting on sugars are involved in the formation of deoxysugars. Sub-classes are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.17.1), oxygen (EC 1.17.3), a cytochrome (EC 1.17.2), a disulfide (EC 1.17.4), a quinone or similar compound (EC 1.17.5), another, known, physiological acceptors (EC 1.17.98) or an unknown, physiological acceptor (EC 1.17.99).

EC 1.17.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.17.1.1

Accepted name: CDP-4-dehydro-6-deoxyglucose reductase
Reaction: CDP-4-dehydro-3,6-dideoxy-D-glucose + NAD(P)⁺ + H₂O = CDP-4-dehydro-6-deoxy-D-glucose + NAD(P)H + H⁺
Other name(s): CDP-4-keto-6-deoxyglucose reductase; cytidine diphospho-4-keto-6-deoxy-D-glucose reductase; cytidine diphosphate 4-keto-6-deoxy-D-glucose-3-dehydrogenase; CDP-4-keto-deoxy-glucose reductase; CDP-4-keto-6-deoxy-D-glucose-3-dehydrogenase system; NAD(P)H:CDP-4-keto-6-deoxy-D-glucose oxidoreductase
Systematic name: CDP-4-dehydro-3,6-dideoxy-D-glucose:NAD(P)⁺ 3-oxidoreductase
Comments: The enzyme consists of two proteins. One forms an enzyme-bound adduct of the CDP-4-dehydro-6-deoxyglucose with pyridoxamine phosphate, in which the 3-hydroxy group has been removed. The second catalyses the reduction of this adduct by NAD(P)H and release of the CDP-4-dehydro-3,6-dideoxy-D-glucose and pyridoxamine phosphate.
References: [2935, 3248, 2279]

[EC 1.17.1.1 created 1972, modified 2005]

[1.17.1.2 *Transferred entry. 4-hydroxy-3-methylbut-2-enyl diphosphate reductase, now classified as EC 1.17.7.4, 4-hydroxy-3-methylbut-2-enyl diphosphate reductase.*]

[EC 1.17.1.2 created 2003, modified 2009, deleted 2016]

EC 1.17.1.3

Accepted name: leucoanthocyanidin reductase
Reaction: (2*R*,3*S*)-catechin + NADP⁺ + H₂O = 2,3-*trans*-3,4-*cis*-leucocyanidin + NADPH + H⁺
Other name(s): leucocyanidin reductase
Systematic name: (2*R*,3*S*)-catechin:NADP⁺ 4-oxidoreductase

Comments: The enzyme catalyses the synthesis of catechin, catechin-4 β -ol (leucocyanidin) and the related flavan-3-ols afzelechin and gallo catechin, which are initiating monomers in the synthesis of plant polymeric proanthocyanidins or condensed tannins. While 2,3-*trans*-3,4-*cis*-leucocyanidin is the preferred flavan-3,4-diol substrate, 2,3-*trans*-3,4-*cis*-leucodelphinidin and 2,3-*trans*-3,4-*cis*-leucopelargonidin can also act as substrates, but more slowly. NADH can replace NADPH but is oxidized more slowly.

References: [3818, 3817]

[EC 1.17.1.3 created 2003]

EC 1.17.1.4

Accepted name: xanthine dehydrogenase

Reaction: xanthine + NAD⁺ + H₂O = urate + NADH + H⁺

Other name(s): NAD⁺-xanthine dehydrogenase; xanthine-NAD⁺ oxidoreductase; xanthine/NAD⁺ oxidoreductase; xanthine oxidoreductase

Systematic name: xanthine:NAD⁺ oxidoreductase

Comments: Acts on a variety of purines and aldehydes, including hypoxanthine. The mammalian enzyme can also convert *all-trans* retinol to *all-trans*-retinoate, while the substrate is bound to a retinoid-binding protein [3778]. The enzyme from eukaryotes contains [2Fe-2S], FAD and a molybdenum centre. The mammalian enzyme predominantly exists as the NAD-dependent dehydrogenase (EC 1.17.1.4). During purification the enzyme is largely converted to an O₂-dependent form, xanthine oxidase (EC 1.17.3.2). The conversion can be triggered by several mechanisms, including the oxidation of cysteine thiols to form disulfide bonds [2,6,8,15] [which can be catalysed by EC 1.8.4.7, enzyme-thiol transhydrogenase (glutathione-disulfide) in the presence of glutathione disulfide] or limited proteolysis, which results in irreversible conversion. The conversion can also occur *in vivo* [2,7,15].

References: [213, 667, 2950, 3111, 3565, 1636, 950, 3286, 2947, 1625, 956, 3933, 1502, 3778, 2798]

[EC 1.17.1.4 created 1972 as EC 1.2.1.37, transferred 1984 to EC 1.1.1.204, modified 1989, transferred 2004 to EC 1.17.1.4, modified 2011]

EC 1.17.1.5

Accepted name: nicotinate dehydrogenase

Reaction: nicotinate + H₂O + NADP⁺ = 6-hydroxynicotinate + NADPH + H⁺

Other name(s): nicotinic acid hydroxylase; nicotinate hydroxylase

Systematic name: nicotinate:NADP⁺ 6-oxidoreductase (hydroxylating)

Comments: A flavoprotein containing non-heme iron. The enzyme is capable of acting on a variety of nicotinate analogues to varying degrees, including pyrazine-2-carboxylate, pyrazine 2,3-dicarboxylate, trigonelline and 6-methylnicotinate. The enzyme from *Clostridium barkeri* also possesses a catalytically essential, labile selenium that can be removed by reaction with cyanide.

References: [1537, 1214, 1213, 828, 827, 2690]

[EC 1.17.1.5 created 1972 as EC 1.5.1.13, transferred 2004 to EC 1.17.1.5]

[1.17.1.6 Transferred entry. bile-acid 7 α -dehydroxylase. Now EC 1.17.99.5, bile-acid 7 α -dehydroxylase. It is now known that FAD is the acceptor and not NAD⁺ as was thought previously]

[EC 1.17.1.6 created 2005, deleted 2006]

[1.17.1.7 Transferred entry. 3-oxo-5,6-dehydrosuberyl-CoA semialdehyde dehydrogenase. Now EC 1.2.1.91, 3-oxo-5,6-dehydrosuberyl-CoA semialdehyde dehydrogenase]

[EC 1.17.1.7 created 2011, deleted 2014]

EC 1.17.1.8

Accepted name: 4-hydroxy-tetrahydrodipicolinate reductase

Reaction: (S)-2,3,4,5-tetrahydropyridine-2,6-dicarboxylate + NAD(P)⁺ + H₂O = (2S,4S)-4-hydroxy-2,3,4,5-tetrahydrodipicolinate + NAD(P)H + H⁺

Other name(s): dihydrodipicolinate reductase (incorrect); dihydrodipicolinic acid reductase (incorrect); 2,3,4,5-tetrahydrodipicolinate:NAD(P)⁺ oxidoreductase (incorrect); *dapB* (gene name)
Systematic name: (S)-2,3,4,5-tetrahydropyridine-2,6-dicarboxylate:NAD(P)⁺ 4-oxidoreductase
Comments: Studies [803] of the enzyme from the bacterium *Escherichia coli* have shown that the enzyme accepts (2S,4S)-4-hydroxy-2,3,4,5-tetrahydrodipicolinate and not (S)-2,3-dihydrodipicolinate as originally thought [987].
References: [987, 803]

[EC 1.17.1.8 created 1976 as EC 1.3.1.26, transferred 2013 to EC 1.17.1.8]

EC 1.17.1.9

Accepted name: formate dehydrogenase
Reaction: formate + NAD⁺ = CO₂ + NADH
Other name(s): formate-NAD⁺ oxidoreductase; FDH I; FDH II; N-FDH; formic hydrogen-lyase; formate hydrogenlyase; hydrogenlyase; NAD⁺-linked formate dehydrogenase; NAD⁺-dependent formate dehydrogenase; formate dehydrogenase (NAD⁺); NAD⁺-formate dehydrogenase; formate benzyl-viologen oxidoreductase; formic acid dehydrogenase
Systematic name: formate:NAD⁺ oxidoreductase
Comments: The enzyme from most aerobic organisms is devoid of redox-active centres but that from the proteobacterium *Methylosinus trichosporium* contains iron-sulfur centres, flavin and a molybdenum centre [1767]. Together with EC 1.12.1.2 hydrogen dehydrogenase, forms a system previously known as formate hydrogenlyase.
References: [756, 3090, 1767]

[EC 1.17.1.9 created 1961 as EC 1.2.1.2, transferred 2017 to EC 1.17.1.9]

EC 1.17.1.10

Accepted name: formate dehydrogenase (NADP⁺)
Reaction: formate + NADP⁺ = CO₂ + NADPH
Other name(s): NADP⁺-dependent formate dehydrogenase
Systematic name: formate:NADP⁺ oxidoreductase
Comments: A tungsten-selenium-iron protein characterized from the bacterium *Moorella thermoacetica*. It is extremely sensitive to oxygen.
References: [87, 4316]

[EC 1.17.1.10 created 1978 as EC 1.2.1.43, transferred 2017 to EC 1.17.1.10]

EC 1.17.1.11

Accepted name: formate dehydrogenase (NAD⁺, ferredoxin)
Reaction: 2 formate + NAD⁺ + 2 oxidized ferredoxin [iron-sulfur] cluster = 2 CO₂ + NADH + H⁺ + 2 reduced ferredoxin [iron-sulfur] cluster
Other name(s): electron-bifurcating formate dehydrogenase
Systematic name: formate:NAD⁺, ferredoxin oxidoreductase
Comments: The enzyme complex, isolated from the bacterium *Gottschalkia acidurici*, couples the reduction of NAD⁺ and the reduction of ferredoxin with formate via flavin-based electron bifurcation.
References: [4118]

[EC 1.17.1.11 created 2015 as EC 1.2.1.93, transferred 2017 to EC 1.17.1.11]

EC 1.17.2 With a cytochrome as acceptor

EC 1.17.2.1

- Accepted name:** nicotinate dehydrogenase (cytochrome)
Reaction: nicotinate + a ferricytochrome + H₂O = 6-hydroxynicotinate + a ferrocyclochrome + 2 H⁺
Other name(s): nicotinic acid hydroxylase; nicotinate hydroxylase
Systematic name: nicotinate:cytochrome 6-oxidoreductase (hydroxylating)
Comments: This two-component enzyme from *Pseudomonas* belongs to the family of xanthine dehydrogenases, but differs from most other members of this family. While most members contain an FAD cofactor, the large subunit of this enzyme contains three *c*-type cytochromes, enabling it to interact with the electron transfer chain, probably by delivering the electrons to a cytochrome oxidase. The small subunit contains a typical molybdopterin cytosine dinucleotide(MCD) cofactor and two [2Fe-2S] clusters [1743].
References: [1743, 4340]

[EC 1.17.2.1 created 2010]

EC 1.17.2.2

- Accepted name:** lupanine 17-hydroxylase (cytochrome *c*)
Reaction: lupanine + 2 ferricytochrome *c* + H₂O = 17-hydroxylupanine + 2 ferrocyclochrome *c* + 2 H⁺
Other name(s): lupanine dehydrogenase (cytochrome *c*)
Systematic name: lupanine:cytochrome *c*-oxidoreductase (17-hydroxylating)
Comments: The enzyme isolated from *Pseudomonas putida* contains heme *c* and requires pyrroloquinoline quinone (PQQ) for activity
References: [1564, 1563]

[EC 1.17.2.2 created 2012]

EC 1.17.2.3

- Accepted name:** formate dehydrogenase (cytochrome-*c*-553)
Reaction: formate + 2 ferricytochrome *c*-553 = CO₂ + 2 ferrocyclochrome *c*-553 + H⁺
Systematic name: formate:ferricytochrome-*c*-553 oxidoreductase
Comments: The enzyme has been characterized from the bacterium *Desulfovibrio vulgaris*. *In vitro*, yeast cytochrome *c*, ferricyanide and phenazine methosulfate can act as acceptors.
References: [4297, 4298]

[EC 1.17.2.3 created 1981 as EC 1.2.2.3, transferred 2017 to EC 1.17.2.3]

EC 1.17.3 With oxygen as acceptor

EC 1.17.3.1

- Accepted name:** pteridine oxidase
Reaction: 2-amino-4-hydroxypteridine + O₂ = 2-amino-4,7-dihydroxypteridine + (?)
Systematic name: 2-amino-4-hydroxypteridine:oxygen oxidoreductase (7-hydroxylating)
Comments: Different from EC 1.17.3.2 xanthine oxidase; does not act on hypoxanthine.
References: [4370]

[EC 1.17.3.1 created 1983]

EC 1.17.3.2

- Accepted name:** xanthine oxidase
Reaction: xanthine + H₂O + O₂ = urate + H₂O₂
Other name(s): hypoxanthine oxidase; hypoxanthine:oxygen oxidoreductase; Schardinger enzyme; xanthine oxidoreductase; hypoxanthine-xanthine oxidase; xanthine:O₂ oxidoreductase; xanthine:xanthine oxidase

Systematic name: xanthine:oxygen oxidoreductase

Comments: An iron-molybdenum flavoprotein (FAD) containing [2Fe-2S] centres. Also oxidizes hypoxanthine, some other purines and pterins, and aldehydes, but is distinct from EC 1.2.3.1, aldehyde oxidase. Under some conditions the product is mainly superoxide rather than peroxide: $\text{RH} + \text{H}_2\text{O} + 2 \text{O}_2 = \text{ROH} + 2 \text{O}_2^{\cdot -} + 2 \text{H}^+$. The mammalian enzyme predominantly exists as an NAD-dependent dehydrogenase (EC 1.17.1.4, xanthine dehydrogenase). During purification the enzyme is largely converted to the O_2 -dependent xanthine oxidase form (EC 1.17.3.2). The conversion can be triggered by several mechanisms, including the oxidation of cysteine thiols to form disulfide bonds [4,5,7,10] [which can be catalysed by EC 1.8.4.7, enzyme-thiol transhydrogenase (glutathione-disulfide) in the presence of glutathione disulfide] or limited proteolysis, which results in irreversible conversion. The conversion can also occur *in vivo* [4,6,10].

References: [146, 213, 389, 667, 1636, 950, 3286, 510, 924, 2798]

[EC 1.17.3.2 created 1961 as EC 1.2.3.2, transferred 1984 to EC 1.1.3.22, modified 1989, transferred 2004 to EC 1.17.3.2, modified 2011]

EC 1.17.3.3

Accepted name: 6-hydroxynicotinate dehydrogenase

Reaction: $6\text{-hydroxynicotinate} + \text{H}_2\text{O} + \text{O}_2 = 2,6\text{-dihydroxynicotinate} + \text{H}_2\text{O}_2$

Other name(s): 6-hydroxynicotinic acid hydroxylase; 6-hydroxynicotinic acid dehydrogenase; 6-hydroxynicotinate hydroxylase; 6-hydroxynicotinate: O_2 oxidoreductase

Systematic name: 6-hydroxynicotinate:oxygen oxidoreductase

Comments: Contains [2Fe-2S] iron-sulfur centres, FAD and molybdenum. It also has a catalytically essential, labile selenium that can be removed by reaction with cyanide. In *Bacillus niacini*, this enzyme is required for growth on nicotinic acid.

References: [2689, 2690]

[EC 1.17.3.3 created 2004]

EC 1.17.3.4

Accepted name: juglone 3-hydroxylase

Reaction: $2 \text{ juglone} + \text{O}_2 = 2 \text{ 3,5-dihydroxy-1,4-naphthoquinone}$ (overall reaction)

(1a) $2 \text{ juglone} + 2 \text{ H}_2\text{O} = 2 \text{ naphthalene-1,2,4,8-tetrol}$

(1b) $2 \text{ naphthalene-1,2,4,8-tetrol} + \text{O}_2 = 2 \text{ 3,5-dihydroxy-1,4-naphthoquinone} + 2 \text{ H}_2\text{O}$

Other name(s): juglone hydroxylase; naphthoquinone hydroxylase; naphthoquinone-hydroxylase

Systematic name: 5-hydroxy-1,4-naphthoquinone,water:oxygen oxidoreductase (3-hydroxylating)

Comments: Even though oxygen is consumed, molecular oxygen is not incorporated into the product. Catalysis starts by incorporation of an oxygen atom from a water molecule into the substrate. The naphthalene-1,2,4,8-tetrol intermediate is then oxidized by molecular oxygen, which is reduced to water. Also acts on 1,4-naphthoquinone, naphthazarin and 2-chloro-1,4-naphthoquinone.

References: [3173]

[EC 1.17.3.4 created 1989 as EC 1.14.99.27, transferred 2016 to EC 1.17.3.4]

EC 1.17.4 With a disulfide as acceptor

EC 1.17.4.1

Accepted name: ribonucleoside-diphosphate reductase

Reaction: $2'\text{-deoxyribonucleoside } 5'\text{-diphosphate} + \text{thioredoxin disulfide} + \text{H}_2\text{O} = \text{ribonucleoside } 5'\text{-diphosphate} + \text{thioredoxin}$

Other name(s): ribonucleotide reductase (ambiguous); CDP reductase; ribonucleoside diphosphate reductase; UDP reductase; ADP reductase; nucleoside diphosphate reductase; ribonucleoside 5'-diphosphate reductase; ribonucleotide diphosphate reductase; 2'-deoxyribonucleoside-diphosphate:oxidized-thioredoxin 2'-oxidoreductase; RR; *nrdB* (gene name); *nrdF* (gene name); *nrdJ* (gene name)

Systematic name: 2'-deoxyribonucleoside-5'-diphosphate:thioredoxin-disulfide 2'-oxidoreductase
Comments: This enzyme is responsible for the *de novo* conversion of ribonucleoside diphosphates into deoxyribonucleoside diphosphates, which are essential for DNA synthesis and repair. There are three types of this enzyme differing in their cofactors. Class Ia enzymes contain a diiron(III)-tyrosyl radical, class Ib enzymes contain a dimanganese-tyrosyl radical, and class II enzymes contain adenosylcobalamin. In all cases the cofactors are involved in generation of a transient thiyl (sulfanyl) radical on a cysteine residue, which attacks the substrate, forming a ribonucleotide 3'-radical, followed by water loss to form a ketyl (α -oxoalkyl) radical. The ketyl radical is reduced to 3'-keto-deoxynucleotide concomitant with formation of a disulfide anion radical between two cysteine residues. A proton-coupled electron-transfer from the disulfide radical to the substrate generates a 3'-deoxynucleotide radical, and the final product is formed when the hydrogen atom that was initially removed from the 3'-position of the nucleotide by the thiyl radical is returned to the same position. The disulfide bridge is reduced by the action of thioredoxin. *cf.* EC 1.1.98.6, ribonucleoside-triphosphate reductase (formate) and EC 1.17.4.2, ribonucleoside-triphosphate reductase (thioredoxin).
References: [2143, 2144, 2605, 2142, 2122, 3693, 2196, 2154, 3082]

[EC 1.17.4.1 created 1972, modified 2017]

EC 1.17.4.2

Accepted name: ribonucleoside-triphosphate reductase (thioredoxin)
Reaction: 2'-deoxyribonucleoside 5'-triphosphate + thioredoxin disulfide + H₂O = ribonucleoside 5'-triphosphate + thioredoxin
Other name(s): ribonucleotide reductase (ambiguous); 2'-deoxyribonucleoside-triphosphate:oxidized-thioredoxin 2'-oxidoreductase
Systematic name: 2'-deoxyribonucleoside-5'-triphosphate:thioredoxin-disulfide 2'-oxidoreductase
Comments: The enzyme, characterized from the bacterium *Lactobacillus leichmannii*, is similar to class II ribonucleoside-diphosphate reductase (*cf.* EC 1.17.4.1). However, it is specific for the triphosphate versions of its substrates. The enzyme contains an adenosylcobalamin cofactor that is involved in generation of a transient thiyl (sulfanyl) radical on a cysteine residue. This radical attacks the substrate, forming a ribonucleotide 3'-radical, followed by water loss to form a ketyl (α -oxoalkyl) radical. The ketyl radical is reduced to 3'-keto-deoxynucleotide concomitant with formation of a disulfide anion radical between two cysteine residues. A proton-coupled electron-transfer from the disulfide radical to the substrate generates a 3'-deoxynucleotide radical, and the final product is formed when the hydrogen atom that was initially removed from the 3'-position of the nucleotide by the thiyl radical is returned to the same position. The disulfide bridge is reduced by the action of thioredoxin. *cf.* EC 1.1.98.6, ribonucleoside-triphosphate reductase (formate).
References: [314, 1253, 3692, 130, 2156, 2245]

[EC 1.17.4.2 created 1972, modified 2017]

[1.17.4.3 *Transferred entry. 4-hydroxy-3-methylbut-2-en-1-yl diphosphate synthase. As ferredoxin and not protein-disulfide is now known to take part in the reaction, the enzyme has been transferred to EC 1.17.7.1, (E)-4-hydroxy-3-methylbut-2-enyl-diphosphate synthase.*]

[EC 1.17.4.3 created 2003, deleted 2009]

EC 1.17.4.4

Accepted name: vitamin-K-epoxide reductase (warfarin-sensitive)
Reaction: (1) phylloquinone + a protein with a disulfide bond + H₂O = 2,3-epoxyphylloquinone + a protein with reduced L-cysteine residues
(2) phylloquinol + a protein with a disulfide bond = phylloquinone + a protein with reduced L-cysteine residues
Other name(s): VKORC1 (gene name); VKORC1L1 (gene name)
Systematic name: phylloquinone:disulfide oxidoreductase

Comments: The enzyme catalyses the reduction of vitamin K 2,3-epoxide, which is formed by the activity of EC 4.1.1.90, peptidyl-glutamate 4-carboxylase, back to its phyloquinol active form. The enzyme forms a tight complex with EC 5.3.4.1, protein disulfide-isomerase, which transfers the required electrons from newly-synthesized proteins by catalysing the formation of disulfide bridges. The enzyme acts on the epoxide forms of both phyloquinone (vitamin K₁) and menaquinone (vitamin K₂). Inhibited strongly by (*S*)-warfarin and ferulenol.

References: [4196, 2171, 2647, 2233, 4081, 3606, 3398]

[EC 1.17.4.4 created 1989 as EC 1.1.4.1, transferred 2014 to EC 1.17.4.4, modified 2018]

EC 1.17.4.5

Accepted name: vitamin-K-epoxide reductase (warfarin-insensitive)

Reaction: 3-hydroxy-2-methyl-3-phytyl-2,3-dihydro-1,4-naphthoquinone + oxidized dithiothreitol = 2,3-epoxy-2-methyl-3-phytyl-2,3-dihydro-1,4-naphthoquinone + 1,4-dithiothreitol

Systematic name: 3-hydroxy-2-methyl-3-phytyl-2,3-dihydronaphthoquinone:oxidized-dithiothreitol oxidoreductase

Comments: Vitamin K 2,3-epoxide is reduced to 3-hydroxy- (and 2-hydroxy-) vitamin K by 1,4-dithiothreitol, which is oxidized to a disulfide. Not inhibited by warfarin [*cf.* EC 1.17.4.4, vitamin-K-epoxide reductase (warfarin-sensitive)].

References: [2647]

[EC 1.17.4.5 created 1989 as EC 1.1.4.2, transferred 2014 to EC 1.17.4.5]

EC 1.17.5 With a quinone or similar compound as acceptor

EC 1.17.5.1

Accepted name: phenylacetyl-CoA dehydrogenase

Reaction: phenylacetyl-CoA + H₂O + 2 quinone = phenylglyoxylyl-CoA + 2 quinol

Other name(s): phenylacetyl-CoA:acceptor oxidoreductase

Systematic name: phenylacetyl-CoA:quinone oxidoreductase

Comments: The enzyme from *Thauera aromatica* is a membrane-bound molybdenum—iron—sulfur protein. The enzyme is specific for phenylacetyl-CoA as substrate. Phenylacetate, acetyl-CoA, benzoyl-CoA, propanoyl-CoA, crotonyl-CoA, succinyl-CoA and 3-hydroxybenzoyl-CoA cannot act as substrates. The oxygen atom introduced into the product, phenylglyoxylyl-CoA, is derived from water and not molecular oxygen. Duroquinone, menaquinone and 2,6-dichlorophenolindophenol (DCPIP) can act as acceptor, but the likely physiological acceptor is ubiquinone [3175]. A second enzyme, EC 3.1.2.25, phenylacetyl-CoA hydrolase, converts the phenylglyoxylyl-CoA formed into phenylglyoxylate.

References: [3175, 3384]

[EC 1.17.5.1 created 2004]

EC 1.17.5.2

Accepted name: caffeine dehydrogenase

Reaction: caffeine + ubiquinone + H₂O = 1,3,7-trimethylurate + ubiquinol

Systematic name: caffeine:ubiquinone oxidoreductase

Comments: This enzyme, characterized from the soil bacterium *Pseudomonas* sp. CBB1, catalyses the incorporation of an oxygen atom originating from a water molecule into position C-8 of caffeine. The enzyme utilizes short-tail ubiquinones as the preferred electron acceptor.

References: [4399]

[EC 1.17.5.2 created 2010]

EC 1.17.5.3

Accepted name: formate dehydrogenase-N
Reaction: formate + a quinone = CO₂ + a quinol
Other name(s): Fdh-N; FdnGHI; nitrate-inducible formate dehydrogenase; formate dehydrogenase N; FDH-N; nitrate inducible Fdn; nitrate inducible formate dehydrogenase
Systematic name: formate:quinone oxidoreductase
Comments: The enzyme contains molybdopterin-guanine dinucleotides, five [4Fe-4S] clusters and two heme *b* groups. Formate dehydrogenase-N oxidizes formate in the periplasm, transferring electrons via the menaquinone pool in the cytoplasmic membrane to a dissimilatory nitrate reductase (EC 1.7.5.1), which transfers electrons to nitrate in the cytoplasm. The system generates proton motive force under anaerobic conditions [1775].
References: [954, 1776, 1775]

[EC 1.17.5.3 created 2010 as EC 1.1.5.6, transferred 2017 to EC 1.17.5.3]

EC 1.17.7 With an iron-sulfur protein as acceptor

EC 1.17.7.1

Accepted name: (*E*)-4-hydroxy-3-methylbut-2-enyl-diphosphate synthase (ferredoxin)
Reaction: (*E*)-4-hydroxy-3-methylbut-2-en-1-yl diphosphate + H₂O + 2 oxidized ferredoxin = 2-*C*-methyl-D-erythritol 2,4-cyclodiphosphate + 2 reduced ferredoxin
Other name(s): 4-hydroxy-3-methylbut-2-en-1-yl diphosphate synthase (ambiguous); (*E*)-4-hydroxy-3-methylbut-2-en-1-yl-diphosphate:protein-disulfide oxidoreductase (hydrating) (incorrect); (*E*)-4-hydroxy-3-methylbut-2-enyl diphosphate synthase (ambiguous); *gcpE* (gene name); ISPG (gene name); (*E*)-4-hydroxy-3-methylbut-2-enyl-diphosphate synthase
Systematic name: (*E*)-4-hydroxy-3-methylbut-2-en-1-yl-diphosphate:oxidized ferredoxin oxidoreductase
Comments: An iron-sulfur protein found in plant chloroplasts and cyanobacteria that contains a [4Fe-4S] cluster [2858]. Forms part of an alternative non-mevalonate pathway for isoprenoid biosynthesis. Bacteria have a similar enzyme that uses flavodoxin rather than ferredoxin (*cf.* EC 1.17.7.3). The enzyme from the plant *Arabidopsis thaliana* is active with photoreduced 5-deazaflavin but not with flavodoxin [2858].
References: [2858, 3428, 3427, 3426]

[EC 1.17.7.1 created 2003 as EC 1.17.4.3, transferred 2009 to EC 1.17.7.1, modified 2014]

EC 1.17.7.2

Accepted name: 7-hydroxymethyl chlorophyll *a* reductase
Reaction: chlorophyll *a* + H₂O + 2 oxidized ferredoxin = 7¹-hydroxychlorophyll *a* + 2 reduced ferredoxin + 2 H⁺
Other name(s): HCAR; 7¹-hydroxychlorophyll-*a*:ferredoxin oxidoreductase
Systematic name: chlorophyll-*a*:ferredoxin oxidoreductase
Comments: Contains FAD and an iron-sulfur center. This enzyme, which is present in plant chloroplasts, carries out the second step in the conversion of chlorophyll *b* to chlorophyll *a*. It similarly reduces chlorophyllide *a*.
References: [2496]

[EC 1.17.7.2 created 2011]

EC 1.17.7.3

Accepted name: (*E*)-4-hydroxy-3-methylbut-2-enyl-diphosphate synthase (flavodoxin)
Reaction: (*E*)-4-hydroxy-3-methylbut-2-en-1-yl diphosphate + H₂O + oxidized flavodoxin = 2-*C*-methyl-D-erythritol 2,4-cyclodiphosphate + reduced flavodoxin
Other name(s): 4-hydroxy-3-methylbut-2-en-1-yl diphosphate synthase (ambiguous); (*E*)-4-hydroxy-3-methylbut-2-en-1-yl-diphosphate:protein-disulfide oxidoreductase (hydrating) (incorrect); (*E*)-4-hydroxy-3-methylbut-2-enyl diphosphate synthase (ambiguous); *ispG* (gene name)

Systematic name: (*E*)-4-hydroxy-3-methylbut-2-en-1-yl-diphosphate:oxidized flavodoxin oxidoreductase
Comments: A bacterial iron-sulfur protein that contains a [4Fe-4S] cluster. Forms part of an alternative non-mevalonate pathway for isoprenoid biosynthesis that is found in most bacteria [4435]. Plants and cyanobacteria have a similar enzyme that utilizes ferredoxin rather than flavodoxin (*cf.* EC 1.17.7.1).
References: [1449, 4435, 3072]

[EC 1.17.7.3 created 2014]

EC 1.17.7.4

Accepted name: 4-hydroxy-3-methylbut-2-en-1-yl diphosphate reductase
Reaction: (1) isopentenyl diphosphate + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O = (*E*)-4-hydroxy-3-methylbut-2-en-1-yl diphosphate + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺
(2) dimethylallyl diphosphate + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O = (*E*)-4-hydroxy-3-methylbut-2-en-1-yl diphosphate + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺
Other name(s): isopentenyl-diphosphate:NADP⁺ oxidoreductase; LytB; (*E*)-4-hydroxy-3-methylbut-2-en-1-yl diphosphate reductase; HMBPP reductase; IspH; LytB/IspH
Systematic name: isopentenyl-diphosphate:ferredoxin oxidoreductase
Comments: An iron-sulfur protein that contains either a [3Fe-4S] [1264] or a [4Fe-4S] [4241] cluster. This enzyme forms a system with a ferredoxin or a flavodoxin and an NAD(P)H-dependent reductase. This is the last enzyme in the non-mevalonate pathway for isoprenoid biosynthesis. This pathway, also known as the 1-deoxy-D-xylulose 5-phosphate (DOXP) or as the 2-C-methyl-D-erythritol-4-phosphate (MEP) pathway, is found in most bacteria and in plant chloroplasts. The enzyme acts in the reverse direction, producing a 5:1 mixture of isopentenyl diphosphate and dimethylallyl diphosphate.
References: [3219, 1512, 550, 3220, 4241, 1264]

[EC 1.17.7.4 created 2003 as EC 1.17.1.2, modified 2009, transferred 2016 to EC 1.17.7.4]

EC 1.17.8 With a flavin as acceptor

EC 1.17.8.1

Accepted name: hydroxysqualene dehydroxylase
Reaction: squalene + FAD + H₂O = hydroxysqualene + FADH₂
Other name(s): *hpnE* (gene name)
Systematic name: squalene:FAD oxidoreductase (hydroxylating)
Comments: This enzyme, isolated from the bacteria *Rhodopseudomonas palustris* and *Zymomonas mobilis*, participates, along with EC 2.5.1.103, presqualene diphosphate synthase, and EC 4.2.3.156, hydroxysqualene synthase, in the conversion of *all-trans*-farnesyl diphosphate to squalene. Eukaryotes achieve the same goal in a single step, catalysed by EC 2.5.1.21, squalene synthase.
References: [2929]

[EC 1.17.8.1 created 2016]

EC 1.17.9 With a flavin as acceptor

EC 1.17.9.1

Accepted name: 4-methylphenol dehydrogenase (hydroxylating)
Reaction: 4-methylphenol + 4 oxidized azurin + H₂O = 4-hydroxybenzaldehyde + 4 reduced azurin + 4 H⁺ (overall reaction)
(1a) 4-methylphenol + 2 oxidized azurin + H₂O = 4-hydroxybenzyl alcohol + 2 reduced azurin + 2 H⁺
(1b) 4-hydroxybenzyl alcohol + 2 oxidized azurin = 4-hydroxybenzaldehyde + 2 reduced azurin + 2 H⁺

Other name(s): *pchCF* (gene names); *p*-cresol-(acceptor) oxidoreductase (hydroxylating); *p*-cresol methylhydroxylase; 4-cresol dehydrogenase (hydroxylating)

Systematic name: 4-methylphenol:oxidized azurin oxidoreductase (methyl-hydroxylating)

Comments: This bacterial enzyme contains a flavin (FAD) subunit and a cytochrome *c* subunit. The flavin subunit abstracts two hydrogen atoms from the substrate, forming a quinone methide intermediate, then hydrates the latter at the benzylic carbon with a hydroxyl group derived from water. The protons are lost to the bulk solvent, while the electrons are passed to the heme on the cytochrome subunit, and from there to azurin, a small copper-binding protein that is co-localized with the enzyme in the periplasm. The first hydroxylation forms 4-hydroxybenzyl alcohol; a second hydroxylation converts this into 4-hydroxybenzaldehyde.

References: [1565, 2486, 1562, 362, 3153, 2985, 1750]

[EC 1.17.9.1 created 1983 as EC 1.17.99.1, modified 2001, modified 2011, modified 2015, transferred 2018 to EC 1.17.9.1]

EC 1.17.98 With other, known, physiological acceptors

[1.17.98.1 Deleted entry. *bile-acid 7 α -dehydroxylase*. Now known to be catalyzed by multiple enzymes.]

[EC 1.17.98.1 created 2005 as EC 1.17.1.6, transferred 2006 to EC 1.17.99.5, transferred 2014 to EC 1.17.98.1, deleted 2016]

EC 1.17.98.2

Accepted name: bacteriochlorophyllide *c* C-7¹-hydroxylase

Reaction: 2 *S*-adenosyl-L-methionine + a bacteriochlorophyllide *c* + H₂O = a bacteriochlorophyllide *e* + 2 5'-deoxyadenosine + 2 L-methionine (overall reaction)

(1a) *S*-adenosyl-L-methionine + a bacteriochlorophyllide *c* + H₂O = a 7-(hydroxymethyl)bacteriochlorophyllide *c* + 5'-deoxyadenosine + L-methionine

(1b) *S*-adenosyl-L-methionine + a 7-(hydroxymethyl)bacteriochlorophyllide *c* + H₂O = a 7-(dihydroxymethyl)bacteriochlorophyllide *c* + 5'-deoxyadenosine + L-methionine

(1c) a 7-(dihydroxymethyl)bacteriochlorophyllide *c* = a bacteriochlorophyllide *e* + H₂O (spontaneous)

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

Systematic name: bacteriochlorophyllide-*c*:*S*-adenosyl-L-methionine oxidoreductase (C-7¹-hydroxylating)

Comments: The enzyme, found in green sulfur bacteria (Chlorobiaceae), is a radical *S*-adenosyl-L-methionine (AdoMet) enzyme and contains a [4Fe-4S] cluster. It catalyses two consecutive hydroxylation reactions of the C-7 methyl group of bacteriochlorophyllide *c* to form a geminal diol intermediate that spontaneously dehydrates to produce the formyl group of bacteriochlorophyllide *e*.

References: [1389, 3883]

[EC 1.17.98.2 created 2016, modified 2017]

EC 1.17.98.3

Accepted name: formate dehydrogenase (coenzyme F₄₂₀)

Reaction: formate + oxidized coenzyme F₄₂₀ = CO₂ + reduced coenzyme F₄₂₀

Other name(s): coenzyme F₄₂₀ reducing formate dehydrogenase; coenzyme F₄₂₀-dependent formate dehydrogenase

Systematic name: formate:coenzyme-F₄₂₀ oxidoreductase

Comments: The enzyme, characterized from methanogenic archaea, is involved in formate-dependent H₂ production. It contains noncovalently bound FAD [3351].

References: [3351, 3352, 2323]

[EC 1.17.98.3 created 2014 as EC 1.2.99.9, transferred 2017 to EC 1.17.98.3]

EC 1.17.99 With unknown physiological acceptors

[1.17.99.1 Transferred entry. 4-methylphenol dehydrogenase (hydroxylating). Now EC 1.17.9.1, 4-methylphenol dehydrogenase (hydroxylating)]

[EC 1.17.99.1 created 1983, modified 2001, modified 2011, modified 2015, deleted 2018]

EC 1.17.99.2

Accepted name: ethylbenzene hydroxylase
Reaction: ethylbenzene + H₂O + acceptor = (S)-1-phenylethanol + reduced acceptor
Other name(s): ethylbenzene dehydrogenase; ethylbenzene:(acceptor) oxidoreductase
Systematic name: ethylbenzene:acceptor oxidoreductase
Comments: Involved in the anaerobic catabolism of ethylbenzene by denitrifying bacteria. Ethylbenzene is the preferred substrate; the enzyme from some strains oxidizes propylbenzene, 1-ethyl-4-fluorobenzene, 3-methylpent-2-ene and ethylidenecyclohexane. Toluene is not oxidized. *p*-Benzoquinone or ferrocenium can act as electron acceptor. Contains molybdopterin, [4Fe-4S] clusters and heme *b*.
References: [1974, 1757]

[EC 1.17.99.2 created 2001]

EC 1.17.99.3

Accepted name: 3 α ,7 α ,12 α -trihydroxy-5 β -cholestanoyl-CoA 24-hydroxylase
Reaction: (25*R*)-3 α ,7 α ,12 α -trihydroxy-5 β -cholestan-26-oyl-CoA + H₂O + acceptor = (24*R*,25*R*)-3 α ,7 α ,12 α ,24-tetrahydroxy-5 β -cholestan-26-oyl-CoA + reduced acceptor
Other name(s): trihydroxycoprostanoyl-CoA oxidase; THC-CoA oxidase; THCA-CoA oxidase; 3 α ,7 α ,12 α -trihydroxy-5 β -cholestanoyl-CoA oxidase; 3 α ,7 α ,12 α -trihydroxy-5 β -cholestan-26-oate 24-hydroxylase
Systematic name: (25*R*)-3 α ,7 α ,12 α -trihydroxy-5 β -cholestan-26-oyl-CoA:acceptor 24-oxidoreductase (24*R*-hydroxylating)
Comments: Requires ATP. The reaction in mammals possibly involves dehydrogenation to give a 24(25)-double bond followed by hydration [1323]. However, in amphibians such as the Oriental fire-bellied toad (*Bombina orientalis*), it is probable that the product is formed via direct hydroxylation of the saturated side chain of (25*R*)-3 α ,7 α ,12 α -trihydroxy-5 β -cholestan-26-oate and not via hydration of a 24(25) double bond [2973]. In microsomes, the free acid is preferred to the coenzyme A ester, whereas in mitochondria, the coenzyme A ester is preferred to the free-acid form of the substrate [1323].
References: [1323, 3359, 823, 824, 2973, 3263]

[EC 1.17.99.3 created 2005]

EC 1.17.99.4

Accepted name: uracil/thymine dehydrogenase
Reaction: (1) uracil + H₂O + acceptor = barbiturate + reduced acceptor
(2) thymine + H₂O + acceptor = 5-methylbarbiturate + reduced acceptor
Other name(s): uracil oxidase; uracil-thymine oxidase; uracil dehydrogenase
Systematic name: uracil:acceptor oxidoreductase
Comments: Forms part of the oxidative pyrimidine-degrading pathway in some microorganisms, along with EC 3.5.2.1 (barbiturase) and EC 3.5.1.95 (*N*-malonylurea hydrolase). Mammals, plants and other microorganisms utilize the reductive pathway, comprising EC 1.3.1.1 [dihydrouracil dehydrogenase (NAD⁺)] or EC 1.3.1.2 [dihydropyrimidine dehydrogenase (NADP⁺)], EC 3.5.2.2 (dihydropyrimidinase) and EC 3.5.1.6 (β -ureidopropionase), with the ultimate degradation products being an L-amino acid, NH₃ and CO₂ [3586].
References: [1432, 4122, 4123, 2135, 3586]

[EC 1.17.99.4 created 1961 as EC 1.2.99.1, transferred 1984 to EC 1.1.99.19, transferred 2006 to EC 1.17.99.4]

[1.17.99.5 Transferred entry. bile-acid 7 α -dehydroxylase. Now classified as EC 1.17.98.1, bile-acid 7 α -dehydroxylase.]

[EC 1.17.99.5 created 2005 as EC 1.17.1.6, transferred 2006 to EC 1.17.99.5, deleted 2014]

EC 1.17.99.6

Accepted name: epoxyqueuosine reductase
Reaction: queuosine³⁴ in tRNA + acceptor + H₂O = epoxyqueuosine³⁴ in tRNA + reduced acceptor
Other name(s): oQ reductase; *queG* (gene name); *queH* (gene name)
Systematic name: queuosine³⁴ in tRNA:acceptor oxidoreductase
Comments: This enzyme catalyses the last step in the bacterial biosynthetic pathway to queuosine, the modified guanosine base in the wobble position in tRNAs specific for Tyr, His, Asp or Asn.
References: [2541, 4422]

[EC 1.17.99.6 created 2014]

EC 1.17.99.7

Accepted name: formate dehydrogenase (acceptor)
Reaction: formate + acceptor = CO₂ + reduced acceptor
Other name(s): FDHH; FDH-H; FDH-O; formate dehydrogenase H; formate dehydrogenase O
Systematic name: formate:acceptor oxidoreductase
Comments: Formate dehydrogenase H is a cytoplasmic enzyme that oxidizes formate without oxygen transfer, transferring electrons to a hydrogenase. The two enzymes form the formate-hydrogen lyase complex [149]. The enzyme contains an [4Fe-4S] cluster, a selenocysteine residue and a molybdopterin cofactor [149].
References: [149, 1212, 1895]

[EC 1.17.99.7 created 2010 as EC 1.1.99.33, transferred 2017 to EC 1.17.99.7]

EC 1.18 Acting on iron-sulfur proteins as donors

This subclass contains enzymes that act on iron-sulfur proteins as donors. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.18.1) and dinitrogen (EC 1.18.6).

EC 1.18.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.18.1.1

Accepted name: rubredoxin—NAD⁺ reductase
Reaction: 2 reduced rubredoxin + NAD⁺ + H⁺ = 2 oxidized rubredoxin + NADH
Other name(s): rubredoxin reductase; rubredoxin-nicotinamide adenine dinucleotide reductase; dihydronicotinamide adenine dinucleotide-rubredoxin reductase; reduced nicotinamide adenine dinucleotide-rubredoxin reductase; NADH-rubredoxin reductase; rubredoxin-NAD reductase; NADH: rubredoxin oxidoreductase; DPNH-rubredoxin reductase; NADH-rubredoxin oxidoreductase
Systematic name: rubredoxin:NAD⁺ oxidoreductase
Comments: Requires FAD. The enzyme from *Clostridium acetobutylicum* reduces rubredoxin, ferricyanide and dichlorophenolindophenol, but not ferredoxin or flavodoxin. The reaction does not occur when NADPH is substituted for NADH. Contains iron at the redox centre.
References: [2988, 3960, 3961, 2992]

[EC 1.18.1.1 created 1972 as EC 1.6.7.2, transferred 1978 to EC 1.18.1.1, modified 2001]

EC 1.18.1.2

Accepted name: ferredoxin—NADP⁺ reductase
Reaction: 2 reduced ferredoxin + NADP⁺ + H⁺ = 2 oxidized ferredoxin + NADPH
Other name(s): ferredoxin-nicotinamide adenine dinucleotide phosphate reductase; ferredoxin-NADP⁺ reductase; TPNH-ferredoxin reductase; ferredoxin-NADP⁺ oxidoreductase; NADP⁺:ferredoxin oxidoreductase; ferredoxin-TPN reductase; ferredoxin-NADP⁺-oxidoreductase; NADPH:ferredoxin oxidoreductase; ferredoxin-nicotinamide-adenine dinucleotide phosphate (oxidized) reductase
Systematic name: ferredoxin:NADP⁺ oxidoreductase
Comments: A flavoprotein (FAD). In chloroplasts and cyanobacteria the enzyme acts on plant-type [2Fe-2S] ferredoxins, but in other bacteria it can also reduce bacterial [4Fe-4S] ferredoxins and flavodoxin.
References: [3509, 1970, 1818, 2610]

[EC 1.18.1.2 created 1965 as EC 1.6.99.4, transferred 1972 as EC 1.6.7.1, transferred 1978 to EC 1.18.1.2, part transferred 2012 to EC 1.18.1.6, modified 2012]

EC 1.18.1.3

Accepted name: ferredoxin—NAD⁺ reductase
Reaction: (1) 2 reduced [2Fe-2S] ferredoxin + NAD⁺ + H⁺ = 2 oxidized [2Fe-2S] ferredoxin + NADH
 (2) reduced 2[4Fe-4S] ferredoxin + NAD⁺ + H⁺ = oxidized 2[4Fe-4S] ferredoxin + NADH
Other name(s): ferredoxin-nicotinamide adenine dinucleotide reductase; ferredoxin reductase (ambiguous); NAD⁺-ferredoxin reductase; NADH-ferredoxin oxidoreductase; reductase, reduced nicotinamide adenine dinucleotide-ferredoxin; ferredoxin-NAD⁺ reductase; NADH-ferredoxin reductase; NADH₂-ferredoxin oxidoreductase; NADH flavodoxin oxidoreductase; NADH-ferredoxin NAP reductase (component of naphthalene dioxygenase multicomponent enzyme system); ferredoxin-linked NAD⁺ reductase; NADH-ferredoxin TOL reductase (component of toluene dioxygenase); ferredoxin—NAD reductase
Systematic name: ferredoxin:NAD⁺ oxidoreductase
Comments: Contains FAD. Reaction (1) is written for a [2Fe-2S] ferredoxin, which is characteristic of some mono- and dioxygenase systems. The alternative reaction (2) is written for a 2[4Fe-4S] ferredoxin, which transfers two electrons, and occurs in metabolism of anaerobic bacteria.
References: [1785, 1342, 3115, 3467]

[EC 1.18.1.3 created 1976 as EC 1.6.7.3, transferred 1978 to EC 1.18.1.3, modified 2011]

EC 1.18.1.4

Accepted name: rubredoxin—NAD(P)⁺ reductase
Reaction: 2 reduced rubredoxin + NAD(P)⁺ + H⁺ = 2 oxidized rubredoxin + NAD(P)H
Other name(s): rubredoxin-nicotinamide adenine dinucleotide (phosphate) reductase; rubredoxin-nicotinamide adenine; dinucleotide phosphate reductase; NAD(P)⁺-rubredoxin oxidoreductase; NAD(P)H-rubredoxin oxidoreductase
Systematic name: rubredoxin:NAD(P)⁺ oxidoreductase
Comments: The enzyme from *Pyrococcus furiosus* requires FAD. It reduces a number of electron carriers, including benzyl viologen, menadione and 2,6-dichloroindophenol, but rubredoxin is the most efficient. Ferredoxin is not utilized.
References: [2991, 2329]

[EC 1.18.1.4 created 1984, modified 2001, modified 2011]

EC 1.18.1.5

Accepted name: putidaredoxin—NAD⁺ reductase
Reaction: reduced putidaredoxin + NAD⁺ = oxidized putidaredoxin + NADH + H⁺
Other name(s): putidaredoxin reductase; *camA* (gene name)
Systematic name: putidaredoxin:NAD⁺ oxidoreductase
Comments: Requires FAD. The enzyme from *Pseudomonas putida* reduces putidaredoxin. It contains a [2Fe-2S] cluster. Involved in the camphor monoxygenase system (see EC 1.14.15.1, camphor 5-monoxygenase).

References: [3229, 1998, 2989, 3454, 3451, 3452, 3563]

[EC 1.18.1.5 created 2012]

EC 1.18.1.6

Accepted name: adrenodoxin-NADP⁺ reductase
Reaction: 2 reduced adrenodoxin + NADP⁺ + H⁺ = 2 oxidized adrenodoxin + NADPH
Other name(s): adrenodoxin reductase; nicotinamide adenine dinucleotide phosphate-adrenodoxin reductase; AdR; NADPH:adrenal ferredoxin oxidoreductase; NADPH-adrenodoxin reductase
Systematic name: reduced adrenodoxin:NADP⁺ oxidoreductase
Comments: A flavoprotein (FAD). The enzyme, which transfers electrons from NADPH to adrenodoxin molecules, is the first component of the mitochondrial cytochrome *P*-450 electron transfer systems, and is involved in the biosynthesis of all steroid hormones.
References: [2884, 620, 3718, 1381, 1380, 1379, 4487]

[EC 1.18.1.6 created 1965 as EC 1.6.99.4, transferred 1972 as EC 1.6.7.1, transferred 1978 to EC 1.18.1.2, part transferred 2012 to EC 1.18.1.6, modified 2016]

EC 1.18.1.7

Accepted name: ferredoxin—NAD(P)⁺ reductase (naphthalene dioxygenase ferredoxin-specific)
Reaction: 2 reduced [2Fe-2S] ferredoxin + NAD(P)⁺ + H⁺ = 2 oxidized [2Fe-2S] ferredoxin + NAD(P)H
Other name(s): NADH-ferredoxin(NAP) reductase
Systematic name: ferredoxin:NAD(P)⁺ oxidoreductase
Comments: The enzyme from the aerobic bacterium *Ralstonia* sp. U2 donates electrons to both EC 1.14.12.12, naphthalene 1,2-dioxygenase and EC 1.14.13.172, salicylate 5-hydroxylase [4472]. The enzyme from *Pseudomonas* NCIB 9816 is specific for the ferredoxin associated with naphthalene dioxygenase; it contains FAD and a [2Fe-2S] cluster.
References: [4472, 1342]

[EC 1.18.1.7 created 2013]

[1.18.1.8 *Transferred entry. ferredoxin-NAD⁺ oxidoreductase (Na⁺-transporting). Now EC 7.2.1.2, ferredoxin—NAD⁺ oxidoreductase (Na⁺-transporting)*]

[EC 1.18.1.8 created 2015, deleted 2018]

EC 1.18.2 With dinitrogen as acceptor (deleted sub-subclass)

[1.18.2.1 *Transferred entry. now EC 1.18.6.1, nitrogenase*]

[EC 1.18.2.1 created 1978, deleted 1984]

EC 1.18.3 With H⁺ as acceptor (deleted sub-subclass)

[1.18.3.1 *Transferred entry. hydrogenase. Now EC 1.12.7.2, ferredoxin hydrogenase*]

[EC 1.18.3.1 created 1978, deleted 1984]

EC 1.18.6 With dinitrogen as acceptor

EC 1.18.6.1

Accepted name: nitrogenase

Reaction: 8 reduced ferredoxin + 8 H⁺ + N₂ + 16 ATP + 16 H₂O = 8 oxidized ferredoxin + H₂ + 2 NH₃ + 16 ADP + 16 phosphate

Other name(s): reduced ferredoxin:dinitrogen oxidoreductase (ATP-hydrolysing)

Systematic name: ferredoxin:dinitrogen oxidoreductase (ATP-hydrolysing, molybdenum-dependent)

Comments: Requires Mg²⁺. The enzyme is a complex of two components (namely dinitrogen reductase and dinitrogenase). Dinitrogen reductase is a [4Fe-4S] protein, which, in the presence of two molecules of ATP, transfers an electron from ferredoxin to the dinitrogenase component. Dinitrogenase is a molybdenum-iron protein that reduces dinitrogen to two molecules of ammonia in three successive two-electron reductions via diazene and hydrazine. The reduction is initiated by formation of hydrogen in stoichiometric amounts [2241]. Acetylene is reduced to ethylene (but only very slowly to ethane), azide to nitrogen and ammonia, and cyanide to methane and ammonia. In the absence of a suitable substrate, hydrogen is slowly formed. Ferredoxin may be replaced by flavodoxin [see EC 1.19.6.1 nitrogenase (flavodoxin)]. The enzyme does not reduce CO (*cf.* EC 1.18.6.2, vanadium-dependent nitrogenase).

References: [4499, 2241, 735, 536]

[EC 1.18.6.1 created 1978 as EC 1.18.2.1, transferred 1984 to EC 1.18.6.1, modified 2005, modified 2018]

EC 1.18.6.2

Accepted name: vanadium-dependent nitrogenase

Reaction: 12 reduced ferredoxin + 12 H⁺ + N₂ + 40 ATP + 40 H₂O = 12 oxidized ferredoxin + 3 H₂ + 2 NH₃ + 40 ADP + 40 phosphate

Other name(s): *vnfD* (gene name); *vnfG* (gene name); *vnfK* (gene name)

Systematic name: ferredoxin:dinitrogen oxidoreductase (ATP-hydrolysing, vanadium-dependent)

Comments: Requires Mg²⁺. This enzyme, originally isolated from the bacterium *Azotobacter vinelandii*, is a complex of two components (namely dinitrogen reductase and dinitrogenase). Dinitrogen reductase is a [4Fe-4S] protein, which, in the presence of ATP, transfers an electron from ferredoxin to the dinitrogenase component. Dinitrogenase is a vanadium-iron protein that reduces dinitrogen to two molecules of ammonia in three successive two-electron reductions via diazine and hydrazine. Compared with molybdenum-dependent nitrogenase (EC 1.18.6.1), this enzyme produces more dihydrogen and consumes more ATP per dinitrogen molecule being reduced. Unlike EC 1.18.6.1, this enzyme can also use CO as substrate, producing ethene, ethane and propane [2165, 3540].

References: [905, 2547, 3878, 829, 830, 900, 2165, 2166, 3540]

[EC 1.18.6.2 created 2018]

EC 1.18.96 With other, known, acceptors (deleted sub-subclass)

[1.18.96.1 *Transferred entry. superoxide reductase. Now EC 1.15.1.2, superoxide reductase*]

[EC 1.18.96.1 created 2001, deleted 2001]

EC 1.18.99 With H⁺ as acceptor (deleted sub-subclass)

[1.18.99.1 *Transferred entry. hydrogenase. Now EC 1.12.7.2, ferredoxin hydrogenase*]

[EC 1.18.99.1 created 1961 as EC 1.98.1.1, transferred 1965 to EC 1.12.1.1, transferred 1972 to EC 1.12.7.1, transferred 1978 to EC 1.18.3.1, transferred 1984 to EC 1.18.99.1, deleted 2002]

EC 1.19 Acting on reduced flavodoxin as donor

This subclass contains enzymes that act on reduced flavodoxin as donors. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.19.1) and dinitrogen (EC 1.19.6).

EC 1.19.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.19.1.1

- Accepted name:** flavodoxin—NADP⁺ reductase
Reaction: reduced flavodoxin + NADP⁺ = oxidized flavodoxin + NADPH + H⁺
Other name(s): FPR
Systematic name: flavodoxin:NADP⁺ oxidoreductase
Comments: A flavoprotein (FAD). This activity occurs in some prokaryotes and algae that possess flavodoxin, and provides low-potential electrons for a variety of reactions such as nitrogen fixation, sulfur assimilation and amino acid biosynthesis. In photosynthetic organisms it is involved in the photosynthetic electron transport chain. The enzyme also catalyses EC 1.18.1.2, ferredoxin—NADP⁺ reductase.
References: [2487, 2160, 4101, 357, 358, 3548]

[EC 1.19.1.1 created 2016]

EC 1.19.6 With dinitrogen as acceptor

EC 1.19.6.1

- Accepted name:** nitrogenase (flavodoxin)
Reaction: 4 reduced flavodoxin + N₂ + 16 ATP + 16 H₂O = 4 oxidized flavodoxin + H₂ + 2 NH₃ + 16 ADP + 16 phosphate
Systematic name: reduced flavodoxin:dinitrogen oxidoreductase (ATP-hydrolysing)
Comments: Requires Mg²⁺. It is composed of two components, dinitrogen reductase and dinitrogenase, that can be separated but are both required for nitrogenase activity. Dinitrogen reductase is a [4Fe-4S] protein, which, at the expense of ATP, transfers electrons from a dedicated flavodoxin to dinitrogenase. Dinitrogenase is a protein complex that contains either a molybdenum-iron cofactor, a vanadium-iron cofactor, or an iron-iron cofactor, that reduces dinitrogen in three successive two-electron reductions from nitrogen to diimine to hydrazine to two molecules of ammonia. The reduction is initiated by formation of hydrogen. The enzyme can also reduce acetylene to ethylene (but only very slowly to ethane), azide to nitrogen and ammonia, and cyanide to methane and ammonia. In the absence of a suitable substrate, hydrogen is slowly formed. Some enzymes utilize ferredoxin rather than flavodoxin as the electron donor (see EC 1.18.6.1, nitrogenase).
References: [4498, 906, 778]

[EC 1.19.6.1 created 1984, modified 2014]

EC 1.20 Acting on phosphorus or arsenic in donors

This subclass contains enzymes that act on phosphorus or arsenic in donors. Sub-subclasses are based on the acceptor: NAD⁺ or NADP⁺ (EC 1.20.1), disulfide (EC 1.20.4), other, known, acceptors (EC 1.20.98), or some other acceptor (EC 1.20.99).

EC 1.20.1 With NAD⁺ or NADP⁺ as acceptor

EC 1.20.1.1

- Accepted name:** phosphonate dehydrogenase
Reaction: phosphonate + NAD⁺ + H₂O = phosphate + NADH + H⁺
Other name(s): NAD:phosphite oxidoreductase; phosphite dehydrogenase
Systematic name: phosphonate:NAD⁺ oxidoreductase
Comments: NADP⁺ is a poor substitute for NAD⁺ in the enzyme from *Pseudomonas stutzeri* WM88.
References: [672, 4070]

[EC 1.20.1.1 created 2001]

EC 1.20.2 With a cytochrome as acceptor

EC 1.20.2.1

- Accepted name:** arsenate reductase (cytochrome *c*)
Reaction: arsenite + H₂O + 2 oxidized cytochrome *c* = arsenate + 2 reduced cytochrome *c* + 2 H⁺
Other name(s): arsenite oxidase (ambiguous)
Systematic name: arsenite:cytochrome *c* oxidoreductase
Comments: A molybdoenzyme containing iron-sulfur clusters. Isolated from α -proteobacteria. Unlike EC 1.20.9.1, arsenate reductase (azurin), it does not use azurin as acceptor.
References: [4017, 3310, 384, 2251]

[EC 1.20.2.1 created 2011]

EC 1.20.4 With disulfide as acceptor

EC 1.20.4.1

- Accepted name:** arsenate reductase (glutaredoxin)
Reaction: arsenate + glutaredoxin = arsenite + glutaredoxin disulfide + H₂O
Other name(s): ArsC (ambiguous)
Systematic name: arsenate:glutaredoxin oxidoreductase
Comments: A molybdoenzyme. The enzyme is part of a system for detoxifying arsenate. Although the arsenite formed is more toxic than arsenate, it can be extruded from some bacteria by EC 3.6.3.16, arsenite-transporting ATPase; in other organisms, arsenite can be methylated by EC 2.1.1.137, arsenite methyltransferase, in a pathway that produces non-toxic organoarsenical compounds. *cf.* EC 1.20.4.4, arsenate reductase (thioredoxin).
References: [1215, 1216, 1549, 2052, 2413, 3099, 3320, 3481]

[EC 1.20.4.1 created 2000 as EC 1.97.1.5, transferred 2001 to EC 1.20.4.1, modified 2015]

EC 1.20.4.2

- Accepted name:** methylarsonate reductase
Reaction: methylarsonate + 2 glutathione = methylarsonite + glutathione disulfide + H₂O
Other name(s): MMA(V) reductase
Systematic name: methylarsonate:glutathione oxidoreductase
Comments: The product, methylarsonite, is biologically methylated by EC 2.1.1.137, arsenite methyltransferase, to form cacodylic acid.
References: [4421]

[EC 1.20.4.2 created 2000 as EC 1.97.1.7, transferred 2001 to EC 1.20.4.2, modified 2003]

EC 1.20.4.3

- Accepted name:** mycoredoxin
Reaction: arseno-mycothioliol + mycoredoxin = arsenite + mycothiol-mycoredoxin disulfide
Other name(s): Mrx1; MrxI
Systematic name: arseno-mycothioliol:mycoredoxin oxidoreductase
Comments: Reduction of arsenate is part of a defense mechanism of the cell against toxic arsenate. The substrate arseno-mycothioliol is formed by EC 2.8.4.2 (arsenate:mycothiol transferase). A second mycothiol recycles mycoredoxin and forms mycothione.
References: [2894]

[EC 1.20.4.3 created 2010]

EC 1.20.4.4

- Accepted name:** arsenate reductase (thioredoxin)
Reaction: arsenate + thioredoxin = arsenite + thioredoxin disulfide + H₂O
Other name(s): ArsC (ambiguous)
Systematic name: arsenate:thioredoxin oxidoreductase
Comments: The enzyme, characterized in bacteria of the Firmicutes phylum, is specific for thioredoxin [1738]. It has no activity with glutaredoxin [*cf.* EC 1.20.4.1, arsenate reductase (glutaredoxin)]. Although the arsenite formed is more toxic than arsenate, it can be extruded from some bacteria by EC 3.6.3.16, arsenite-transporting ATPase; in other organisms, arsenite can be methylated by EC 2.1.1.137, arsenite methyltransferase, in a pathway that produces non-toxic organoarsenical compounds. The enzyme also has the activity of EC 3.1.3.48, protein-tyrosine-phosphatase [4429].
References: [1738, 2509, 4429, 2510]

[EC 1.20.4.4 created 2015]

EC 1.20.9 With a copper protein as acceptor

EC 1.20.9.1

- Accepted name:** arsenate reductase (azurin)
Reaction: arsenite + H₂O + 2 oxidized azurin = arsenate + 2 reduced azurin + 2 H⁺
Other name(s): arsenite oxidase (ambiguous)
Systematic name: arsenite:azurin oxidoreductase
Comments: Contains a molybdopterin centre comprising two molybdopterin guanosine dinucleotide cofactors bound to molybdenum, a [3Fe-4S] cluster and a Rieske-type [2Fe-2S] cluster. Isolated from β-proteobacteria. Also uses a *c*-type cytochrome or O₂ as acceptors.
References: [83, 941]

[EC 1.20.9.1 created 2001 as EC 1.20.98.1, transferred 2011 to EC 1.20.9.1]

EC 1.20.98 With other, known, physiological acceptors

[1.20.98.1 *Transferred entry. arsenate reductase (azurin). Now EC 1.20.9.1, arsenate reductase (azurin)*]

[EC 1.20.98.1 created 2001, deleted 2011]

EC 1.20.99 With unknown physiological acceptors

EC 1.20.99.1

- Accepted name:** arsenate reductase (donor)
Reaction: arsenite + acceptor = arsenate + reduced acceptor
Other name(s): arsenate:(acceptor) oxidoreductase
Systematic name: arsenate:acceptor oxidoreductase
Comments: Benzyl viologen can act as an acceptor. Unlike EC 1.20.4.1, arsenate reductase (glutaredoxin), reduced glutaredoxin cannot serve as a reductant.
References: [2052, 3099]

[EC 1.20.99.1 created 2000 as EC 1.97.1.6, transferred 2001 to EC 1.20.99.1]

EC 1.21 Catalysing the reaction $X-H + Y-H = X-Y$

This subclass contains enzymes that catalyse the reaction $X-H + Y-H = X-Y$, forming or breaking an X-Y bond. Sub-subclasses are based on the acceptor: oxygen (EC 1.21.3), a disulfide (EC 1.21.4), or some other unidentified acceptor (EC 1.21.99).

EC 1.21.1 Catalysing the reaction $X-H + Y-H = X-Y$

EC 1.21.1.1

- Accepted name:** iodotyrosine deiodinase
Reaction: L-tyrosine + 2 NADP⁺ + 2 iodide = 3,5-diiodo-L-tyrosine + 2 NADPH + 2 H⁺ (overall reaction)
(1a) L-tyrosine + NADP⁺ + iodide = 3-iodo-L-tyrosine + NADPH + H⁺
(1b) 3-iodo-L-tyrosine + NADP⁺ + iodide = 3,5-diiodo-L-tyrosine + NADPH + H⁺
Other name(s): iodotyrosine dehalogenase 1; DEHAL1
Systematic name: L-tyrosine,iodide:NADP⁺ oxidoreductase (iodinating)
Comments: The enzyme activity has only been demonstrated in the direction of 3-deiodination. Present in a trans-membrane flavoprotein. Requires FMN.
References: [3234, 1227, 1070, 3869]

[EC 1.21.1.1 created 2010 as EC 1.22.1.1 transferred 2015 to EC 1.21.1.1]

EC 1.21.1.2

- Accepted name:** 2,4-dichlorobenzoyl-CoA reductase
Reaction: 4-chlorobenzoyl-CoA + NADP⁺ + chloride = 2,4-dichlorobenzoyl-CoA + NADPH + H⁺
Systematic name: 4-chlorobenzoyl-CoA:NADP⁺ oxidoreductase (halogenating)
Comments: The enzyme, characterized from *Corynebacterium* strains able to grow on 2,4-dichlorobenzoate, forms part of the 2,4-dichlorobenzoate degradation pathway.
References: [3226]

[EC 1.21.1.2 created 2000 as EC 1.3.1.63, modified 2011, transferred 2015 to EC 1.21.1.2]

EC 1.21.3 With oxygen as acceptor

EC 1.21.3.1

- Accepted name:** isopenicillin-N synthase
Reaction: *N*-[(5*S*)-5-amino-5-carboxypentanoyl]-L-cysteinyl-D-valine + O₂ = isopenicillin N + 2 H₂O
Other name(s): isopenicillin N synthetase
Systematic name: *N*-[(5*S*)-5-amino-5-carboxypentanoyl]-L-cysteinyl-D-valine:oxygen oxidoreductase (cyclizing)
Comments: Forms part of the penicillin biosynthesis pathway (for pathway, click here).
References: [1603, 3199]

[EC 1.21.3.1 created 2002]

EC 1.21.3.2

- Accepted name:** columbamine oxidase
Reaction: 2 columbamine + O₂ = 2 berberine + 2 H₂O
Other name(s): berberine synthase
Systematic name: columbamine:oxygen oxidoreductase (cyclizing)
Comments: An iron protein. Oxidation of the *O*-methoxyphenol structure forms the methylenedioxy group of berberine.
References: [3253]

[EC 1.21.3.2 created 1989 as EC 1.1.3.26, transferred 2002 to EC 1.21.3.2]

EC 1.21.3.3

Accepted name: reticuline oxidase
Reaction: (*S*)-reticuline + O₂ = (*S*)-scoulerine + H₂O₂
Other name(s): BBE; berberine bridge enzyme; berberine-bridge-forming enzyme; tetrahydroprotoberberine synthase
Systematic name: (*S*)-reticuline:oxygen oxidoreductase (methylene-bridge-forming)
Comments: Contains FAD. The enzyme from the plant *Eschscholtzia californica* binds the cofactor covalently [2099]. Acts on (*S*)-reticuline and related compounds, converting the *N*-methyl group into the methylene bridge ('berberine bridge') of (*S*)-tetrahydroprotoberberines. The product of the reaction, (*S*)-scoulerine, is a precursor of protopine, protoberberine and benzophenanthridine alkaloid biosynthesis in plants.
References: [3631, 833, 2099]

[EC 1.21.3.3 created 1989 as EC 1.5.3.9, transferred 2002 to EC 1.21.3.3]

EC 1.21.3.4

Accepted name: sulochrin oxidase [(+)-bisdechlorogeodin-forming]
Reaction: 2 sulochrin + O₂ = 2 (+)-bisdechlorogeodin + 2 H₂O
Other name(s): sulochrin oxidase
Systematic name: sulochrin:oxygen oxidoreductase (cyclizing, (+)-specific)
Comments: Also acts on several diphenols and phenylenediamines, but has low affinity for these substrates. Involved in the biosynthesis of mould metabolites related to the antibiotic griseofulvin.
References: [2818]

[EC 1.21.3.4 created 1986 as EC 1.10.3.7, transferred 2002 to EC 1.21.3.4]

EC 1.21.3.5

Accepted name: sulochrin oxidase [(-)-bisdechlorogeodin-forming]
Reaction: 2 sulochrin + O₂ = 2 (-)-bisdechlorogeodin + 2 H₂O
Other name(s): sulochrin oxidase
Systematic name: sulochrin:oxygen oxidoreductase (cyclizing, (-)-specific)
Comments: Also acts on several diphenols and phenylenediamines, but has low affinity for these substrates. Involved in the biosynthesis of mould metabolites related to the antibiotic griseofulvin.
References: [2818]

[EC 1.21.3.5 created 1986 as EC 1.10.3.8, transferred 2002 to EC 1.21.3.5]

EC 1.21.3.6

Accepted name: aureusidin synthase
Reaction: (1) 2',4,4',6'-tetrahydroxychalcone 4'-*O*-β-D-glucoside + O₂ = aureusidin 6-*O*-β-D-glucoside + H₂O
(2) 2',3,4,4',6'-pentahydroxychalcone 4'-*O*-β-D-glucoside + $\frac{1}{2}$ O₂ = aureusidin 6-*O*-β-D-glucoside + H₂O
(3) 2',3,4,4',6'-pentahydroxychalcone 4'-*O*-β-D-glucoside + O₂ = bracteatin 6-*O*-β-D-glucoside + H₂O
Other name(s): AmAS1
Systematic name: 2',4,4',6'-tetrahydroxychalcone 4'-*O*-β-D-glucoside:oxygen oxidoreductase
Comments: A copper-containing glycoprotein that plays a key role in the yellow coloration of flowers such as *Antirrhinum majus* (snapdragon). The enzyme is a homologue of plant polyphenol oxidase [2723] and catalyses two separate chemical transformations, i.e. 3-hydroxylation and oxidative cyclization (2',-dehydrogenation). H₂O₂ activates reaction (1) but inhibits reaction (2). Originally considered to act on the phenol but now thought to act mainly on the 4'-*O*-β-D-glucoside *in vivo* [2888].
References: [2723, 2722, 3321, 2888]

[EC 1.21.3.6 created 2003, modified 2012]

EC 1.21.3.7

- Accepted name:** tetrahydrocannabinolic acid synthase
Reaction: cannabigerolate + O₂ = Δ⁹-tetrahydrocannabinolate + H₂O₂
Other name(s): THCA synthase; Δ¹-tetrahydrocannabinolic acid synthase
Systematic name: cannabigerolate:oxygen oxidoreductase (cyclizing, Δ⁹-tetrahydrocannabinolate-forming)
Comments: A flavoprotein (FAD). The cofactor is covalently bound. Part of the cannabinoids biosynthetic pathway in the plant *Cannabis sativa*. The enzyme can also convert cannabinerolate (the (Z)-isomer of cannabigerolate) to Δ⁹-THCA with lower efficiency. Whereas the product was originally called Δ¹-tetrahydrocannabinolate, the recommended name according to systematic peripheral numbering is Δ⁹-tetrahydrocannabinolate.
References: [3826, 3542, 3521, 3522]

[EC 1.21.3.7 created 2012]

EC 1.21.3.8

- Accepted name:** cannabidiolic acid synthase
Reaction: cannabigerolate + O₂ = cannabidiolate + H₂O₂
Other name(s): CBDA synthase
Systematic name: cannabigerolate:oxygen oxidoreductase (cyclizing, cannabidiolate-forming)
Comments: Binds FAD covalently. Part of the cannabinoids biosynthetic pathway of the plant *Cannabis sativa*. The enzyme can also convert cannabinerolate to cannabidiolate with lower efficiency.
References: [3825, 3827]

[EC 1.21.3.8 created 2012]

[1.21.3.9 Transferred entry. dichlorochromopyrrolate synthase, now classified as EC 1.21.98.2, dichlorochromopyrrolate synthase]

[EC 1.21.3.9 created 2010 as EC 4.3.1.26, transferred 2013 to EC 1.21.3.9, deleted 2016]

EC 1.21.4 With a disulfide as acceptor

EC 1.21.4.1

- Accepted name:** D-proline reductase
Reaction: 5-aminopentanoate + a [PrdC protein with a selenide-sulfide bridge] = D-proline + a [PrdC protein with thiol/selenol residues]
Other name(s): *prdAB* (gene names); D-proline reductase (dithiol)
Systematic name: 5-aminopentanoate:[PrdC protein] oxidoreductase (cyclizing)
Comments: A pyruvoyl- and L-selenocysteine-containing enzyme found in a number of Clostridial species. The pyruvoyl group, located on the PrdA subunit, binds the substrate, while the selenocysteine residue, located on the PrdB subunit, attacks the α-C-atom of D-proline, leading to a reductive cleavage of the C-N-bond of the pyrrolidine ring and formation of a selenoether. The selenoether is cleaved by a cysteine residue of PrdB, resulting in a mixed selenide-sulfide bridge, which is restored to its reduced state by another selenocysteine protein, PrdC. 5-aminopentanoate is released from PrdA by hydrolysis, regenerating the pyruvoyl moiety. The resulting mixed selenide-sulfide bridge in PrdC is reduced by NADH.
References: [3616, 1530, 1790, 240, 1027]

[EC 1.21.4.1 created 1972 as EC 1.4.4.1, modified 1982 (EC 1.4.1.6 created 1961, incorporated 1982), transferred 2003 to EC 1.21.4.1, modified 2018]

EC 1.21.4.2

- Accepted name:** glycine reductase
Reaction: acetyl phosphate + NH₃ + thioredoxin disulfide + H₂O = glycine + phosphate + thioredoxin
Systematic name: acetyl-phosphate ammonia:thioredoxin disulfide oxidoreductase (glycine-forming)
Comments: The reaction is observed only in the direction of glycine reduction. The enzyme from *Eubacterium acidaminophilum* consists of subunits A, B and C. Subunit B contains selenocysteine and a pyruvoyl group, and is responsible for glycine binding and ammonia release. Subunit A, which also contains selenocysteine, is reduced by thioredoxin, and is needed to convert the carboxymethyl group into a ketene equivalent, in turn used by subunit C to produce acetyl phosphate. Only subunit B distinguishes this enzyme from EC 1.21.4.3 (sarcosine reductase) and EC 1.21.4.4 (betaine reductase).
References: [4079, 240]

[EC 1.21.4.2 created 2003]

EC 1.21.4.3

- Accepted name:** sarcosine reductase
Reaction: acetyl phosphate + methylamine + thioredoxin disulfide + H₂O = *N*-methylglycine + phosphate + thioredoxin
Systematic name: acetyl-phosphate methylamine:thioredoxin disulfide oxidoreductase (*N*-methylglycine-forming)
Comments: The reaction is observed only in the direction of sarcosine reduction. The enzyme from *Eubacterium acidaminophilum* consists of subunits A, B and C. Subunit B contains selenocysteine and a pyruvoyl group, and is responsible for sarcosine binding and methylamine release. Subunit A, which also contains selenocysteine, is reduced by thioredoxin, and is needed to convert the carboxymethyl group into a ketene equivalent, in turn used by subunit C to produce acetyl phosphate. Only subunit B distinguishes this enzyme from EC 1.21.4.2 (glycine reductase) and EC 1.21.4.4 (betaine reductase).
References: [4079, 1572]

[EC 1.21.4.3 created 2003]

EC 1.21.4.4

- Accepted name:** betaine reductase
Reaction: acetyl phosphate + trimethylamine + thioredoxin disulfide + H₂O = betaine + phosphate + thioredoxin
Other name(s): acetyl-phosphate trimethylamine:thioredoxin disulfide oxidoreductase (*N,N,N*-trimethylglycine-forming)
Systematic name: acetyl-phosphate trimethylamine:thioredoxin disulfide oxidoreductase (betaine-forming)
Comments: The reaction is observed only in the direction of betaine reduction. The enzyme from *Eubacterium acidaminophilum* consists of subunits A, B and C. Subunit B contains selenocysteine and a pyruvoyl group, and is responsible for betaine binding and trimethylamine release. Subunit A, which also contains selenocysteine, is reduced by thioredoxin, and is needed to convert the carboxymethyl group into a ketene equivalent, in turn used by subunit C to produce acetyl phosphate. Only subunit B distinguishes this enzyme from EC 1.21.4.2 (glycine reductase) and EC 1.21.4.3 (sarcosine reductase).
References: [4079, 240]

[EC 1.21.4.4 created 2003, modified 2010]

EC 1.21.4.5

- Accepted name:** tetrachlorohydroquinone reductive dehalogenase
Reaction: (1) 2,6-dichlorohydroquinone + Cl⁻ + glutathione disulfide = 2,3,6-trichlorohydroquinone + 2 glutathione
(2) 2,3,6-trichlorohydroquinone + Cl⁻ + glutathione disulfide = 2,3,5,6-tetrachlorohydroquinone + 2 glutathione
Other name(s): *pcpC* (gene name)
Systematic name: glutathione disulfide:2,6-dichlorohydroquinone (chlorinating)

Comments: The enzyme, characterized from the bacterium *Sphingobium chlorophenicum*, converts tetrachloro-hydroquinone to 2,6-dichlorohydroquinone in two steps, via 2,3,6-trichlorohydroquinone, using glutathione as the reducing agent. The enzyme is sensitive to oxidation - when an internal L-cysteine residue is oxidized, the enzyme produces 2,3,5-trichloro-6-(glutathion-S-yl)-hydroquinone and 2,6-dichloro-3-(glutathion-S-yl)-hydroquinone instead of its normal products.

References: [4294, 2477]

[EC 1.21.4.5 created 2018]

EC 1.21.98 With other, known, physiological acceptors

EC 1.21.98.1

Accepted name: cyclic dehydroporphyrinyl futalosine synthase
Reaction: dehydroporphyrin futalosine + *S*-adenosyl-L-methionine = cyclic dehydroporphyrin futalosine + 5'-deoxyadenosine + L-methionine
Other name(s): MqnC; dehydroporphyrinyl futalosine cyclase
Systematic name: dehydroporphyrin futalosine:*S*-adenosyl-L-methionine oxidoreductase (cyclizing)
Comments: This enzyme is a member of the 'AdoMet radical' (radical SAM) family. The enzyme, found in several bacterial species, is part of the futalosine pathway for menaquinone biosynthesis.
References: [1519, 654]

[EC 1.21.98.1 created 2014 as EC 1.21.99.2, transferred 2014 to EC 1.21.98.1]

EC 1.21.98.2

Accepted name: dichlorochromopyrrolate synthase
Reaction: 2 3-(7-chloroindol-3-yl)-2-imino-propanoate + H₂O₂ = dichlorochromopyrrolate + NH₃ + 2 H₂O
Other name(s): RebD; chromopyrrolic acid synthase; chromopyrrolate synthase
Systematic name: 3-(7-chloroindol-3-yl)-2-imino-propanoate ammonia-lyase (dichlorochromopyrrolate-forming)
Comments: This enzyme catalyses a step in the biosynthesis of rebeccamycin, an indolocarbazole alkaloid produced by the bacterium *Lechevalieria aerocolonigenes*. The enzyme is a dimeric heme-protein oxidase that catalyses the oxidative dimerization of two L-tryptophan-derived molecules to form dichlorochromopyrrolic acid, the precursor for the fused six-ring indolocarbazole scaffold of rebeccamycin [2802]. Contains one molecule of heme *b* per monomer, as well as non-heme iron that is not part of an iron-sulfur center [1585]. *In vivo* the enzyme uses hydrogen peroxide, formed by the enzyme upstream in the biosynthetic pathway (EC 1.4.3.23, 7-chloro-L-tryptophan oxidase) as the electron acceptor. However, the enzyme is also able to catalyse the reaction using molecular oxygen [3607].
References: [2802, 1585, 3607]

[EC 1.21.98.2 created 2010 as EC 4.3.1.26, transferred 2013 to EC 1.21.3.9, transferred 2016 to EC 1.21.98.2]

EC 1.21.98.3

Accepted name: anaerobic magnesium-protoporphyrin IX monomethyl ester cyclase
Reaction: magnesium-protoporphyrin IX 13-monomethyl ester + 3 *S*-adenosyl-L-methionine + H₂O = 3,8-divinyl protochlorophyllide *a* + 3 5'-deoxyadenosine + 3 L-methionine (overall reaction)
(1a) magnesium-protoporphyrin IX 13-monomethyl ester + *S*-adenosyl-L-methionine + H₂O = 13¹-hydroxy-magnesium-protoporphyrin IX 13-monomethyl ester + 5'-deoxyadenosine + L-methionine
(1b) 13¹-hydroxy-magnesium-protoporphyrin IX 13-monomethyl ester + *S*-adenosyl-L-methionine = 13¹-oxo-magnesium-protoporphyrin IX 13-monomethyl ester + 5'-deoxyadenosine + L-methionine
(1c) 13¹-oxo-magnesium-protoporphyrin IX 13-monomethyl ester + *S*-adenosyl-L-methionine = 3,8-divinyl protochlorophyllide *a* + 5'-deoxyadenosine + L-methionine
Other name(s): *bchE* (gene name); MPE cyclase (ambiguous)

Systematic name: magnesium-protoporphyrin-IX 13-monomethyl ester,*S*-adenosyl-L-methionine:H₂O oxidoreductase (hydroxylating)

Comments: This radical AdoMet enzyme participates in the biosynthesis of chlorophyllide *a* in anaerobic bacteria, catalysing the formation of an isocyclic ring. Contains a [4Fe-4S] cluster and a cobalamin cofactor. The same transformation is achieved in aerobic organisms by the oxygen-dependent EC 1.14.13.81, magnesium-protoporphyrin IX monomethyl ester (oxidative) cyclase. Some facultative phototrophic bacteria, such as *Rubrivivax gelatinosus*, possess both enzymes.

References: [4346, 1251, 2916, 350]

[EC 1.21.98.3 created 2016]

EC 1.21.98.4

Accepted name: PqqA peptide cyclase

Reaction: a PqqA peptide + *S*-adenosyl-L-methionine = a PqqA peptide with linked Glu-Tyr residues + 5'-deoxyadenosine + L-methionine

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

Systematic name: PqqA peptide:*S*-adenosyl-L-methionine oxidoreductase (cyclizing)

Comments: This bacterial enzyme, which is a member of the radical SAM protein family, catalyses the formation of a C-C bond between C-4 of glutamate and C-3 of tyrosine residues of the PqqA protein (which are separated by three amino acid residues). This is the first enzymic step in the biosynthesis of the bacterial enzyme cofactor pyrroloquinoline quinone (PQQ). The reaction is dependent on the presence of a reductant (flavodoxin) and the accessory protein PqqD.

References: [4154, 2146, 204]

[EC 1.21.98.4 created 2018]

EC 1.21.99 With unknown physiological acceptors

EC 1.21.99.1

Accepted name: β-cyclopiazonate dehydrogenase

Reaction: β-cyclopiazonate + acceptor = α-cyclopiazonate + reduced acceptor

Other name(s): β-cyclopiazonate oxidocyclase; β-cyclopiazonic oxidocyclase; β-cyclopiazonate:(acceptor) oxidoreductase (cyclizing)

Systematic name: β-cyclopiazonate:acceptor oxidoreductase (cyclizing)

Comments: A flavoprotein (FAD). Cytochrome *c* and various dyes can act as acceptor. Cyclopiazonate is a microbial toxin.

References: [920, 3341]

[EC 1.21.99.1 created 1976 as EC 1.3.99.9, transferred 2002 to EC 1.21.99.1]

[1.21.99.2 *Transferred entry. EC 1.21.99.2, cyclic dehydropoxanthinyl futasolose synthase. Now classified as EC 1.21.98.1, cyclic dehydropoxanthinyl futasolose synthase.*]

[EC 1.21.99.2 created 2014, deleted 2014]

EC 1.21.99.3

Accepted name: thyroxine 5-deiodinase

Reaction: 3,3',5'-triiodo-L-thyronine + iodide + acceptor + H⁺ = L-thyroxine + reduced acceptor

Other name(s): diiodothyronine 5'-deiodinase (ambiguous); iodothyronine 5-deiodinase; iodothyronine inner ring monodeiodinase; type III iodothyronine deiodinase

Systematic name: 3,3',5'-triiodo-L-thyronine,iodide:acceptor oxidoreductase (iodinating)

Comments: The enzyme activity has only been demonstrated in the direction of 5-deiodination. This removal of the 5-iodine, i.e. from the inner ring, largely inactivates the hormone thyroxine.

References: [613, 2032]

[EC 1.21.99.3 created 2003 as EC 1.97.1.11, transferred 2015 to EC 1.21.99.3]

EC 1.21.99.4

- Accepted name:** thyroxine 5'-deiodinase
Reaction: 3,3',5-triiodo-L-thyronine + iodide + acceptor + H⁺ = L-thyroxine + reduced acceptor
Other name(s): diiodothyronine 5'-deiodinase [ambiguous]; iodothyronine 5'-deiodinase; iodothyronine outer ring monodeiodinase; type I iodothyronine deiodinase; type II iodothyronine deiodinase; thyroxine 5-deiodinase [misleading]; L-thyroxine iodohydrolase (reducing)
Systematic name: 3,3',5-triiodo-L-thyronine,iodide:acceptor oxidoreductase (iodinating)
Comments: The enzyme activity has only been demonstrated in the direction of 5'-deiodination, which renders the thyroid hormone more active. The enzyme consists of type I and type II enzymes, both containing selenocysteine, but with different kinetics. For the type I enzyme the first reaction is a reductive deiodination converting the -Se-H group of the enzyme into an -Se-I group; the reductant then reconverts this into -Se-H, releasing iodide.
References: [613, 1248, 3554, 2032]

[EC 1.21.99.4 created 1984 as EC 3.8.1.4, transferred 2003 to EC 1.97.1.10, transferred 2015 to EC 1.21.99.4]

EC 1.21.99.5

- Accepted name:** tetrachloroethene reductive dehalogenase
Reaction: trichloroethene + chloride + acceptor = tetrachloroethene + reduced acceptor
Other name(s): tetrachloroethene reductase
Systematic name: acceptor:trichloroethene oxidoreductase (chlorinating)
Comments: This enzyme allows the common pollutant tetrachloroethene to support bacterial growth and is responsible for disposal of a number of chlorinated hydrocarbons. The reaction occurs in the reverse direction. The enzyme also reduces trichloroethene to dichloroethene. Although the physiological reductant is unknown, the supply of reductant in some organisms involves menaquinol, which is reduced by molecular hydrogen via the action of EC 1.12.5.1, hydrogen:quinone oxidoreductase. The enzyme contains a corrinoid and two iron-sulfur clusters. Methylviologen can act as electron donor *in vitro*.
References: [1543, 1224, 2769, 3404, 3403]

[EC 1.21.99.5 created 2001 as EC 1.97.1.8, transferred 2017 to EC 1.21.99.5]

EC 1.22 Acting on halogen in donors

EC 1.22.1 With NAD⁺ or NADP⁺ as acceptor

[1.22.1.1 Transferred entry. iodytyrosine deiodinase. Now EC 1.21.1.1, iodytyrosine deiodinase]

[EC 1.22.1.1 created 2010, deleted 2015]

EC 1.23 Reducing C-O-C group as acceptor

EC 1.23.1 With NADH or NADPH as donor

EC 1.23.1.1

- Accepted name:** (+)-pinoresinol reductase
Reaction: (+)-lariciresinol + NADP⁺ = (+)-pinoresinol + NADPH + H⁺

Other name(s): pinoresinol/lariciresinol reductase; pinoresinol-lariciresinol reductases; (+)-pinoresinol/(+)-lariciresinol; (+)-pinoresinol-(+)-lariciresinol reductase; PLR
Systematic name: (+)-lariciresinol:NADP⁺ oxidoreductase
Comments: The reaction is catalysed *in vivo* in the opposite direction to that shown. A multifunctional enzyme that further reduces the product to the lignan (–)-secoisolariciresinol [EC 1.23.1.2, (+)-lariciresinol reductase]. Isolated from the plants *Forsythia intermedia* [619, 832], *Thuja plicata* (western red cedar) [1098], *Linum perenne* (perennial flax) [1474] and *Linum corymbulosum* [224]. The 4-*pro-R* hydrogen of NADH is transferred to the 7-*pro-R* position of lariciresinol [619].
References: [619, 832, 1098, 2551, 1474, 224]

[EC 1.23.1.1 created 2013]

EC 1.23.1.2

Accepted name: (+)-lariciresinol reductase
Reaction: (–)-secoisolariciresinol + NADP⁺ = (+)-lariciresinol + NADPH + H⁺
Other name(s): pinoresinol/lariciresinol reductase; pinoresinol-lariciresinol reductases; (+)-pinoresinol/(+)-lariciresinol; (+)-pinoresinol-(+)-lariciresinol reductase; PLR
Systematic name: (–)-secoisolariciresinol:NADP⁺ oxidoreductase
Comments: The reaction is catalysed *in vivo* in the opposite direction to that shown. A multifunctional enzyme that also reduces (+)-pinoresinol [EC 1.23.1.1, (+)-pinoresinol reductase]. Isolated from the plants *Forsythia intermedia* [619, 832], *Thuja plicata* (western red cedar) [1098], *Linum perenne* (perennial flax) [1474] and *Linum corymbulosum* [224].
References: [619, 832, 1098, 2551, 1474, 224]

[EC 1.23.1.2 created 2013]

EC 1.23.1.3

Accepted name: (–)-pinoresinol reductase
Reaction: (–)-lariciresinol + NADP⁺ = (–)-pinoresinol + NADPH + H⁺
Other name(s): pinoresinol/lariciresinol reductase; pinoresinol-lariciresinol reductases; (–)-pinoresinol-(–)-lariciresinol reductase; PLR
Systematic name: (–)-lariciresinol:NADP⁺ oxidoreductase
Comments: The reaction is catalysed *in vivo* in the opposite direction to that shown. A multifunctional enzyme that usually further reduces the product to (+)-secoisolariciresinol [EC 1.23.1.4, (–)-lariciresinol reductase]. Isolated from the plants *Thuja plicata* (western red cedar) [1098], *Linum perenne* (perennial flax) [1474] and *Arabidopsis thaliana* (thale cress) [2719].
References: [1098, 1474, 2719]

[EC 1.23.1.3 created 2013]

EC 1.23.1.4

Accepted name: (–)-lariciresinol reductase
Reaction: (+)-secoisolariciresinol + NADP⁺ = (–)-lariciresinol + NADPH + H⁺
Other name(s): pinoresinol/lariciresinol reductase; pinoresinol-lariciresinol reductases; (–)-pinoresinol-(–)-lariciresinol reductase; PLR
Systematic name: (+)-secoisolariciresinol:NADP⁺ oxidoreductase
Comments: The reaction is catalysed *in vivo* in the opposite direction to that shown. A multifunctional enzyme that also reduces (–)-pinoresinol [EC 1.23.1.3, (–)-pinoresinol reductase]. Isolated from the plants *Thuja plicata* (western red cedar) [1098] and *Linum corymbulosum* [1474].
References: [1098, 1474]

[EC 1.23.1.4 created 2013]

EC 1.23.5 With a quinone or similar compound as acceptor

EC 1.23.5.1

- Accepted name:** violaxanthin de-epoxidase
Reaction: violaxanthin + 2 L-ascorbate = zeaxanthin + 2 L-dehydroascorbate + 2 H₂O (overall reaction)
(1a) violaxanthin + L-ascorbate = antheraxanthin + L-dehydroascorbate + H₂O
(1b) antheraxanthin + L-ascorbate = zeaxanthin + L-dehydroascorbate + H₂O
- Other name(s):** VDE
Systematic name: violaxanthin:ascorbate oxidoreductase
Comments: Along with EC 1.14.15.21, zeaxanthin epoxidase, this enzyme forms part of the xanthophyll (or violaxanthin) cycle for controlling the concentration of zeaxanthin in chloroplasts. It is activated by a low pH of the thylakoid lumen (produced by high light intensity). Zeaxanthin induces the dissipation of excitation energy in the chlorophyll of the light-harvesting protein complex of photosystem II. In higher plants the enzyme reacts with *all-trans*-diepoxides, such as violaxanthin, and *all-trans*-monoepoxides, but in the alga *Mantoniella squamata*, only the diepoxides are good substrates.
References: [4315, 3208, 443, 2103, 2148, 1247, 2147]

[EC 1.23.5.1 created 2005 as EC 1.10.99.3, transferred 2015 to EC 1.23.5.1]

EC 1.97 Other oxidoreductases

This subclass contains a single sub-subclass (EC 1.97.1) and is reserved for oxidoreductases not included in the previous categories.

EC 1.97.1 Sole sub-subclass for oxidoreductases that do not belong in the other subclasses

EC 1.97.1.1

- Accepted name:** chlorate reductase
Reaction: reduced acceptor + chlorate = acceptor + H₂O + chlorite
Other name(s): chlorate reductase C
Systematic name: chlorite:acceptor oxidoreductase
Comments: Flavins or benzylviologen can act as acceptor.
References: [153]

[EC 1.97.1.1 created 1978]

EC 1.97.1.2

- Accepted name:** pyrogallol hydroxytransferase
Reaction: 1,2,3,5-tetrahydroxybenzene + 1,2,3-trihydroxybenzene = 1,3,5-trihydroxybenzene + 1,2,3,5-tetrahydroxybenzene
Other name(s): 1,2,3,5-tetrahydroxybenzene hydroxyltransferase; 1,2,3,5-tetrahydroxybenzene:pyrogallol transhydroxylase; 1,2,3,5-tetrahydroxybenzene-pyrogallol hydroxyltransferase (transhydroxylase); pyrogallol hydroxyltransferase; 1,2,3,5-tetrahydroxybenzene:1,2,3-trihydroxybenzene hydroxyltransferase
Systematic name: 1,2,3,5-tetrahydroxybenzene:1,2,3-trihydroxybenzene hydroxytransferase
Comments: 1,2,3,5-Tetrahydroxybenzene acts as a co-substrate for the conversion of pyrogallol into phloroglucinol, and for a number of similar isomerizations. The enzyme is provisionally listed here, but might be considered as the basis for a new class in the transferases, analogous to the aminotransferases.
References: [428]

[EC 1.97.1.2 created 1992]

[1.97.1.3 Transferred entry. sulfur reductase. Now EC 1.12.98.4, sulfhydrogenase, since hydrogen is known to be the electron donor.]

[EC 1.97.1.3 created 1992, deleted 2013]

EC 1.97.1.4

Accepted name: [formate-*C*-acetyltransferase]-activating enzyme
Reaction: *S*-adenosyl-L-methionine + dihydroflavodoxin + [formate *C*-acetyltransferase]-glycine = 5'-deoxyadenosine + L-methionine + flavodoxin semiquinone + [formate *C*-acetyltransferase]-glycyl radical
Other name(s): PFL activase; PFL-glycine:*S*-adenosyl-L-methionine H transferase (flavodoxin-oxidizing, *S*-adenosyl-L-methionine-cleaving); formate acetyltransferase activating enzyme; formate acetyltransferase-glycine dihydroflavodoxin:*S*-adenosyl-L-methionine oxidoreductase (*S*-adenosyl-L-methionine cleaving); pyruvate formate-lyase activating enzyme; pyruvate formate-lyase 1 activating enzyme
Systematic name: [formate *C*-acetyltransferase]-glycine dihydroflavodoxin:*S*-adenosyl-L-methionine oxidoreductase (*S*-adenosyl-L-methionine cleaving)
Comments: An iron-sulfur protein. A single glycine residue in EC 2.3.1.54, formate *C*-acetyltransferase, is oxidized to the corresponding radical by transfer of H from its CH₂ to AdoMet with concomitant cleavage of the latter. The reaction requires Fe²⁺. The first stage is reduction of the AdoMet to give methionine and the 5'-deoxyadenosin-5'-yl radical, which then abstracts a hydrogen radical from the glycine residue.
References: [1064, 4078, 1066]

[EC 1.97.1.4 created 1999, modified 2004]

[1.97.1.5 Transferred entry. arsenate reductase (glutaredoxin). Now EC 1.20.4.1, arsenate reductase (glutaredoxin)]

[EC 1.97.1.5 created 2000 deleted 2001]

[1.97.1.6 Transferred entry. arsenate reductase (donor). Now EC 1.20.99.1, arsenate reductase (donor)]

[EC 1.97.1.6 created 2000 deleted 2001]

[1.97.1.7 Transferred entry. methylarsonate reductase. Now EC 1.20.4.2, methylarsonate reductase]

[EC 1.97.1.7 created 2000, deleted 2001]

[1.97.1.8 Transferred entry. tetrachloroethene reductive dehalogenase. Now EC 1.21.99.5, tetrachloroethene reductive dehalogenase]

[EC 1.97.1.8 created 2001, deleted 2017]

EC 1.97.1.9

Accepted name: selenate reductase
Reaction: selenite + H₂O + acceptor = selenate + reduced acceptor
Systematic name: selenite:reduced acceptor oxidoreductase
Comments: The periplasmic enzyme from *Thauera selenatis* is a complex comprising three heterologous subunits (α , β and γ) that contains molybdenum, iron, acid-labile sulfide and heme b as cofactor constituents. Nitrate, nitrite, chlorate and sulfate are not substrates. A number of compounds, including acetate, lactate, pyruvate, and certain sugars, amino acids, fatty acids, di- and tricarboxylic acids, and benzoate can serve as electron donors.
References: [3393, 2351, 2051, 3663]

[EC 1.97.1.9 created 2003]

[1.97.1.10 Transferred entry. thyroxine 5'-deiodinase. Now EC 1.21.99.4 thyroxine 5'-deiodinase]

[EC 1.97.1.10 created 1984 as EC 3.8.1.4, transferred 2003 to EC 1.97.1.10, deleted 2015]

[1.97.1.11 *Transferred entry. thyroxine 5-deiodinase. Now EC 1.21.99.3 thyroxine 5-deiodinase.*]

[EC 1.97.1.11 created 2003, deleted 2015]

EC 1.97.1.12

Accepted name: photosystem I
Reaction: reduced plastocyanin + oxidized ferredoxin + $h\nu$ = oxidized plastocyanin + reduced ferredoxin
Systematic name: plastocyanin:ferredoxin oxidoreductase (light-dependent)
Comments: Contains chlorophyll, phylloquinones, carotenoids and [4Fe-4S] clusters. Cytochrome c_6 can act as an alternative electron donor, and flavodoxin as an alternative acceptor in some species.
References: [3779, 4013, 598, 78]

[EC 1.97.1.12 created 2011]

EC 1.98 Enzymes using H_2 as reductant (deleted subclass)

EC 1.98.1 Enzymes using H_2 as reductant (deleted subclass)

[1.98.1.1 *Transferred entry. Now EC 1.12.7.2, ferredoxin hydrogenase*]

[EC 1.98.1.1 created 1961, deleted 1965]

EC 1.99 Other enzymes using O_2 as oxidant (deleted subclass)

EC 1.99.1 Hydroxylases (now covered by EC 1.14)

[1.99.1.1 *Transferred entry. Now EC 1.12.7.2, ferredoxin hydrogenase*]

[EC 1.99.1.1 created 1961, deleted 1965]

[1.99.1.2 *Transferred entry. Now EC 1.14.16.1, phenylalanine 4-monooxygenase*]

[EC 1.99.1.2 created 1961, deleted 1965]

[1.99.1.3 *Deleted entry. nicotinate 6-hydroxylase*]

[EC 1.99.1.3 created 1961, deleted 1965]

[1.99.1.4 *Deleted entry. tryptophan 5-hydroxylase*]

[EC 1.99.1.4 created 1961, deleted 1965]

[1.99.1.5 *Transferred entry. Now EC 1.14.13.9, kynurenine 3-monooxygenase*]

[EC 1.99.1.5 created 1961, deleted 1965]

[1.99.1.6 *Deleted entry. steroid 11 α -hydroxylase*]

[EC 1.99.1.6 created 1961, deleted 1965]

[1.99.1.7 *Transferred entry. Now EC 1.14.15.4, steroid 11 β -monooxygenase*]

[EC 1.99.1.7 created 1961, deleted 1965]

[1.99.1.8 *Deleted entry. steroid 6 β -hydroxylase*]

[EC 1.99.1.8 created 1961, deleted 1965]

[1.99.1.9 *Transferred entry. Now EC 1.14.99.9, steroid 17 α -monooxygenase*]

[EC 1.99.1.9 created 1961, deleted 1965]

[1.99.1.10 *Deleted entry. steroid 19-hydroxylase*]

[EC 1.99.1.10 created 1961, deleted 1965]

[1.99.1.11 *Transferred entry. Now EC 1.14.99.10, steroid 21-monooxygenase*]

[EC 1.99.1.11 created 1961, deleted 1965]

[1.99.1.12 *Deleted entry. alkoxyaryl hydroxylase*]

[EC 1.99.1.12 created 1961, deleted 1965]

[1.99.1.13 *Deleted entry. squalene cyclohydroxylase, covered by EC 1.14.99.7 (squalene monooxygenase) and by EC 5.4.99.7 (lanosterol synthase)*]

[EC 1.99.1.13 created 1961, deleted 1965]

[1.99.1.14 *Transferred entry. Now EC 1.13.11.27, 4-hydroxyphenylpyruvate dioxygenase*]

[EC 1.99.1.14 created 1961, deleted 1965]

EC 1.99.2 Oxygenases (now covered by EC 1.13)

[1.99.2.1 *Transferred entry. Now EC 1.13.11.12, lipoxygenase*]

[EC 1.99.2.1 created 1961, deleted 1965]

[1.99.2.2 *Transferred entry. Now EC 1.13.11.1, catechol 1,2-dioxygenase*]

[EC 1.99.2.2 created 1961, deleted 1965]

[1.99.2.3 *Transferred entry. Now EC 1.13.11.3, protocatechuate 3,4-dioxygenase*]

[EC 1.99.2.3 created 1961, deleted 1965]

[1.99.2.4 *Transferred entry. Now EC 1.13.11.4, gentisate 1,2-dioxygenase*]

[EC 1.99.2.4 created 1961, deleted 1965]

[1.99.2.5 *Transferred entry. Now EC 1.13.11.5, homogentisate 1,2-dioxygenase*]

[EC 1.99.2.5 created 1961, deleted 1965]

[1.99.2.6 *Transferred entry. Now EC 1.13.99.1, inositol oxygenase*]

[EC 1.99.2.6 created 1961, deleted 1965]

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