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;

nase; 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: [424, 1953, 3035, 4121, 4257]

[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 sec-

ondary alcohols. May be identical with EC 1.1.1.19 (L-glucuronate reductase), EC 1.1.1.33 [meval-date reductase (NADPH)] and EC 1.1.1.55 [lactaldehyde reductase (NADPH)]. *Re*-specific with re-

spect to NADPH.

References: [400, 875, 3484, 4157]

[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: [346, 4007, 4440]

[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; butyleneglycol dehydrogenase; D-butanediol dehydrogenase; D-butan

lene 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⁺ oxidoreduc-

tase; 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: [4059, 4228]

[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: [148, 506, 2488]

[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: [3796]

[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-glycerophosphate dehydrogenase; L-glycerophosphate 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: [214, 451, 3127, 4546, 60, 2188]

[EC 1.1.1.8 created 1961, modified 2005]

Accepted name: D-xylulose reductase

Reaction: $xylitol + NAD^+ = D-xylulose + NADH + H^+$

Other name(s): NAD⁺-dependent xylitol dehydrogenase; xylitol dehydrogenase (ambiguous); erythritol dehydrogenase

nase; 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: [649, 1639, 1882]

[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: [955, 1639, 1697, 4316]

[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: [2487, 4666]

[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: [649, 650]

[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: [650]

[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-iditol:NAD⁺ 5-oxidoreductase; L-iditol (sorbitol)

dehydrogenase; glucitol dehydrogenase; L-iditol:NAD+ oxidoreductase; NAD+-dependent sorbitol

dehydrogenase; NAD+-sorbitol dehydrogenase

Systematic name: L-iditol:NAD⁺ 2-oxidoreductase

Comments: This enzyme is widely distributed and has been described in archaea, bacteria, yeast, plants and an-

imals. It acts on a number of sugar alcohols, including (but not limited to) L-iditol, 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: [183, 499, 2413, 3036, 3126, 3056]

[EC 1.1.1.14 created 1961, modified 2011]

EC 1.1.1.15

Accepted name: D-iditol 2-dehydrogenase

Reaction: D-iditol + NAD⁺ = D-sorbose + NADH + H⁺

Other name(s): D-sorbitol dehydrogenase

Systematic name: D-iditol:NAD+ 2-oxidoreductase

Comments: Also converts xylitol into L-xylulose and L-glucitol into L-fructose.

References: [3832]

[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: [3832, 4615]

[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: [2656, 4653, 4654]

[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: [302, 2355, 4448]

[EC 1.1.1.18 created 1961]

Accepted name: glucuronate reductase

Reaction: L-gulonate + NADP $^+$ = D-glucuronate + NADPH + H $^+$

Other name(s): L-hexonate: NADP dehydrogenase; TPN-L-gulonate dehydrogenase; NADP-L-gulonate dehydrogenase; TPN-L-gulonate dehydrogenase; NADP-L-gulonate dehydrogenase; TPN-L-gulonate dehydrogenase; NADP-L-gulonate de

nase; 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: [3919, 4470, 4804]

[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: [4138]

[EC 1.1.1.20 created 1961]

EC 1.1.1.21

Accepted name: aldose reductase

Reaction: alditol + NAD(P)⁺ = aldose + NAD(P)H + H⁺

Other name(s): polyol dehydrogenase (NADP⁺); ALR2; alditol:NADP⁺ oxidoreductase; alditol:NADP⁺ 1-

oxidoreductase; NADPH-aldopentose reductase; NADPH-aldose reductase; aldehyde reductase (mis-

leading)

Systematic name: alditol:NAD(P) $^+$ 1-oxidoreductase

Comments: Has wide specificity. **References:** [152, 372, 1630, 3712]

[EC 1.1.1.21 created 1961 (EC 1.1.1.139 created 1972, incorporated 1978), modified 2019]

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

 $\label{eq:comments:} \textbf{Comments:} \quad \text{Also acts on UDP-α-D-2-deoxyglucose}.$

References: [970, 2728, 4072, 4073]

[EC 1.1.1.22 created 1961]

EC 1.1.1.23

Accepted name: histidinol dehydrogenase

Reaction: L-histidinol + 2 NAD⁺ + $H_2O = L$ -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: [21, 22, 2538, 4829]

[EC 1.1.1.23 created 1961]

EC 1.1.1.24

Accepted name: quinate/shikimate dehydrogenase (NAD⁺)

Reaction: L-quinate + NAD $^+$ = 3-dehydroquinate + NADH + H $^+$

Other name(s): quinate dehydrogenase (ambiguous); quinic dehydrogenase (ambiguous); quinate:NAD oxidoreduc-

tase; quinate 5-dehydrogenase (ambiguous); quinate:NAD+ 5-oxidoreductase

Systematic name: L-quinate:NAD⁺ 3-oxidoreductase

Comments: The enzyme, found mostly in bacteria (mostly, but not exclusively in Gram-positive bacteria),

fungi, and plants, participates in the degradation of quinate and shikimate with a strong preference for NAD⁺ as a cofactor. While the enzyme can act on both quinate and shikimate, activity is higher with the former. *cf.* EC 1.1.5.8, quinate/shikimate dehydrogenase (quinone), EC 1.1.1.282, quinate/shikimate dehydrogenase [NAD(P)⁺], and EC 1.1.1.25, shikimate dehydrogenase (NADP⁺).

References: [2833, 1266, 1569, 3910, 4243, 2272, 3280]

[EC 1.1.1.24 created 1961, modified 1976, modified 2004, modified 2021]

EC 1.1.1.25

Accepted name: shikimate dehydrogenase (NADP⁺)

Reaction: shikimate + NADP $^+$ = 3-dehydroshikimate + NADPH + H $^+$

Other name(s): shikimate dehydrogenase; dehydroshikimic reductase; shikimate oxidoreductase; shikimate:NADP⁺

oxidoreductase; 5-dehydroshikimate reductase; shikimate 5-dehydrogenase; 5-dehydroshikimic re-

ductase; DHS reductase; shikimate:NADP+ 5-oxidoreductase; AroE

Systematic name: shikimate:NADP⁺ 3-oxidoreductase

Comments: NAD⁺ cannot replace NADP⁺ [200]. In higher organisms, this enzyme forms part of a multienzyme

complex with EC 4.2.1.10, 3-dehydroquinate dehydratase [617]. *cf.* EC 1.1.1.24, quinate/shikimate dehydrogenase (NAD⁺), EC 1.1.5.8, quinate/shikimate dehydrogenase (quinone), and EC 1.1.1.282,

quinate/shikimate dehydrogenase $[NAD(P)^+]$.

References: [2833, 4776, 200, 617, 110, 4783]

[EC 1.1.1.25 created 1961, modified 1976, modified 2004, modified 2021]

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: [4866, 4867]

[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 dehydro-

genase; 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: [882, 1072, 1689, 3702]

[EC 1.1.1.27 created 1961]

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: [882]

[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: [1704, 4000]

[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 de-

hydrogenase; D- β -hydroxybutyrate dehydrogenase; D-3-hydroxybutyrate dehydrogenase; D-(-)-3-hydroxybutyrate dehydrogenase; β -hydroxybutyric acid dehydrogenase; 3-D-hydroxybutyrate dehydroxybutyrate dehydrox

drogenase; β-hydroxybutyric dehydrogenase

Systematic name: (R)-3-hydroxybutanoate:NAD⁺ oxidoreductase

Comments: Also oxidizes other 3-hydroxymonocarboxylic acids.

References: [299, 871, 2407]

[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: [3540]

[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: [3723]

[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)

(R)-mevalonate:NADP+ oxidoreductase **Systematic name:**

> May be identical with EC 1.1.1.2 [alcohol dehydrogenase (NADP⁺)]. **Comments:**

References: [726, 4470]

[EC 1.1.1.33 created 1961]

EC 1.1.1.34

hydroxymethylglutaryl-CoA reductase (NADPH) Accepted name:

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 phos-

> phate); 3-hydroxy-3-methylglutaryl-CoA reductase (ambiguous); β-hydroxy-β-methylglutaryl coenzyme A reductase (ambiguous); hydroxymethylglutaryl CoA reductase (NADPH); S-3-hydroxy-3methylglutaryl-CoA reductase (ambiguous); NADPH-hydroxymethylglutaryl-CoA reductase; HMG-CoA reductase-mevalonate: NADP-oxidoreductase (acetylating-CoA); 3-hydroxy-3-methylglutaryl

CoA reductase (NADPH); hydroxymethylglutaryl-CoA reductase (NADPH₂)

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

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: [486, 990, 2040]

[EC 1.1.1.34 created 1961]

EC 1.1.1.35

Accepted name: 3-hydroxyacyl-CoA dehydrogenase

(S)-3-hydroxyacyl-CoA + NAD⁺ = 3-oxoacyl-CoA + NADH + H⁺ Reaction:

β-hydroxyacyl dehydrogenase; β-keto-reductase; 3-keto reductase; 3-hydroxyacyl coenzyme A de-Other name(s):

> hydrogenase; β-hydroxyacyl-coenzyme A synthetase; β-hydroxyacylcoenzyme A dehydrogenase; β-hydroxybutyrylcoenzyme A dehydrogenase; L-3hydroxyacyl 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 en-

zymes act, more slowly, with NADP⁺. Broad specificity to acyl chain-length (cf. EC 1.1.1.211 [long-

chain-3-hydroxyacyl-CoA dehydrogenase]).

References: [1656, 2406, 4024, 4492]

[EC 1.1.1.35 created 1961]

EC 1.1.1.36

Accepted name: acetoacetyl-CoA reductase

> (R)-3-hydroxyacyl-CoA + NADP⁺ = 3-oxoacyl-CoA + NADPH + H⁺ Reaction:

Other name(s): acetoacetyl coenzyme A reductase; hydroxyacyl coenzyme-A dehydrogenase; NADP-linked ace-

toacetyl 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: [4491]

[EC 1.1.1.36 created 1961]

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 dehydro

genase; 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 (ambiguous); L-malate-NAD⁺ oxidore-

ductase

Systematic name: (S)-malate:NAD⁺ oxidoreductase

Comments: There are several forms of malate dehydrogenases that differ by their use of substrate and cofac-

tors. This NAD $^+$ -dependent enzyme forms oxaloacetate and unlike EC 1.1.1.38, malate dehydrogenase (oxaloacetate-decarboxylating), is unable to convert it to pyruvate. Also oxidizes some other 2-hydroxydicarboxylic acids. cf. EC 1.1.1.82, malate dehydrogenase (NADP $^+$); EC 1.1.1.299, malate

dehydrogenase [NAD(P)⁺]; and EC 1.1.5.4, malate dehydrogenase (quinone).

References: [207, 1439, 2756, 4655]

[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 + CO_2

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: [2037, 4729]

[EC 1.1.1.38 created 1961]

EC 1.1.1.39

Accepted name: malate dehydrogenase (decarboxylating)

Reaction: (S)-malate + NAD⁺ = pyruvate + CO_2 + NADH

Other name(s): 'malic' enzyme (ambiguous); pyruvic-malic carboxylase (ambiguous); NAD-specific malic enzyme

(ambiguous); NAD-malic enzyme (ambiguous); malate dehydrogenase (decarboxylating) (ambigu-

ous)

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 exogeneously-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: [2596, 1432, 4568, 4567]

[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 + CO_2 + NADPH

(2) oxaloacetate = $pyruvate + CO_2$

Other name(s): 'malic' enzyme (ambiguous); pyruvic-malic carboxylase (ambiguous); malate dehydrogenase (de-

carboxylating, 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 di-

valent 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: [1529, 3130, 3609, 4028, 4029, 4496]

[EC 1.1.1.40 created 1961, modified 1976]

EC 1.1.1.41

Accepted name: isocitrate dehydrogenase (NAD⁺)

Reaction: isocitrate + NAD⁺ = 2-oxoglutarate + CO_2 + NADH

Other name(s): isocitric dehydrogenase; β-ketoglutaric-isocitric carboxylase; isocitric acid dehydrogenase; NAD de-

pendent 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⁺), oxalo-

succinate 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 [532]. The en-

zyme from some species can also use NADP⁺ but much more slowly [1813].

References: [1560, 2235, 3335, 3336, 3442, 4446, 532, 2114, 1813]

[EC 1.1.1.41 created 1961, modified 2005]

EC 1.1.1.42

Accepted name: isocitrate dehydrogenase (NADP⁺)

Reaction: isocitrate + NADP $^+$ = 2-oxoglutarate + CO $_2$ + NADPH + H $^+$ (overall reaction)

(1a) isocitrate + $NADP^+$ = oxalosuccinate + $NADPH + H^+$

(1b) oxalosuccinate = 2-oxoglutarate + CO_2

Other name(s): oxalosuccinate decarboxylase; oxalsuccinic decarboxylase; isocitrate (NADP) dehydrogenase; isoc-

itrate (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 isoci-

trate 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⁺), oxalo-

succinate 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 [532]. The en-

zyme from some species can also use NAD⁺ but much more slowly [532, 4010].

References: [37, 2913, 3335, 3899, 4446, 532, 4010, 2196, 581]

[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 dehy-

drogenase; 6-phosphogluconate dehydrogenase (NAD); 2-keto-6-phosphogluconate reductase

Systematic name: 6-phospho-D-gluconate:NAD(P)⁺ 2-oxidoreductase

References: [1160]

[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 car-

boxylase; 6-phosphogluconate dehydrogenase (decarboxylating); 6-phospho-D-gluconate dehydroge-

nase

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 pur-

pose 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: [903, 3353, 3772, 3773, 440, 4802, 4857]

[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 dehydroge-

nase

Systematic name: L-gulonate:NAD⁺ 3-oxidoreductase

Comments: Also oxidizes other L-3-hydroxyacids.

References: [994, 3932]

[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: [4576]

[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: [208, 441, 3266, 4060, 4275, 1215]

[EC 1.1.1.47 created 1961, modified 2013]

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: [2438, 1746]

[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; Zwischenferment; Zwischenferment; Zwischenferment; Zwischenferment; Zwischenferment; Zwischenferment; Zwischenferment; Zwischenferment; Zwischenferment; Zw

nase; 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: [1047, 1340, 1959, 3098, 2794, 3166, 1513, 1785, 1864, 669]

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

EC 1.1.1.50

Accepted name: 3α-hydroxysteroid 3-dehydrogenase (*Si*-specific)

Reaction: a 3α -hydroxysteroid + NAD(P)⁺ = a 3-oxosteroid + NAD(P)H + H⁺

Other name(s): hydroxyprostaglandin dehydrogenase; 3α-hydroxysteroid oxidoreductase; sterognost 3α; 3α-

hydroxysteroid dehydrogenase (B-specific); 3α-hydroxysteroid 3-dehydrogenase (B-specific); 3α-

hydroxysteroid:NAD(P)⁺ 3-oxidoreductase (B-specific)

Systematic name: 3α -hydroxysteroid:NAD(P)⁺ 3-oxidoreductase (*Si*-specific)

Comments: The enzyme acts on androsterone and other 3α -hydroxysteroids and on 9-, 11- and 15-

hydroxyprostaglandin. Si-specific with respect to NAD⁺ or NADP⁺. cf. EC 1.1.1.213, 3α-

hydroxysteroid 3-dehydrogenase (Re-specific).

References: [1892, 2180, 2647, 3287]

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

EC 1.1.1.51

Accepted name: $3(\text{or }17)\beta$ -hydroxysteroid dehydrogenase

Reaction: testosterone + NAD(P) $^+$ = androstenedione + NAD(P)H + H $^+$

Other name(s): β-hydroxy steroid dehydrogenase; 17-ketoreductase; 17β-hydroxy steroid dehydrogenase; 3β-

hydroxysteroid dehydrogenase; 3β-hydroxy steroid dehydrogenase

Systematic name: $3(\text{or }17)\beta$ -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 dehydroge-

nase.

References: [801, 2571, 2647, 3754, 4190]

[EC 1.1.1.51 created 1961]

Accepted name: 3α -hydroxycholanate dehydrogenase (NAD⁺)

Reaction: lithocholate + NAD⁺ = 3-oxo- 5β -cholan-24-oate + NADH + H⁺

Other name(s): α -hydroxy-cholanate dehydrogenase; lithocholate:NAD⁺ oxidoreductase; 3α -hydroxycholanate dehydrogenase; 3α -hydroxycholanate dehydrogenase; 3α -hydroxycholanate dehydrogenase; 3α -hydroxycholanate dehydroxycholanate dehydro

drogenase

Systematic name: lithocholate:NAD⁺ 3-oxidoreductase

Comments: Also acts on other 3α -hydroxysteroids with an acidic side-chain. cf. EC 1.1.1.392, 3α -

hydroxycholanate dehydrogenase (NADP⁺).

References: [1574]

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

EC 1.1.1.53

Accepted name: 3α(or 20β)-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; 20 β -hydroxy steroid dehydrogenase;

 Δ^4 -3-ketosteroid hydrogenase; 20 β -hydroxysteroid dehydrogenase; 3 α ,20 β -hydroxysteroid:NAD⁺-

oxidoreductase; NADH-20β-hydroxysteroid dehydrogenase; 20β-HSD

Systematic name: 3α (or 20β)-hydroxysteroid:NAD⁺ oxidoreductase

Comments: The 3α -hydroxy group or 20β -hydroxy group of pregnane and androstane steroids can act as donor.

References: [1021, 1760, 1761, 2571, 4064, 4150]

[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: [3206]

[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: [1450]

[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 en-

zyme with different properties); ribitol dehydrogenase D (mutant enzyme with different properties)

Systematic name: ribitol:NAD⁺ 2-oxidoreductase

References: [1697, 3104, 4666]

[EC 1.1.1.56 created 1965]

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: [1640, 2089]

[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: [1640]

[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: [877]

[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: [1372]

[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: [3072]

[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 dehydro-

genase; estradiol dehydrogenase; estrogen 17-oxidoreductase; 17 β -HSD; HSD17B7

Systematic name: 17β-estradiol:NAD(P) $^+$ 17-oxidoreductase

The enzyme oxidizes or reduces the hydroxy/keto group on C₁₇ of estrogens and androgens in mam-**Comments:**

> mals 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 [2650]. 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: [2039, 2347, 2650]

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

[1.1.1.63 Transferred entry. testosterone 17β -dehydrogenase. Now EC 1.1.1.239, $3\alpha(17\beta)$ -hydroxysteroid dehydrogenase (NAD^+)

[EC 1.1.1.63 created 1965, deleted 2012]

EC 1.1.1.64

Accepted name: testosterone 17β-dehydrogenase (NADP⁺)

> testosterone + $NADP^+$ = androstenedione + $NADPH + H^+$ Reaction:

Other name(s): 17-ketoreductase; NADP-dependent testosterone-17β-oxidoreductase; testosterone 17β-

dehydrogenase (NADP)

17β-hydroxysteroid:NADP⁺ 17-oxidoreductase **Systematic name:**

Comments: Also oxidizes 3-hydroxyhexobarbital to 3-oxohexobarbital.

References: [1044, 4149, 4452]

[EC 1.1.1.64 created 1965]

EC 1.1.1.65

Accepted name: pyridoxine 4-dehydrogenase

> **Reaction:** $pyridoxine + NADP^+ = pyridoxal + NADPH + H^+$

pyridoxin dehydrogenase; pyridoxol dehydrogenase; pyridoxine dehydrogenase Other name(s):

pyridoxine:NADP+ 4-oxidoreductase **Systematic name: Comments:** Also oxidizes pyridoxine phosphate.

> References: [1705]

> > [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: [1983, 2836]

[EC 1.1.1.66 created 1965]

EC 1.1.1.67

mannitol 2-dehydrogenase Accepted name:

Reaction: D-mannitol + NAD $^+$ = D-fructose + NADH + H $^+$ Other name(s): D-mannitol dehydrogenase; mannitol dehydrogenase

D-mannitol:NAD+ 2-oxidoreductase **Systematic name:**

> **References:** [2670]

> > [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: [77, 2437, 3156]

[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: [1115]

[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: [2234, 4299]

[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: [3542]

[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]

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:** [866, 4354, 4355]

[EC 1.1.1.75 created 1972]

EC 1.1.1.76

Accepted name: (*S*,*S*)-butanediol dehydrogenase

Reaction: (2S,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: [4228, 553, 4189]

[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: [4292]

[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: [4291, 3466]

[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: [567, 2152]

[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: [1735, 1736]

[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: [2150, 2151, 2201]

[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:** [721, 1932, 1933]

[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 (de-

carboxylating)

Systematic name: (*R*)-malate:NAD⁺ oxidoreductase (decarboxylating)

References: [4025]

[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 + CO_2 + NADH

Other name(s): β , β -dimethylmalate dehydrogenase

Systematic name: (*R*)-3,3-dimethylmalate:NAD⁺ oxidoreductase (decarboxylating) **Comments:** Requires K^+ or NH_4^+ and Mn^{2+} or Co^{2+} ; also acts on (*R*)-malate.

References: [2607]

[EC 1.1.1.84 created 1972]

Accepted name: 3-isopropylmalate dehydrogenase

Reaction: (2R,3S)-3-isopropylmalate + NAD⁺ = 4-methyl-2-oxopentanoate + CO₂ + NADH + H⁺ (overall reac-

tion)

(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 -isopropylmalate dehydrogenase; threo-D_s-3-isopropylmalate dehydrogenase

nase; 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: [501, 3248, 3041, 531]

[EC 1.1.1.85 created 1972, modified 1976]

EC 1.1.1.86

Accepted name: ketol-acid reductoisomerase (NADP⁺)

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

 $NADPH + H^{+}$

Other name(s): dihydroxyisovalerate dehydrogenase (isomerizing); acetohydroxy acid isomeroreductase; ketol acid

reductoisomerase; α -keto- β -hydroxylacyl reductoisomerase; 2-hydroxy-3-keto acid reductoisomerase; acetohydroxy 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: [130, 1652, 2126, 3675, 443]

[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: (1R,2S)-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; homoisoc-

itric dehydrogenase; (-)-1-hydroxy-1,2,4-butanetricarboxylate:NAD+ oxidoreductase (decarboxylat-

ing); 3-carboxy-2-hydroxyadipate:NAD⁺ oxidoreductase (decarboxylating); HICDH

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

Comments: Forms part of the lysine biosynthesis pathway in fungi [4851].

References: [4054, 3584, 4851]

[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 + $CoA + 2NAD^+ = 3$ -hydroxy-3-methylglutaryl- $CoA + 2NADH + 2H^+$

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

reductase (ambiguous); 3-hydroxy-3-methylglutaryl coenzyme A reductase (ambiguous); hydrox-

ymethylglutaryl coenzyme A reductase (ambiguous)

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

References: [1123]

[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 dehydro

genase

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: [4107, 4745]

[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 dehy-

drogenase; 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: [1426]

[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: [2200]

[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 Mn^{2+} and a monovalent cation.

References: [2203]

[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: [2140, 1015, 1016, 1017]

[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 de-

hydrogenase; 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 ser-

ine 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

[4900].

References: [3332, 4507, 3926, 4096, 3751, 4900, 9, 897]

[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 halo-

genated derivatives. Compounds with hydroxy or amino groups in the 3 or 5 position are inactive.

References: [4860]

[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: [1146]

[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: [2430]

[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: [2430]

[EC 1.1.1.99 created 1972]

EC 1.1.1.100

Accepted name: 3-oxoacyl-[acyl-carrier-protein] reductase

Reaction: a (3R)-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 -

doreductase

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: [3375, 3866, 4312]

[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; palmi-

toyl dihydroxyacetone phosphate reductase

Systematic name: 1-palmitoylglycerol-3-phosphate:NADP⁺ oxidoreductase

Comments: Also acts on alkylglycerone 3-phosphate and alkylglycerol 3-phosphate.

References: [2321]

[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 reduc-

tase; 3-oxosphinganine:NADPH oxidoreductase; D-3-oxosphinganine:B-NADPH oxidoreductase

Systematic name: D-erythro-dihydrosphingosine:NADP⁺ 3-oxidoreductase

References: [4039, 4040]

[EC 1.1.1.102 created 1972]

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 thre-

onine to glycine. This threonine-degradation pathway is common to prokaryotic and eukaryotic cells and the two enzymes involved form a complex [1542]. In aqueous solution, the product L-2-amino-3-

oxobutanoate can spontaneously decarboxylate to form aminoacetone.

References: [1397, 1542, 3054, 1057]

[EC 1.1.1.103 created 1972]

EC 1.1.1.104

Accepted name: 4-oxoproline reductase

Reaction: cis-4-hydroxy-L-proline + NAD⁺ = 4-oxo-L-proline + NADH + H⁺

Other name(s): *cis*-hydroxy-L-proline oxidase

Systematic name: *cis*-4-hydroxy-L-proline:NAD⁺ oxidoreductase (4-oxo-L-proline forming)

Comments: The enzyme, isolated from animals, is specific for 4-oxo-L-proline and *cis*-4-hydroxy-L-proline. It has

no activity with trans-4-hydroxy-L-proline.

References: [3946, 2319]

[EC 1.1.1.104 created 1972, modified 2022]

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]

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 pref-

erence 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 [1375]. No activity with 11-cis-retinol or 11-cis-retinal (cf. EC 1.1.1.315, 11-cis retinol dehydrogenase). Also active

with 3α -hydroxysteroids [1375].

References: [2190, 1375, 2721, 2396]

[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: [1362]

[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: [495]

[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: [157, 3745]

[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+ oxidore-

ductase

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: [1895, 1323, 364, 906, 936]

[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: [732, 743]

[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: $3(20)\alpha$ -Hydroxysteroids are also oxidized, more slowly.

References: [334, 1523]

[EC 1.1.1.112 created 1972]

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: [4367]

[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-apiose reductase; D-apiitol reductase

Systematic name: D-apiitol:NAD⁺ 1-oxidoreductase

References: [1508, 3029]

[EC 1.1.1.114 created 1972]

EC 1.1.1.115

Accepted name: ribose 1-dehydrogenase (NADP⁺)

Reaction: D-ribose + NADP⁺ + H_2O = 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: [3712, 3719]

[EC 1.1.1.115 created 1972]

EC 1.1.1.116

Accepted name: D-arabinose 1-dehydrogenase (NAD⁺)

 $\begin{tabular}{ll} \textbf{Reaction:} & D-arabinose + NAD^+ = D-arabinono-1, 4-lactone + NADH + H^+ \\ \textbf{Other name(s):} & NAD^+-pentose-dehydrogenase; arabinose(fucose) dehydrogenase \\ \end{tabular}$

Systematic name: D-arabinose:NAD⁺ 1-oxidoreductase

References: [3224, 3719]

[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: [706, 704, 705]

[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-aldohexose dehydrogenase; glucose 1-dehydrogenase (NAD)

Systematic name: D-glucose:NAD⁺ 1-oxidoreductase

References: [1746]

[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 aldo-

hexose 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, 158]

[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: [706, 704, 705, 3718]

[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: [706, 704, 705]

[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 (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: [3666, 3698]

[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: [1049]

[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-keto-fructose 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: [81, 160]

[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: [1029]

[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 (ambiguous); 2-keto-3-deoxygluconate dehydrogenase

(ambiguous)

Systematic name: 2-dehydro-3-deoxy-D-gluconate:NADP⁺ 6-oxidoreductase

References: [3371]

[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⁺ = (4*S*)-4,6-dihydroxy-2,5-dioxohexanoate + NADH + H⁺ **Other name(s):** 2-keto-3-deoxygluconate 5-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 (ambiguous)

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: [719, 3372]

[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 $^+$ threonate dehydrogenase; L-threonic acid dehydrogenase

Systematic name: L-threonate:NAD⁺ 3-oxidoreductase

References: [149]

[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-keto-L-gulonate dehydrogenase;

3-ketogulonate dehydrogenase

Systematic name: 3-dehydro-L-gulonate:NAD(P)⁺ 2-oxidoreductase

References: [4466]

[EC 1.1.1.130 created 1972]

EC 1.1.1.131

Accepted name: mannuronate reductase

Reaction: D-mannonate + NAD(P)⁺ = D-mannuronate + NAD(P)H + H⁺

Other name(s): mannonate dehydrogenase; mannonate (nicotinamide adenine dinucleotide (phos-

phate)) dehydrogenase; mannonate dehydrogenase; mannuronate reductase; mannonate dehydrogenase (NAD(P) $^+$); D-mannonate:nicotinamide adenine dinucleotide (phosphate oxidoreductase (D-

mannuronate-forming))

Systematic name: D-mannonate:NAD(P)⁺ 6-oxidoreductase

References: [1091]

[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⁺ + H_2O = GDP-D-mannuronate + 2 NADH + 2 H⁺

Other name(s): guanosine diphosphomannose dehydrogenase; GDP-mannose dehydrogenase; guanosine diphospho-

mannose 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: [3370]

[EC 1.1.1.132 created 1972]

EC 1.1.1.133

Accepted name: dTDP-4-dehydrorhamnose reductase

Reaction: $dTDP-\beta-L$ -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 re-

ductase; 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: [2767]

[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 an-

other enzyme that catalyses epimerization at C-3 and C-5.

References: [1285]

[EC 1.1.1.134 created 1972]

EC 1.1.1.135

Accepted name: GDP-6-deoxy-D-talose 4-dehydrogenase

Reaction: GDP-6-deoxy- α -D-talose + NAD(P)⁺ = GDP-4-dehydro- α -D-rhamnose + NAD(P)H + H⁺ 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: [2653]

[EC 1.1.1.135 created 1972, modified 1976]

EC 1.1.1.136

Accepted name: UDP-*N*-acetylglucosamine 6-dehydrogenase

 $\textbf{Reaction:} \quad \text{UDP-N-acetyl-}\alpha\text{-D-glucosamine} + \textbf{2} \text{ NAD}^+ + \text{H}_2\text{O} = \text{UDP-2-acetamido-2-deoxy-}\alpha\text{-D-glucuronate} + \textbf{2} \text{ NAD}^+ + \textbf{M}_2\text{O} = \textbf{M}_2\text{O} + \textbf{M}_2\text{O} +$

2 NADH + 2 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 lipopolysaccha-

ride.

References: [1082, 2815]

[EC 1.1.1.136 created 1972, modified 2012]

EC 1.1.1.137

Accepted name: ribitol-5-phosphate 2-dehydrogenase

Reaction: D-ribitol 5-phosphate + NAD(P) $^+$ = D-ribulose 5-phosphate + NAD(P)H + 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: [1339]

[EC 1.1.1.137 created 1972, modified 2017]

Accepted name: mannitol 2-dehydrogenase (NADP⁺)

Reaction: D-mannitol + NADP $^+$ = D-fructose + NADPH + H $^+$

Other name(s): mannitol 2-dehydrogenase (NADP)
Systematic name: D-mannitol:NADP⁺ 2-oxidoreductase

References: [1919, 4071]

[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: D-sorbitol 6-phosphate + NAD $^+$ = D-fructose 6-phosphate + NADH + 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 dehydroge-

nase

Systematic name: D-sorbitol-6-phosphate:NAD⁺ 2-oxidoreductase

References: [4300, 2506]

[EC 1.1.1.140 created 1972]

EC 1.1.1.141

Accepted name: 15-hydroxyprostaglandin dehydrogenase (NAD⁺)

Reaction: $(5Z,13E,15S)-11\alpha,15$ -dihydroxy-9-oxoprost-5,13-dienoate + NAD⁺ = $(5Z,13E)-11\alpha$ -hydroxy-9,15-

dioxoprost-5,13-dienoate + NADH + H⁺

Other name(s): NAD⁺-dependent 15-hydroxyprostaglandin dehydrogenase (type I); PGDH; 11\alpha,15-dihydroxy-9-

oxoprost-13-enoate:NAD⁺ 15-oxidoreductase; 15-OH-PGDH; 15-hydroxyprostaglandin dehydrogenase; 15-hydroxyprostanoic dehydrogenase; NAD⁺-specific 15-hydroxyprostaglandin dehydrogenase; prostaglandin dehydrogenase; 15-hydroxyprostaglandin dehydrogenase (NAD⁺); (5*Z*,13*E*)-(15*S*)-

11α,15-dihydroxy-9-oxoprost-13-enoate:NAD⁺ 15-oxidoreductase

Systematic name: $(5Z,13E,15S)-11\alpha,15$ -dihydroxy-9-oxoprost-5,13-dienoate:NAD⁺ 15-oxidoreductase

Comments: Acts on prostaglandin E_2 , $F_{2\alpha}$ and B_1 , but not on prostaglandin D_2 . cf. EC 1.1.1.196 15-

hydroxyprostaglandin-D dehydrogenase (NADP⁺) and EC 1.1.1.197 15-hydroxyprostaglandin de-

hydrogenase (NADP⁺).

References: [104, 422, 2393, 2395]

[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: [3603]

[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: [3603]

[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: [201]

[EC 1.1.1.144 created 1972]

EC 1.1.1.145

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

Reaction: a 3β -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;

drogenase; 3β-hydroxy steroid dehydrogenase/isomerase; 3β-hydroxy- Δ^5 - C_{27} -steroid dehydrogenase/isomerase; 3β-hydroxy- Δ^5 - C_{27} -steroid oxidoreductase; 3β-hydroxy-5-ene-steroid oxidoreductase; steroid- Δ^5 -3β-ol dehydrogenase; 3β-HSDH; 5-ene-3-β-hydroxysteroid dehydrogenase; 3β-

hydroxy-5-ene-steroid dehydrogenase

Systematic name: 3β -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 in-

termediate of cholesterol degradation.

References: [623, 2233, 3053]

[EC 1.1.1.145 created 1972]

EC 1.1.1.146

Accepted name: 11β-hydroxysteroid dehydrogenase

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

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

nase; corticosteroid 11-reductase; dehydrogenase, 11β -hydroxy steroid

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

References: [32, 509, 2327, 3314]

[EC 1.1.1.146 created 1972]

EC 1.1.1.147

Accepted name: 16α-hydroxysteroid dehydrogenase

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

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

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

References: [2763]

[EC 1.1.1.147 created 1972]

EC 1.1.1.148

Accepted name: estradiol 17α -dehydrogenase

Reaction: estradiol- $17\alpha + \text{NAD}(P)^+ = \text{estrone} + \text{NAD}(P)H + H^+$

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

tase; 17α-hydroxysteroid oxidoreductase; estradiol 17α-oxidoreductase

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

References: [3501]

[EC 1.1.1.148 created 1972]

EC 1.1.1.149

Accepted name: 20α-hydroxysteroid dehydrogenase

Reaction: $17\alpha,20\alpha$ -dihydroxypregn-4-en-3-one + NAD(P)⁺ = 17α -hydroxyprogesterone + NAD(P)H + H⁺

Other name(s): 20α-hydroxy steroid dehydrogenase; 20α-HSD; 20α-HSDH

Systematic name: 20α -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: [3860, 4065]

[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: [2867]

[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 phos-

phate) 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: [2867]

[EC 1.1.1.151 created 1972]

EC 1.1.1.152

Accepted name: 3α -hydroxy- 5β -androstane-17-one 3α -dehydrogenase

Reaction: 3α -hydroxy- 5β -androstane-17-one + NAD⁺ = 5β -androstane-3,17-dione + NADH + H⁺

Other name(s): etiocholanolone 3α-dehydrogenase; etiocholanolone 3α-dehydrogenase; 3α-hydroxy-5β-steroid de-

hydrogenase

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

References: [3551]

[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): S

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: [2025, 2696, 4591, 2111]

[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: [4402]

[EC 1.1.1.154 created 1976]

[1.1.1.155 Deleted entry. homoisocitrate dehydrogenase. The enzyme is identical to EC 1.1.1.87, homoisocitrate 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: [281]

[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: [2598]

[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-5 β -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 con-

jugated forms. The Bacteroides fragilis and Clostridium enzymes can also utilize NADP⁺.

References: [1552, 2583, 2585, 2586]

[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'-hydroxypropoxyp

butylamino)-2'-hydroxypropoxy]-3,4-dihydro-1(2H)-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: [2411]

[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-monooxygenase]

[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 NAD⁺ is also utilized, but more slowly.

References: [4368, 4366]

[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: [1408, 1859]

[EC 1.1.1.163 created 1976]

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 C_8 to C_{16} . The Euglena enzyme also oxidizes the

corresponding aldehydes to fatty acids.

References: [2211, 4038]

[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-butynal + 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: [2847]

[EC 1.1.1.165 created 1976]

EC 1.1.1.166

Accepted name: hydroxycyclohexanecarboxylate dehydrogenase

Reaction: (1S,3R,4S)-3,4-dihydroxycyclohexane-1-carboxylate + NAD⁺ = (1S,4S)-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 hy-

droxy group at C-3 and an equatorial hydroxy or carbonyl group at C-4, including (-)-quinate and

(-)-shikimate.

References: [4608]

[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: [1958]

[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 re-

ductase (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: [2120, 4627]

[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 reduc-

tase; ketopantoic acid reductase

Systematic name: (R)-pantoate:NADP $^+$ 2-oxidoreductase

References: [2120]

[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 participates in the biosynthesis of several important sterols such as ergosterol and choles-

terol. It is part of a three enzyme system that removes methyl groups from the C-4 position of steroid molecules. The first enzyme, EC 1.14.18.9, 4α -methylsterol monooxygenase, catalyses three successive oxidations of the methyl group, resulting in a carboxyl group; the second enzyme, EC 1.1.1.170, catalyses an oxidative decarboxylation that results in a reduction of the 3β -hydroxy group at the C-3 carbon to an oxo group; and the last enzyme, EC 1.1.1.270, 3β -hydroxysteroid 3-dehydrogenase, reduces the 3-oxo group back to a 3β -hydroxyl. If a second methyl group remains at the C-4 position, this enzyme also catalyses its epimerization from 4β to 4α orientation, so it could serve as a substrate for a second round of demethylation. cf. EC 1.1.1.418, plant 3β -hydroxysteroid- 4α -carboxylate 3-

dehydrogenase (decarboxylating).

References: [3831, 3430, 420, 1247, 528]

[EC 1.1.1.170 created 1978, modified 2002, modified 2012, modified 2019]

[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: [4090]

[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: [3521, 3522]

[EC 1.1.1.173 created 1978]

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: [837]

[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: [4744]

[EC 1.1.1.175 created 1978]

EC 1.1.1.176

Accepted name: 12α-hydroxysteroid dehydrogenase

Reaction: cholate + NADP⁺ = 3α , 7α -dihydroxy-12-oxo-5 β -cholan-24-oate + NADPH + H⁺

Other name(s): 12α-hydroxy steroid dehydrogenase; NAD⁺-dependent 12α-hydroxysteroid dehydrogenase; NADP⁺-

12α-hydroxysteroid dehydrogenase

Systematic name: 12α -hydroxysteroid:NADP⁺ 12-oxidoreductase

Comments: Catalyses the oxidation of the 12α -hydroxy group of bile acids, both in their free and conjugated

form. Also acts on bile alcohols.

References: [2582, 2619]

[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: [1346, 4665]

[EC 1.1.1.177 created 1980, modified 1980]

EC 1.1.1.178

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

Reaction: (2S,3S)-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-butyryl CoA dehydrogenase

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

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

References: [724]

[EC 1.1.1.178 created 1981]

Accepted name: D-xylose 1-dehydrogenase (NADP⁺, D-xylono-1,5-lactone-forming)

Reaction: D-xylose + NADP $^+$ = D-xylono-1,5-lactone + NADPH + H $^+$

Other name(s): D-xylose (nicotinamide adenine dinucleotide phosphate) dehydrogenase (ambiguous); D-xylose-

NADP dehydrogenase (ambiguous); D-xylose:NADP⁺ oxidoreductase (ambiguous); D-xylose 1-

dehydrogenase (NADP) (ambiguous)

Systematic name: D-xylose:NADP⁺ 1-oxidoreductase (D-xylono-1,5-lactone-forming)

Comments: The enzyme, characterized from pig arterial vessels and eye lens, also acts, more slowly, on L-

arabinose and D-ribose. cf. EC 1.1.1.424, D-xylose 1-dehydrogenase (NADP+, D-xylono-1,4-lactone-

forming).

References: [4645, 4646]

[EC 1.1.1.179 created 1982, modified 2020]

[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): 3β -hydroxy- Δ^5 -C₂₇-steroid oxidoreductase (ambiguous) Systematic name: cholest-5-ene- 3β ,7α-diol:NAD⁺ 3-oxidoreductase

Comments: Highly specific for 3β , 7α -dihydroxy- C_{27} -steroids with Δ^5 -double bond.

References: [4623, 3769]

[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 + $^+$

Systematic name: geraniol:NADP⁺ oxidoreductase

Comments: Also acts, more slowly on farnesol but not on nerol. The enzyme produces a mixture known as cit-

ral, which includes geranial and neral. It is still not known whether neral is produced directly by the

enzyme, or by isomerization of geranial.

References: [3360, 3794, 3636]

[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: [39, 2494, 4589]

[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) oxi-

doreductase; 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 com-

pound. In the reverse direction, vicinal diketones, glyceraldehyde, glyoxal, methylglyoxal, 2-oxo-

hydroxyketones and 2-ketoacid esters can be reduced.

References: [303]

[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: [2009]

[EC 1.1.1.186 created 1984, modified 2002]

EC 1.1.1.187

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

Reaction: (1) GDP- α -D-rhamnose + NAD(P)⁺ = GDP-4-dehydro- α -D-rhamnose + NAD(P)H + H⁺

(2) GDP-6-deoxy- α -D-talose + NAD(P)⁺ = GDP-4-dehydro- α -D-rhamnose + NAD(P)H + 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

 $\textbf{Comments:} \quad \text{The enzyme, which operates in the opposite direction to that shown, forms a mixture of GDP-α-D-}$

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: [215, 4640]

[EC 1.1.1.187 created 1984]

EC 1.1.1.188

Accepted name: prostaglandin-F synthase

Reaction: $(5Z,13E)-(15S)-9\alpha,11\alpha,15$ -trihydroxyprosta-5,13-dienoate + NADP⁺ = $(5Z,13E)-(15S)-9\alpha,15$ -

dihydroxy-11-oxoprosta-5,13-dienoate + NADPH + H+

Other name(s): prostaglandin-D₂ 11-reductase; reductase, 15-hydroxy-11-oxoprostaglandin; PGD₂ 11-ketoreductase;

 $PGF_{2\alpha}$ synthetase; prostaglandin 11-ketoreductase; prostaglandin D_2 -ketoreductase; prostaglandin F synthetase; prostaglandin $F_{2\alpha}$; PGF synthetase; NADPH-

dependent prostaglandin D₂ 11-keto reductase; prostaglandin 11-keto reductase

Systematic name: (5Z,13E)-(15S)- 9α , 11α , 15-trihydroxyprosta-5, 13-dienoate: NADP+ 11-oxidoreductase

Comments: Reduces prostaglandin D_2 and prostaglandin H_2 to prostaglandin F_2 ; prostaglandin D_2 is not an in-

termediate 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: [3491, 4553, 4555, 4661, 4662]

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

Accepted name: prostaglandin-E₂ 9-reductase

Reaction: $(5Z,13E)-(15S)-9\alpha,11\alpha,15$ -trihydroxyprosta-5,13-dienoate + NADP⁺ = $(5Z,13E)-(15S)-11\alpha,15$ -

dihydroxy-9-oxoprosta-5,13-dienoate + NADPH + 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 E₂-9-oxoreductase

Systematic name: (5Z,13E)-(15S)- 9α , 11α , 15-trihydroxyprosta-5, 13-dienoate: NADP⁺ 9-oxidoreductase

Comments: Reduces prostaglandin E_2 to prostaglandin $F_2\alpha$. 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: [2394, 3721, 4166, 4561]

[EC 1.1.1.189 created 1984, modified 1989]

EC 1.1.1.190

Accepted name: indole-3-acetaldehyde reductase (NADH)

Reaction: (indol-3-yl)ethanol + NAD⁺ = (indol-3-yl)acetaldehyde + NADH + H⁺

Other name(s): indoleacetaldehyde reductase; indole-3-acetaldehyde reductase (NADH); indole-3-ethanol:NAD+

oxidoreductase

Systematic name: (indol-3-yl)ethanol:NAD⁺ oxidoreductase

References: [460]

[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: [460]

[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⁺ + H_2O = 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: [2398]

[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-ribitylamino)uracil

ribosylamino)uracil + NADPH + H⁺

Other name(s): aminodioxyphosphoribosylaminopyrimidine reductase

Systematic name: 5-amino-6-(5-phospho-D-ribitylamino)uracil:NADP⁺ 1'-oxidoreductase

References: [502]

[EC 1.1.1.193 created 1984, modified 2011]

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

hol.

References: [2640, 4691]

[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: [3665, 4691, 4692]

[EC 1.1.1.195 created 1984]

EC 1.1.1.196

Accepted name: 15-hydroxyprostaglandin-D dehydrogenase (NADP⁺)

Reaction: (5Z,13E)-(15S)- 9α ,15-dihydroxy-11-oxoprosta-5,13-dienoate + NADP⁺ = (5Z,13E)- 9α -hydroxy-

11,15-dioxoprosta-5,13-dienoate + NADPH + H⁺

Other name(s): prostaglandin-D 15-dehydrogenase (NADP); dehydrogenase, prostaglandin D₂; NADP-PGD₂ de-

hydrogenase; 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)-9α,15-dihydroxy-11-oxoprosta-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: [4554]

[EC 1.1.1.196 created 1984, modified 1990]

EC 1.1.1.197

Accepted name: 15-hydroxyprostaglandin dehydrogenase (NADP⁺)

Reaction: (13E)-(15S)- 11α , 15-dihydroxy-9-oxoprost-13-enoate + NADP⁺ = (13E)- 11α -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 (NADP)

Systematic name: (13*E*)-(15*S*)-11α,15-dihydroxy-9-oxoprost-13-enoate:NADP⁺ 15-oxidoreductase

Comments: Acts on prostaglandins E_2 , $F_{2\alpha}$ and B_1 , but not on prostaglandin D_2 [cf. EC 1.1.1.141 15-

 $hydroxyprostagland in \ dehydrogen as e \ (NAD^+) \ and \ EC \ 1.1.1.196 \ 15-hydroxyprostagland in-D \ dehydroxyprostagland in-D \ dehydrox$

drogenase (NADP⁺)]. May be identical with EC 1.1.1.189 prostaglandin-E₂ 9-reductase.

References: [2393, 2395]

[EC 1.1.1.197 created 1984]

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: [773, 862]

[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: (6*R*)-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: [1065]

[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: [3037]

[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: [1667, 2583, 2584]

[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⁺ oxi-

doreductase; 1,3-propanediol dehydrogenase

Systematic name: propane-1,3-diol:NAD⁺ 1-oxidoreductase

References: [2, 1137]

[EC 1.1.1.202 created 1984]

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 Mg^{2+} . 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 [3242]. The 1,5-lactone product is rather stable at cytosolic pH and

does not hydrolyse spontaneously at a substantial rate.

References: [2090, 368, 89, 3242]

[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 1.17.1.4, 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: $IMP + NAD^+ + H_2O = XMP + NADH + H^+$

Other name(s): inosine-5'-phosphate dehydrogenase; inosinic acid dehydrogenase; inosinate dehydrogenase; inosine

5'-monophosphate dehydrogenase; inosine monophosphate dehydrogenase; IMP oxidoreductase; ino-

sine monophosphate oxidoreductase

Systematic name: IMP:NAD⁺ oxidoreductase

Comments: The enzyme acts on the hydroxy group of the hydrated derivative of the substrate.

References: [2606, 4353]

[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 tropan- 3α -ols, but not the corresponding β -derivatives [2189]. This enzyme along

with EC 1.1.1.236, tropinone reductase II, represents a branch point in tropane alkaloid metabolism [961]. 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 [961]. Both enzymes are always found together in any given tropane-alkaloid-producing species, have a common substrate, tropinone, and are strictly stereospecific [2977].

References: [2189, 749, 2977, 961]

[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 cy-

clohexanols and cyclohexenols.

References: [2146]

[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 cyclohex-

anols and cyclohexenols.

References: [2146]

[EC 1.1.1.208 created 1984]

EC 1.1.1.209

Accepted name: 3(or 17)α-hydroxysteroid dehydrogenase

Reaction: androsterone + NAD(P)⁺ = 5α -androstane-3,17-dione + NAD(P)H + H⁺

Other name(s): $3(17)\alpha$ -hydroxysteroid dehydrogenase

Systematic name: $3(\text{or }17)\alpha$ -hydroxysteroid:NAD(P)⁺ oxidoreductase

Comments: Acts on the 3α -hydroxy group of androgens of the 5α -androstane series; and also, more slowly, on

the 17α -hydroxy group of both androgenic and estrogenic substrates (cf. EC 1.1.1.51 3(or 17) β -

hydroxysteroid dehydrogenase).

References: [2363, 2364]

[EC 1.1.1.209 created 1986]

EC 1.1.1.210

Accepted name: 3β (or 20α)-hydroxysteroid dehydrogenase

Reaction: 5α -androstan- 3β , 17β -diol + NADP⁺ = 17β -hydroxy- 5α -androstan-3-one + NADPH + H⁺

Other name(s): progesterone reductase; dehydrogenase, 3β , 20α -hydroxy steroid; 3β , 20α -hydroxy steroid oxidoreduc-

tase

Systematic name: 3β (or 20α)-hydroxysteroid:NADP⁺ oxidoreductase

Comments: Also acts on 20α -hydroxysteroids.

References: [3824]

[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 sub-

strate (cf. EC 1.1.1.35 3-hydroxyacyl-CoA dehydrogenase).

References: [1034]

[EC 1.1.1.211 created 1986]

EC 1.1.1.212

Accepted name: 3-oxoacyl-[acyl-carrier-protein] reductase (NADH)

Reaction: a (3R)-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); (3R)-3-hydroxyacyl-[acyl-carrier-protein]:NAD⁺ oxidore-

ductase

Systematic name: (3R)-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: [575]

[EC 1.1.1.212 created 1986]

EC 1.1.1.213

Accepted name: 3α-hydroxysteroid 3-dehydrogenase (*Re*-specific)

Reaction: a 3α -hydroxysteroid + NAD(P)⁺ = a 3-oxosteroid + NAD(P)H + H⁺

Other name(s): 3α-hydroxysteroid dehydrogenase; 3α-hydroxysteroid:NAD(P)⁺ 3-oxidoreductase (A-specific); 3α-

hydroxysteroid 3-dehydrogenase (A-specific)

Systematic name: 3α -hydroxysteroid:NAD(P)⁺ 3-oxidoreductase (*Re*-specific)

Comments: The enzyme acts on multiple 3α -hydroxysteroids. Re-specific with respect to NAD⁺ or NADP⁺ [cf.

EC 1.1.1.50, 3α -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, 3α -hydroxysteroid

3-dehydrogenase.

References: [340, 4304]

[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; 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 re-

ductase (*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: [4627]

[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, 661]

[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;

nase

Systematic name: (2E,6E)-farnesol:NADP⁺ 1-oxidoreductase

Comments: Also acts, more slowly, on (2Z,6E)-farnesol, geraniol, citronerol and nerol.

References: [1814]

[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 (2*S*,3*S*)-2-methyl-3-hydroxybutanoate; otherwise highly specific.

References: [1237]

[EC 1.1.1.217 created 1989]

EC 1.1.1.218

Accepted name: morphine 6-dehydrogenase

Reaction: morphine + NAD(P) $^+$ = morphine + NAD(P)H + H $^+$

Other name(s): naloxone reductase

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 6α -hydroxy analogue. Activated by 2-sulfanylethan-1-ol (2-

mercaptoethanol).

References: [4750, 4751]

[EC 1.1.1.218 created 1989, modified 1990]

EC 1.1.1.219

Accepted name: dihydroflavonol 4-reductase

Reaction: a (2R,3S,4S)-leucoanthocyanidin + NADP⁺ = a (2R,3R)-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: (2R,3S,4S)-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: [1618, 3999, 1125, 2443]

 $[EC\ 1.1.1.219\ created\ 1989,\ modified\ 2016]$

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: [2816]

[EC 1.1.1.220 created 1989]

EC 1.1.1.221

Accepted name: vomifoliol dehydrogenase

Reaction: (6S,9R)-6-hydroxy-3-oxo- α -ionol + NAD⁺ = (6S)-6-hydroxy-3-oxo- α -ionone + NADH + H⁺

Other name(s): vomifoliol 4'-dehydrogenase; vomifoliol:NAD⁺ 4'-oxidoreductase

Systematic name: (6S,9R)-6-hydroxy-3-oxo- α -ionol:NAD⁺ oxidoreductase

Comments: Oxidizes vomifoliol to dehydrovomifoliol; involved in the metabolism of abscisic acid in *Corynebac*-

terium sp.

References: [1548]

[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 biosyn-

thesis of menthol and related monoterpenes in peppermint (Mentha piperita) leaves.

References: [2147]

[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: [3604]

[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: [2865]

[EC 1.1.1.225 created 1989]

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 deriva-

tive.

References: [3123]

[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: [862]

[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: [862]

[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 (2R,3R)-2-methyl-3-hydroxysuccinate + NADP⁺ = diethyl 2-methyl-3-oxosuccinate +

 $NADPH + H^{+}$

Systematic name: diethyl-(2R,3R)-2-methyl-3-hydroxysuccinate:NADP⁺ 3-oxidoreductase

Comments: Also acts on diethyl (2S,3R)-2-methyl-3-hydroxysuccinate; and on the corresponding dimethyl esters.

References: [1238]

[EC 1.1.1.229 created 1990]

EC 1.1.1.230

Accepted name: 3α-hydroxyglycyrrhetinate dehydrogenase

Reaction: 3α -hydroxyglycyrrhetinate + NADP⁺ = 3-oxoglycyrrhetinate + NADPH + H⁺

Systematic name: 3α -hydroxyglycyrrhetinate:NADP⁺ 3-oxidoreductase

Comments: Highly specific to 3α -hydroxy derivatives of glycyrrhetinate and its analogues. Not identical to EC

1.1.1.50 3α-hydroxysteroid dehydrogenase (Si-specific).

References: [47]

[EC 1.1.1.230 created 1990]

Accepted name: 15-hydroxyprostaglandin-I dehydrogenase (NADP⁺)

Reaction: (5Z,13E)-(15S)- $6,9\alpha$ -epoxy- 11α ,15-dihydroxyprosta-5,13-dienoate + NADP⁺ = (5Z,13E)- $6,9\alpha$ -

epoxy- 11α -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: (5Z,13E)-(15S)- $6,9\alpha$ -epoxy- 11α ,15-dihydroxyprosta-5,13-dienoate:NADP $^+$ 15-oxidoreductase

Comments: Specific for prostaglandin I_2 .

References: [2231]

[EC 1.1.1.231 created 1990]

EC 1.1.1.232

Accepted name: 15-hydroxyicosatetraenoate dehydrogenase

Reaction: (15S)-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: (15S)-15-hydroxy-5,8,11-cis-13-trans-icosatetraenoate:NAD(P)⁺ 15-oxidoreductase

References: [3953]

[EC 1.1.1.232 created 1992]

EC 1.1.1.233

Accepted name: *N*-acylmannosamine 1-dehydrogenase

Reaction: N-acyl-D-mannosamine + NAD+ = N-acyl-D-mannosaminolactone + NADH + H+

Other name(s): N-acylmannosamine dehydrogenase; N-acetyl-D-mannosamine dehydrogenase; N-acyl-D-mannosamine dehydrogenase; N-acyl-D-mannosa

 $mannosamine\ dehydrogenase; N\hbox{-acylmannosamine}\ dehydrogenase$

Systematic name: *N*-acyl-D-mannosamine:NAD⁺ 1-oxidoreductase

Comments: Acts on acetyl-D-mannosamine and glycolyl-D-mannosamine. Highly specific.

References: [1727]

[EC 1.1.1.233 created 1992]

EC 1.1.1.234

Accepted name: flavanone 4-reductase

Reaction: (2S)-flavan-4-ol + NADP⁺ = (2S)-flavanone + NADPH + H⁺

Systematic name: (2S)-flavan-4-ol:NADP⁺ 4-oxidoreductase

Comments: Involved in the biosynthesis of 3-deoxyanthocyanidins from flavanones such as naringenin or eriodic-

tyol.

References: [4027]

[EC 1.1.1.234 created 1992]

EC 1.1.1.235

Accepted name: 8-oxocoformycin reductase

Reaction: $coformycin + NADP^+ = 8-oxocoformycin + NADPH + H^+$

Other name(s): 8-ketodeoxycoformycin reductase Systematic name: coformycin:NADP⁺ 8-oxidoreductase

Comments: Si-specific with respect to NADPH. Also reduces 8-oxodeoxy-coformycin to the nucleoside antibiotic

deoxycoformycin.

References: [1521]

[EC 1.1.1.235 created 1992]

Accepted name: tropinone reductase II

Reaction: pseudotropine + NADP $^+$ = tropinone + NADPH + H $^+$

Other name(s): tropinone (ψ-tropine-forming) reductase; pseudotropine forming tropinone reductase; tropinone re-

ductase (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 [2977]. 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 [2977]. Both enzymes are always found together in any given tropane-alkaloid-producing species, have a common substrate, tropinone, and are strictly stereospe-

cific [749].

References: [962, 749, 2977, 961]

[EC 1.1.1.236 created 1992, modified 2007]

EC 1.1.1.237

Accepted name: hydroxyphenylpyruvate reductase

Reaction: (1) (R)-3-(4-hydroxyphenyl)lactate + NAD(P)⁺ = 3-(4-hydroxyphenyl)pyruvate + NAD(P)H + H⁺

(2) (R)-3-(3,4-dihydroxyphenyl)lactate + NAD(P)⁺ = 3-(3,4-dihydroxyphenyl)pyruvate + NAD(P)H +

 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: [3300, 2099, 2112, 4514]

[EC 1.1.1.237 created 1992, modified 2018]

EC 1.1.1.238

Accepted name: 12β-hydroxysteroid dehydrogenase

Reaction: $3\alpha,7\alpha,12\beta$ -trihydroxy-5 β -cholan-24-oate + NADP⁺ = $3\alpha,7\alpha$ -dihydroxy-12-oxo-5 β -cholan-24-oate +

 $NADPH + H^{+}$

Other name(s): 12β-hydroxy steroid (nicotinamide adenine dinucleotide phosphate) dehydrogenase

Systematic name: 12β-hydroxysteroid:NADP⁺ 12-oxidoreductase

Comments: Acts on a number of bile acids, both in their free and conjugated forms.

References: [1012]

[EC 1.1.1.238 created 1992]

EC 1.1.1.239

Accepted name: $3\alpha(17\beta)$ -hydroxysteroid dehydrogenase (NAD⁺)

Reaction: testosterone + NAD $^+$ = androstenedione + NADH + H $^+$

Other name(s): $3\alpha,17\beta$ -hydroxy steroid dehydrogenase; $3\alpha(17\beta)$ -HSD; 17-ketoreductase (ambiguous); 17 β -HSD

(ambiguous); HSD17B6 (gene name); HSD17B8 (gene name)

Systematic name: 3α (or 17 β)-hydroxysteroid:NAD⁺ oxidoreductase

Comments: Also acts on other 17β -hydroxysteroids and on the 3α -hydroxy group of pregnanes and bile acids.

Different from EC 1.1.1.50 3α -hydroxysteroid dehydrogenase (Si-specific) or EC 1.1.1.213 3α -

hydroxysteroid dehydrogenase (Re-specific).

References: [4149, 4452, 1044, 3140]

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

Accepted name: *N*-acetylhexosamine 1-dehydrogenase

Reaction: N-acetyl- α -D-glucosamine + NAD⁺ = N-acetyl-D-glucosaminate + 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 speci-

ficity was tested with N-acetyl-D-glucosamine, and it was shown that the enzyme is specific for the α

anomer.

References: [1728]

[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: [4631]

[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: [1306]

[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: [131]

[EC 1.1.1.244 created 1992]

EC 1.1.1.245

Accepted name: cyclohexanol dehydrogenase

Reaction: cyclohexanol + NAD $^+$ = cyclohexanone + NADH + H $^+$

 $\textbf{Systematic name:} \quad \text{cyclohexanol:} NAD^+ \text{ oxidoreductase}$

Comments: Also oxidizes some other alicyclic alcohols and diols.

References: [823, 951, 4334]

[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]

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: [2416, 2415]

[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 mor-

phinan alkaloids in the poppy plant.

References: [1301]

[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: [4660, 3417]

[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: [4656, 3092, 284]

[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 $^+$ Δ^5 -oxidoreductase

Comments: Reduces 1,3,6,8-tetrahydroxynaphthalene to scytalone and also reduces 1,3,8-trihydroxynaphthalene

to vermelone. Involved with EC 4.2.1.94 scytalone dehydratase in the biosynthesis of melanin in

pathogenic fungi.

References: [4599, 4447, 4273]

[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 carni-

tine 3-dehydrogenase

References: [3804]

[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 additols with a minimum requirement of 2R chi-

rality at the carbon adjacent to the primary carbon undergoing the oxidation. The enzyme is specific

for NAD⁺ and does not use NADP⁺.

References: [4050, 4051, 4637, 4049]

[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: [570, 1411]

[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: [1965]

[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: [951, 1597]

[EC 1.1.1.258 created 2000]

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: [1545]

[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 reduc-

tion in Clostridia pasteurianum, C. tyrobutyricum and Lactobacillus brevis suggest that there may be

at least two sulcatone reductases with different stereospecificities.

References: [276, 4286, 4287]

[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 Zn^{2+} -dependent form in archaea but a Ni^{2+} -dependent form

has been found in Gram-positive bacteria [1442]. 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 un-

saturated archaetidylserine [2889]. Activity of the enzyme is stimulated by K⁺ [3076].

References: [3075, 3076, 2195, 2889, 1497, 1442]

[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-(phosphonooxy)-L-threonine:NAD⁺ oxi-

 $do reduct a se; \hbox{$4$-phosphooxy-L-threonine:} NAD^+ \ oxido reduct a se$

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: [544, 2322, 3920, 212]

[EC 1.1.1.262 created 2000, modified 2006]

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 fruc-

tose.

References: [3644]

[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: [248]

[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: [4410, 3034]

[EC 1.1.1.265 created 2000]

EC 1.1.1.266

Accepted name: dTDP-4-dehydro-6-deoxyglucose reductase

Reaction: $dTDP-\alpha-D-fucopyranose + NAD(P)^+ = dTDP-4-dehydro-6-deoxy-\alpha-D-glucose + NAD(P)H + H^+$ **Other name(s):** $dTDP-4-keto-6-deoxyglucose reductase; <math>dTDP-D-fucose:NADP^+$ oxidoreductase; Fcf1; dTDP-6-deoxyglucose

deoxy-D-xylo-hex-4-ulopyranose reductase

Systematic name: $dTDP-\alpha-D-fucopyranose:NAD(P)^+$ oxidoreductase

Comments: The enzymes from the Gram-negative bacteria *Aggregatibacter actinomycetemcomitans* and *Es*-

cherichia coli O52 are involved in activation of fucose for incorporation into capsular polysaccharide O-antigens [4814, 4525]. 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 [4863]. The enzyme from *Escherichia coli* O52 has a higher catalytic efficiency with NADH

than with NADPH [4525].

References: [4814, 4863, 4525]

 $[EC\ 1.1.1.266\ created\ 2001,\ modified\ 2013]$

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 Mn^{2+} , Co^{2+} or Mg^{2+} for activity, with the first being most effective. The en-

zyme 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 [2934].

References: [4170, 2934]

[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; 2-[2-(R))-

hydroxypropylthio]ethanesulfonate:NAD⁺ oxidoreductase

Systematic name: 2-[(2R)-2-hydroxypropyl]sulfanylethane-1-sulfonate: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: [68]

[EC 1.1.1.268 created 2001]

EC 1.1.1.269

Accepted name: 2-(S)-hydroxypropyl-CoM dehydrogenase

Reaction: (2S)-2-hydroxypropyl-CoM + NAD⁺ = 2-oxopropyl-CoM + NADH + H⁺ **Other name(s):** 2-(2-(S)-hydroxypropylthio)ethanesulfonate dehydrogenase; 2-[2-(S)-

hydroxypropylthiolethanesulfonate:NAD⁺ oxidoreductase

Systematic name: 2-[(2S)-2-hydroxypropyl]sulfanylethanesulfonate:NAD⁺ oxidoreductase

Comments: The enzyme is highly specific for (2S)-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: [68]

[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 [2650].

References: [4151, 333, 1248, 2650]

[EC 1.1.1.270 created 2002, modified 2012]

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: [596, 2724, 2771, 3957]

[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 *As*-

pergillus 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 effi-

ciency. cf. EC 1.1.1.345, (d)-2-hydroxyacid dehydrogenase (NAD⁺).

References: [941, 3870]

[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: [3310]

[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: [3965]

[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: [407]

[EC 1.1.1.275 created 2003]

EC 1.1.1.276

Accepted name: serine 3-dehydrogenase (NADP⁺)

Reaction: L-serine + NADP $^+$ = 2-aminoacetaldehyde + CO $_2$ + NADPH + H $^+$ (overall reaction)

(1a) L-serine + $NADP^+$ = 2-aminomalonate semialdehyde + $NADPH + H^+$

(1b) 2-aminomalonate semialdehyde = 2-aminoacetaldehyde + CO_2 (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: [1209, 681]

[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: [4081, 3788, 2496]

[EC 1.1.1.277 created 2003]

EC 1.1.1.278

Accepted name: 3β -hydroxy- 5α -steroid dehydrogenase

Reaction: 3β -hydroxy- 5α -pregnane-20-one + NADP⁺ = 5α -pregnan-3,20-dione + NADPH + H⁺

Systematic name: 3β-hydroxy-5α-steroid:NADP⁺ 3-oxidoreductase

References: [2496, 4548]

[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: [1608]

[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: [1608]

[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 prod-

uct formed is GDP-α-D-rhamnose. D-Rhamnose is a constituent of lipopolysaccharides of Gram-

negative plant and human pathogenic bacteria.

References: [2165, 2625]

[EC 1.1.1.281 created 2004]

EC 1.1.1.282

Accepted name: quinate/shikimate dehydrogenase [NAD(P)⁺]

Reaction: (1) L-quinate + NAD(P) $^+$ = 3-dehydroquinate + NAD(P)H + H $^+$

(2) shikimate + $NAD(P)^+$ = 3-dehydroshikimate + $NAD(P)H + H^+$

Other name(s): YdiB; quinate/shikimate dehydrogenase (ambiguous)

Systematic name: L-quinate:NAD(P)⁺ 3-oxidoreductase

Comments: This is the second shikimate dehydrogenase enzyme found in Escherichia coli. It can use both quinate

and shikimate as substrates and either NAD⁺ or NADP⁺ as acceptor. The low catalytic efficiency with both quinate and shikimate suggests that neither may be the physiological substrate. *cf.* EC 1.1.1.24, quinate/shikimate dehydrogenase (NAD⁺), EC 1.1.5.8, quinate/shikimate dehydrogenase

(quinone), and EC 1.1.1.25, shikimate dehydrogenase (NADP⁺).

References: [2793, 283]

[EC 1.1.1.282 created 2004, modified 2021]

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-

 $dependent); lactal de hyde: NADP^+\ oxidore du ctase$

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) [2943, 627], 3-methylbutanal [1565], hexane-2,5-dione [2924] and 3-chloro-1-phenylpropan-1-one [674]. 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: [2943, 627, 1565, 2924, 674, 433]

[EC 1.1.1.283 created 2005, modified 2013]

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); GD-FALDH; NAD- and glutathione-dependent formalde-

hyde dehydrogenase; NAD-dependent formaldehyde dehydrogenase (incorrect)

Systematic name: S-(hydroxymethyl)glutathione:NAD⁺ oxidoreductase

Comments: The substrate, S-(hydroxymethyl)glutathione, forms spontaneously from glutathione and formalde-

hyde; 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: [1880, 3573, 2517, 3658, 4412, 3453, 216]

[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: [3891]

[EC 1.1.1.285 created 2005]

EC 1.1.1.286

Accepted name: isocitrate—homoisocitrate dehydrogenase

Reaction: (1) isocitrate + NAD⁺ = 2-oxoglutarate + CO_2 + NADH

(2) (1R,2S)-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 Mn^{2+} and K^{+} or NH_4^{+} 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: [2842]

[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: [2504]

[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 alco-

hols such as ethanol, isopropanol, butanol and cyclohexanol cannot replace xanthoxin as substrate [1361]. 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 [1361].

References: [3907, 3766, 1361]

[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: [1399, 1400, 4099, 3885]

[EC 1.1.1.289 created 2006]

EC 1.1.1.290

Accepted name: 4-phosphoerythronate dehydrogenase

Reaction: 4-phospho-D-erythronate + NAD $^+$ = (3R)-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 [3594].

cf. EC 1.1.1.399, 2-oxoglutarate reductase.

References: [2328, 3272, 4900, 1382, 3743, 3594]

[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: [67]

[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 (ambiguous)

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 [814]. 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 [2276]. 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 com-

mon aldoses and ketoses, or non-sugar aldehydes and ketones [2276].

References: [2276, 814]

[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 -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 -hydroxychlorophyllide-a: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 [1733] and it also forms part of the chlorophyll cycle, which interconverts chlorophyll a and b in response to changing light conditions

[1844, 3592].

References: [3714, 3715, 1733, 1844, 3592]

[EC 1.1.1.294 created 2007]

EC 1.1.1.295

Accepted name: momilactone-A synthase

Reaction: 3β -hydroxy- 9β -pimara-7,15-diene-19, 6β -olide + NAD(P)⁺ = momilactone A + NAD(P)H + H⁺

Other name(s): momilactone A synthase; OsMAS

Systematic name: 3β -hydroxy- 9β -pimara-7,15-diene-19, 6β -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⁺ [151].

References: [151, 3880]

[EC 1.1.1.295 created 2008]

EC 1.1.1.296

Accepted name: dihydrocarveol dehydrogenase

Reaction: menth-8-en-2-ol + NAD⁺ = menth-8-en-2-one + NADH + H^+

Other name(s): carveol dehydrogenase (ambiguous)

Systematic name: 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: [4403]

[EC 1.1.1.296 created 2008]

EC 1.1.1.297

Accepted name: limonene-1,2-diol dehydrogenase

Reaction: menth-8-ene-1,2-diol + NAD $^+$ = 1-hydroxymenth-8-en-2-one + NADH + H $^+$ (general reaction)

(1) (1S,2S,4R)-menth-8-ene-1,2-diol + NAD⁺ = (1S,4R)-1-hydroxymenth-8-en-2-one + NADH + H⁺ (2) (1R,2R,4S)-menth-8-ene-1,2-diol + NAD⁺ = (1R,4S)-1-hydroxymenth-8-en-2-one + NADH + H⁺

Other name(s): NAD+-dependent limonene-1,2-diol dehydrogenase

Systematic name: menth-8-ene-1,2-diol:NAD⁺ oxidoreductase

Comments: While the enzyme from the Gram-positive bacterium *Rhodococcus erythropolis* DCL14 can use both

(1S,2S,4R)- and (1R,2R,4S)-menth-8-ene-1,2-diol as substrate, activity is higher with (1S,2S,4R)-

menth-8-ene-1,2-diol as substrate.

References: [4404]

[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 [4056, 296]. The enzyme from *Chloroflexus aurantiacus* is bifunctional, and also catalyses the upstream reaction in the pathway, EC 1.2.1.75 [1764]. Different from EC 1.1.1.59 [3-hydroxypropionate

dehydrogenase (NAD⁺)] by cofactor preference.

References: [4056, 296, 1764]

[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 dehyrogenase

Systematic name: (S)-malate:NAD(P)⁺ oxidoreductase

Comments: This enzyme, which was characterized from the methanogenic archaeon Methanobacterium ther-

moautotrophicum, catalyses only the reduction of oxaloacetate, and can use NAD⁺ and NADP⁺ with similar specific activity [4271]. 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: [4271]

[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 dehy-

drogenase 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 localiza-

tion 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) [279]. K_m -values for NADP⁺ and NADPH are at least 800-fold lower than those for NAD⁺ and NADH [280, 2052]. This enzyme differs from EC

1.1.1.105, retinol dehydrogenase, which prefers NAD⁺ and NADH.

References: [280, 279, 1468, 2052]

[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 [3363].

References: [3363]

[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(3H)-one + NAD(P)⁺ = 2,5-diamino-6-(5-phospho-D-ribitylamino-6-(5-phospho-D-ribitylamino-6-(5-phospho-D-ribitylamino-6-(5-phospho-D-ribitylamino-6-(5-phospho-D-ribitylamino-6-(5-phospho-D-ribitylamino-6-(5-phospho-D-ribitylamino-6

phospho-D-ribosylamino)pyrimidin-4(3H)-one + NAD(P)H + H⁺

Other name(s): 2,5-diamino-6-ribosylamino-4(3H)-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 [1387].

References: [1387, 614]

[EC 1.1.1.302 created 2010, modified 2011]

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* [1609, 1360]. Different from EC 1.1.1.304, diacetyl reductase [(S)-acetoin

forming].

References: [1609, 1360]

[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 butane-

diol 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*

[1328, 553, 4371]. Different from EC 1.1.1.303, diacetyl reductase [(R)-acetoin forming].

References: [1328, 553, 4371]

[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⁺ 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: [430, 1282, 4633, 1283, 4755]

[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 dehydroge-

nase

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: [2826, 3107, 4459, 3462]

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

Accepted name: D-xylose reductase [NAD(P)H]

Reaction: $xylitol + NAD(P)^+ = D-xylose + NAD(P)H + H^+$

Other name(s): XylR; msXR; dsXR; dual specific xylose reductase; NAD(P)H-dependent xylose reductase; xylose

reductase (ambiguous); D-xylose reductase (ambiguous)

Systematic name: $xylitol:NAD(P)^+$ oxidoreductase

Comments: Xylose reductases catalyse the reduction of xylose to xylitol, the initial reaction in the fungal D-

xylose degradation pathway. Most of the enzymes exhibit a strict requirement for NADPH [cf. EC 1.1.1.431, D-xylose reductase (NADPH)]. However, a few D-xylose reductases, such as those from Neurospora crassa [4668], Yamadazyma tenuis [3045, 1464], Scheffersomyces stipitis [4435], and the thermophilic fungus Chaetomium thermophilum [1480, 3414], have dual coenzyme specificity, though they still prefer NADPH to NADH. Very rarely the enzyme prefers NADH [cf. EC 1.1.1.430,

D-xylose reductase (NADH)].

References: [4435, 3045, 1464, 1480, 4668, 1105, 3414]

[EC 1.1.1.307 created 2010, modified 2022]

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: [2731]

[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 phos-

phinothricin tripeptide, the reduction of phosphonoacetaldehyde to 2-hydroxyethylphosphonate. The

preferred cofactor is NADH, lower activity with NADPH [362].

References: [362]

[EC 1.1.1.309 created 2011]

EC 1.1.1.310

Accepted name: (S)-sulfolactate dehydrogenase

Reaction: (2S)-3-sulfolactate + NAD⁺ = 3-sulfopyruvate + NADH + H⁺

Other name(s): (2S)-3-sulfolactate dehydrogenase; SlcC Systematic name: (2S)-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, (2R)-3-sulfolactate dehydrogenase (NADP⁺), it provides a racemase system that converts (2S)-3-sulfolactate to (2R)-3-sulfolactate, which is degraded further by EC 4.4.1.24, (2R)-sulfolactate sulfo-lyase. The enzyme is specific for

 NAD^{+} .

References: [879]

[EC 1.1.1.310 created 2011, modified 2013]

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: [2168, 1686]

[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-2H-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 [2676]. However, later studies showed that the substrate is the hemiacetal form [2675], and the prod-

uct is 2-oxo-2*H*-pyran-4,6-dicarboxylate [2674, 2679].

References: [2676, 2674, 2675, 2679]

[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 (NADPH)

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 *isfD*2) 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. *cf.* EC

1.1.1.433, sulfoacetaldehyde reductase (NADH).

References: [2259]

[EC 1.1.1.313 created 2011, modified 2022]

[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 [3905] while the substrate is bound to the retinal-binding protein [4686]. 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 [4515].

References: [3905, 4515, 2480, 4686]

[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 path-

way). The activity with NADP⁺ is less than 10% of the activity with NAD⁺.

References: [2795, 1281, 4598, 3136]

[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: [4118, 3576]

[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) [2185, 2543], Clarkia breweri and Petunia hybrida [2186] 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 [2184]. The enzyme from Larrea tridentata (creosote bush) also forms chavicol from a coumaryl ester and can use NADH

[112].

References: [2185, 112, 2543, 2186, 2184]

[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 [2185, 2186]. However in Pimpinella anisum (anise) only

anol is formed *in vivo*, although the cloned enzyme does produce isoeugenol [2184].

References: [2185, 2186, 2184]

[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

[2678].

References: [2677, 2678]

[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: [2223]

[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: [772]

[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: [772]

[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-oxogeranial + **2** NADPH + **2** H⁺ (overall reaction)

(1a) (6*E*)-8-hydroxygeraniol + NADP⁺ = (6*E*)-8-hydroxygeranial + NADPH + H⁺ (1b) (6*E*)-8-hydroxygeraniol + NADP⁺ = (6*E*)-8-oxogeraniol + NADPH + H⁺ (1c) (6*E*)-8-hydroxygeranial + NADP⁺ = (6*E*)-8-oxogeranial + NADPH + H⁺

(1d) (6E)-8-oxogeraniol + NADP⁺ = (6E)-8-oxogeranial + NADPH + H⁺

Other name(s): 8-hydroxygeraniol oxidoreductase; CYP76B10; G10H; CrG10H; SmG10H; acyclic monoterpene pri-

mary alcohol:NADP+ oxidoreductase

Systematic name: (6E)-8-hydroxygeraniol:NADP⁺ oxidoreductase

Comments: Contains Zn^{2+} . The enzyme catalyses the oxidation of (6E)-8-hydroxygeraniol to (6E)-8-oxogeranial

via either (6E)-8-hydroxygeranial 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: [1791, 1483]

[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: [668, 4130]

[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: [3157]

[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 Zn^{2+} . Isolated from *Pseudomonas putida*, and involved in degradation of (+)-camphor.

References: [3509, 2193, 122]

[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: [2801]

[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: [2274, 3042]

[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 (3R)-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 extend-

ing 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 C_{16} to C_{34} , 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 reduc-

tase.

References: [257, 1495, 258]

[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* [4693] and *Podophyllum peltatum* [4693, 4827, 2859].

An intermediate lactol is detected in vitro.

References: [4693, 4827, 2859]

[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: [4505, 4504]

[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 My-

cobacterium 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: [4326]

[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 biosynthe-

sis 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: [1918]

[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-*ribo*-

hex-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 enzyme catalysing the next step the pathway (EC 2.6.1.98, UDP-2-acetamido-2-deoxy-*ribo*-hexuluronate 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: [4596, 2354, 4262, 4263]

[EC 1.1.1.335 created 2012]

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

 $NADH + 2H^{+}$

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 ac-

tivity with NADP⁺.

References: [3006]

[EC 1.1.1.336 created 2012]

EC 1.1.1.337

Accepted name: L-2-hydroxycarboxylate dehydrogenase (NAD⁺)

Reaction: a (2S)-2-hydroxycarboxylate + NAD⁺ = a 2-oxocarboxylate + NADH + H⁺

Other name(s): (R)-sulfolactate:NAD⁺ oxidoreductase; L-sulfolactate dehydrogenase; (R)-sulfolactate dehydrogenase;

nase; 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 (2R)-3-sulfolactate, (S)-malate, (S)-lactate, and (S)-2-

hydroxyglutarate [1380]. Note that (2R)-3-sulfolactate has the same stereo configuration as (2S)-2-

hydroxycarboxylates.

References: [1386, 1385, 1380, 3488]

[EC 1.1.1.337 created 2012]

EC 1.1.1.338

Accepted name: (2R)-3-sulfolactate dehydrogenase (NADP⁺)

Reaction: (2R)-3-sulfolactate + NADP⁺ = 3-sulfopyruvate + NADPH + H⁺

Other name(s): (R)-sulfolactate:NADP⁺ oxidoreductase; L-sulfolactate dehydrogenase; (R)-sulfolactate dehydrogenase;

nase; ComC

Systematic name: (2R)-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 sulfolac-

tate. It can not use (S)-malate and (S)-lactate.

References: [879]

[EC 1.1.1.338 created 2012]

EC 1.1.1.339

Accepted name: dTDP-6-deoxy-L-talose 4-dehydrogenase (NAD⁺)

Reaction: $dTDP-6-deoxy-\beta-L-talose + NAD^+ = dTDP-4-dehydro-\beta-L-rhamnose + NADH + H^+$

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: [2994]

[EC 1.1.1.339 created 2012]

EC 1.1.1.340

Accepted name: 1-deoxy-11β-hydroxypentalenate dehydrogenase

Reaction: 1-deoxy-11β-hydroxypentalenate + NAD⁺ = 1-deoxy-11-oxopentalenate + NADH + H⁺
Other name(s): 1-deoxy-11β-hydroxypentalenic acid dehydrogenase; ptlF (gene name); penF (gene name)

Systematic name: 1-deoxy-11β-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: [4823]

[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* [2074, 4278] and *Salmonella enterica* [2074, 4689].

References: [2074, 4689, 4278]

[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: [4439, 1485]

[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 + CO $_2$ + NADH + H $^+$

Other name(s): 6-PGDH (ambiguous); *gntZ* (gene name); GNDl

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 [658]. *cf.* EC 1.1.1.44, phosphogluconate dehydrogenase (NADP⁺-

dependent, decarboxylating).

References: [2127, 3137, 4857, 658]

[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: [1994]

[EC 1.1.1.344 created 2013]

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 (pyru-

vate and 2-oxobutanoate). cf. EC 1.1.1.272, (d)-2-hydroxyacid dehydrogenase (NADP⁺).

References: [881, 383, 2094, 4484, 589, 2838]

[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 [3966]. 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: [3966, 2809, 4845, 2648, 2085]

[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

[2556]. The enzyme from the prune mite Carpoglyphus lactis also acts (more slowly) on farnesol but

not on nerol [3095].

References: [3095, 2556]

[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: [360, 1446, 1447, 1448, 3821]

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

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: [4717, 4916]

[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⁺ [2102]. cf. EC 1.1.1.154, ureidoglycolate dehydrogenase [NAD(P)⁺].

References: [789, 2102]

[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 pur-

pose 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: [282, 4052, 2436]

[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* [3645]. Involved in aflatoxin

biosynthesis. 5'-Oxoaverantin will spontaneously form averufin by intramolecular ketalisation. cf.

EC 4.2.1.142, 5'-oxoaverantin cyclase.

References: [594, 3645]

[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: [2711, 3862]

[EC 1.1.1.353 created 2013]

EC 1.1.1.354

Accepted name: farnesol dehydrogenase (NAD⁺)

Reaction: (2E,6E)-farnesol + NAD⁺ = (2E,6E)-farnesal + NADH + H⁺

Other name(s): NAD⁺-farnesol dehydrogenase

Systematic name: (2E,6E)-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: [3095]

[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: [4089]

[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 [55].

References: [55]

[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): 3\(\text{a-hydroxysteroid dehydrogenase}\); AKR1C4 (gene name); AKR1C2 (gene name); hsdA (gene name)

Systematic name: 3α -hydroxysteroid:NAD(P)⁺ 3-oxidoreductase

Comments: The enzyme acts on multiple 3α -hydroxysteroids, such as androsterone and 5α -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 stereospecificity 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: [898, 2080, 3189, 2854, 2966]

[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 B_5).

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: [1556]

[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: [1317, 3935, 2334, 4253, 2806, 1469]

[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; glu-

cose/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 galac-

tose 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: [103, 2806]

[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 path-

way.

References: [4441]

[EC 1.1.1.361 created 2013]

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: [905]

[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 dehydro-

genase (NADP⁺) and EC 1.1.1.388, glucose-6-phosphate dehydrogenase (NAD⁺).

References: [3168, 2399, 744, 3425]

[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: $dTDP-6-deoxy-\alpha-D-allose + NAD(P)^+ = dTDP-4-dehydro-6-deoxy-\alpha-D-gulose + NAD(P)H + H^+$ **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: [235, 111, 4280, 2271]

[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 [1825, 35]. The en-

zyme 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 [2296]. Neither

enzyme shows any activity with NADH.

References: [1825, 35, 2296, 2664]

[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: [857]

[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: [2166, 2932, 2837]

[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: [2325]

[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, inos-

itol 2-dehydrogenase, and can also use D-glucose and D-xylose. It shows trace activity with D-ribose and D-fructose [3444]. It is part of a *myo*-inositol/D-*chiro*-inositol degradation pathway leading to

acetyl-CoA.

References: [3444, 4808]

[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: [2891]

[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: [2891]

[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): *gld1* (gene name); *gaaD* (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 glyceralde-

hyde reduction.

References: [2482, 2664]

[EC 1.1.1.372 created 2014]

EC 1.1.1.373

Accepted name: sulfolactaldehyde 3-reductase

Reaction: (2S)-2,3-dihydroxypropane-1-sulfonate + NAD⁺ = (2S)-3-sulfolactaldehyde + NADH + H⁺

Other name(s): yihU (gene name)

Systematic name: (2*S*)-2,3-dihydroxypropane-1-sulfonate:NAD⁺ 3-oxidoreductase

Comments: The enzyme, characterized from the bacterium Escherichia coli, is involved in the degradation path-

way 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: [880, 3826]

[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: [3007]

[EC 1.1.1.374 created 2014]

EC 1.1.1.375

Accepted name: L-2-hydroxycarboxylate dehydrogenase $[NAD(P)^+]$

Reaction: a (2S)-2-hydroxycarboxylate + NAD(P)⁺ = a 2-oxocarboxylate + NAD(P)H + H⁺

Other name(s): MdhII; lactate/malate dehydrogenase

Systematic name: (2S)-2-hydroxycarboxylate:NAD(P) $^+$ oxidoreductase

Comments: The enzyme from the archaeon Methanocaldococcus jannaschii catalyses the reversible oxida-

tion of (2*R*)-3-sulfolactate and (*S*)-malate to 3-sulfopyruvate and oxaloacetate, respectively (note that (2*R*)-3-sulfolactate has the same stereochemical configuration as (2*S*)-2-hydroxycarboxylates) [1386]. The enzyme can use both NADH and NADPH, although activity is higher with NADPH [1386, 2378, 2600]. The oxidation of (2*R*)-3-sulfolactate was observed only in the presence of NADP⁺ [1386]. The same organism also possesses an NAD⁺-specific enzyme with similar activity,

cf. EC 1.1.1.337, L-2-hydroxycarboxylate dehydrogenase (NAD⁺).

References: [1386, 2378, 2600]

[EC 1.1.1.375 created 2014]

EC 1.1.1.376

Accepted name: L-arabinose 1-dehydrogenase $[NAD(P)^+]$

Reaction: α -L-arabinopyranose + NAD(P)⁺ = L-arabinono-1,4-lactone + NAD(P)H + H⁺

Other name(s): L-arabino-aldose dehydrogenase

Systematic name: α -L-arabinopyranose: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. The enzyme is

specific for α -L-arabinopyranose [1927, 135].

References: [3111, 4557, 1927, 135]

[EC 1.1.1.376 created 2014, modified 2022]

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 degra-

dation 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: [2106]

[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: [4559, 4558]

[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 deriva-

tives, 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) [191, 192]. The enzyme transfers the

pro-R-hydrogen from NADH [192].

References: [191, 192]

[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: [729, 4614]

[EC 1.1.1.380 created 2014]

EC 1.1.1.381

Accepted name: 3-hydroxy acid dehydrogenase

Reaction: L-allo-threonine + NADP $^+$ = aminoacetone + CO $_2$ + NADPH + H $^+$ (overall reaction)

(1a) L-allo-threonine + NADP $^+$ = L-2-amino-3-oxobutanoate + NADPH + H $^+$

(1b) L-2-amino-3-oxobutanoate = aminoacetone + CO_2 (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: [1210]

[EC 1.1.1.381 created 2014, modified 2015]

EC 1.1.1.382

Accepted name: ketol-acid reductoisomerase (NAD⁺)

Reaction: (2R)-2,3-dihydroxy-3-methylbutanoate + NAD⁺ = (2S)-2-hydroxy-2-methyl-3-oxobutanoate +

 $NADH + H^{+}$

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

Comments: The enzyme, characterized from the bacteria Thermacetogenium phaeum and Desulfococcus oleovo-

rans 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: [443]

[EC 1.1.1.382 created 2015]

EC 1.1.1.383

Accepted name: ketol-acid reductoisomerase $[NAD(P)^+]$

Reaction: (2R)-2,3-dihydroxy-3-methylbutanoate + NAD(P)⁺ = (2S)-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: [443]

[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: [38, 4520, 1706, 2270]

[EC 1.1.1.384 created 2015]

EC 1.1.1.385

Accepted name: dihydroanticapsin dehydrogenase

Reaction: L-dihydroanticapsin + NAD $^+$ = L-anticapsin + NADH + H $^+$

Other name(s): BacC; *ywfD* (gene name)

Systematic name: L-dihydroanticapsin: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-anticapsin.

References: [3241]

[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: [1121]

[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 + CO $_2$ + 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: [4232]

[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: [3316]

[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: [2397]

[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 sulfo-

quinovose degradation pathway. Activity with NADP⁺ is only 4% of that with NAD⁺.

References: [1098]

[EC 1.1.1.390 created 2015]

EC 1.1.1.391

Accepted name: 3β-hydroxycholanate 3-dehydrogenase (NAD⁺)

Reaction: isolithocholate + NAD⁺ = 3-oxo- 5β -cholan-24-oate + NADH + H⁺

Other name(s): 3β-hydroxysteroid dehydrogenase

Systematic name: isolithocholate:NAD+ 3-oxidoreductase

Comments: This bacterial enzyme is involved, along with EC 1.1.1.52, 3α -hydroxycholanate dehydrogenase

 (NAD^+) , or EC 1.1.1.392, 3α -hydroxycholanate dehydrogenase $(NADP^+)$, in the modification of secondary bile acids to form 3β -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, 3β -

hydroxycholanate 3-dehydrogenase (NADP⁺).

References: [1013, 1014, 892]

[EC 1.1.1.391 created 2016]

EC 1.1.1.392

Accepted name: 3α-hydroxycholanate dehydrogenase (NADP⁺)

Reaction: lithocholate + NADP⁺ = 3-oxo- 5β -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 3β -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, 3α -hydroxycholanate dehydrogenase (NAD⁺).

References: [892]

[EC 1.1.1.392 created 2016]

EC 1.1.1.393

Accepted name: 3β -hydroxycholanate 3-dehydrogenase (NADP⁺)

Reaction: isolithocholate + NADP⁺ = 3-oxo- 5β -cholan-24-oate + NADPH + H⁺

Other name(s): 3β-hydroxysteroid dehydrogenase (ambiguous) Systematic name: isolithocholate:NADP⁺ 3-oxidoreductase

Comments: This bacterial enzyme is involved, along with EC 1.1.1.52, 3α -hydroxycholanate dehydrogenase

 (NAD^+) , or EC 1.1.1.392, 3α -hydroxycholanate dehydrogenase $(NADP^+)$, in the modification of secondary bile acids to form 3β -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, 3β -

hydroxycholanate 3-dehydrogenase (NAD⁺).

References: [46, 892]

[EC 1.1.1.393 created 2016]

EC 1.1.1.394

Accepted name: aurachin B dehydrogenase

Reaction: aurachin B + NAD⁺ + $H_2O = 4-[(2E,6E)-farnesyl]-4-hydroxy-2-methyl-3-oxo-3,4-dihydroquinoline$

1-oxide + NADH + H⁺ (overall reaction)

(1a) $4-[(2E,6E)-farnesyl]-3,4-dihydroxy-2-methyl-3,4-dihydroquinoline 1-oxide + NAD^+ = 4-$

[(2E,6E)-farnesyl]-4-hydroxy-2-methyl-3-oxo-3,4-dihydroquinoline 1-oxide + NADH + H⁺

(1b) aurachin B + $H_2O = 4-[(2E,6E)-farnesyl]-3,4-dihydroxy-2-methyl-3,4-dihydroquinoline 1-oxide$

(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-[(2E,6E)-farnesyl]-4-hydroxy-2-methyl-3-oxo-3,4-dihydroquinoline-1-oxide to form <math>4-[(2E,6E)-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: [2028]

[EC 1.1.1.394 created 2016]

EC 1.1.1.395

Accepted name: 3α-hydroxy bile acid-CoA-ester 3-dehydrogenase

Reaction: a 3α -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: 3α-hydroxy-bile-acid-CoA-ester:NAD⁺ 3-oxidoreductase

Comments: This bacterial enzyme is involved in the 7-dehydroxylation process associated with bile acid degrada-

tion. 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: [2632, 329]

[EC 1.1.1.395 created 2016]

Accepted name: bacteriochlorophyllide *a* dehydrogenase

Reaction: (1) 3-deacetyl-3-(1-hydroxyethyl)bacteriochlorophyllide $a + NAD^+$ = bacteriochlorophyllide $a + NAD^+$

 $NADH + H^{+}$

(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 (bacteriochlorophyl-

lide *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 bacteriochlorophyl-

lide a. The enzyme oxidizes a hydroxyl group on ring A, converting it to an oxo group.

References: [4581, 2749, 2345]

[EC 1.1.1.396 created 2016]

EC 1.1.1.397

Accepted name: β-methylindole-3-pyruvate reductase

Reaction: (2S,3R)-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: (2S,3R)-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: [973]

[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 degra-

dation.

References: [4409]

[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-oxidireductase

Comments: The enzyme catalyses a reversible reaction. The enzyme from the bacterium *Peptoniphilus asaccha-*

rolyticus is specific for (R)-2-hydroxyglutarate [2420, 1938]. 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 [4900].

References: [2420, 1938, 4900]

[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: [1110, 2248]

[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 thermosul-

fidooxidans, 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: [4558, 176]

[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: [3984, 3657, 217]

[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 degrada-

tion of D-threitol.

References: [1753]

[EC 1.1.1.403 created 2016]

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*, par-

ticipates in the degradation of pentachlorophenol.

References: [633, 4718]

[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 Zn^{2+} . The enzyme, characterized in bacteria, is specific for NADP. It is part of the syn-

thesis 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: [4936, 3288, 3289, 247]

[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 subtrate 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 en-

zyme also shows activity with D-tagatose (cf. EC 1.1.1.16, galactitol 2-dehydrogenase).

References: [3736, 556]

[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: [4615]

[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 + CO $_2$ + 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: [4887]

[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 + CO $_2$ + 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 + CO_2 (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: [4887]

[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: [4887]

[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: [4887]

[EC 1.1.1.411 created 2017]

EC 1.1.1.412

Accepted name: 2-alkyl-3-oxoalkanoate reductase

Reaction: a (2R,3S)-2-alkyl-3-hydroxyalkanoate + NADP⁺ = an (R)-2-alkyl-3-oxoalkanoate + NADPH + H⁺

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

Systematic name: (2R,3S)-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: [386]

[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 (3R,4R)-3-[(1S)-1-hydroxyalkyl]-4-(hydroxymethyl)oxolan-2-one + NADP⁺ = a (3R,4R)-3-

alkanoyl-4-(hydroxymethyl)oxolan-2-one + NADPH + H+

Other name(s): barS1 (gene name)

Systematic name: (3R,4R)-3-[(1S)-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) configura-

tion.

References: [3861]

[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, partici-

pates in an L-galactonate degradation pathway.

References: [728, 2280, 1678]

[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: [637, 2464]

[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: [2401]

[EC 1.1.1.416 created 2018]

EC 1.1.1.417

Accepted name: 3β-hydroxysteroid-4β-carboxylate 3-dehydrogenase (decarboxylating)

Reaction: a 3β -hydroxy- 4α -methylsteroid- 4β -carboxylate + NAD(P)⁺ = a 4α -methyl-3-oxosteroid + NAD(P)H

 $+ CO_2 + H^+$

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

Systematic name: 3β -hydroxysteroid- 4β -carboxylate:NAD(P)⁺ 3-oxidoreductase (decarboxylating)

Comments: This bacterial enzyme participates in the biosynthesis of bacterial sterols. Together with EC

1.14.13.246, 4β -methylsterol monooxygenase (SdmA) it forms an enzyme system that removes one methyl group from the C-4 position of 4,4-dimethylated steroid molecules. SdmA catalyses three successive oxidations of the C-4 β methyl group, turning it into a carboxylate group; SdmB is a bifunctional enzyme that catalyses two different activities. As EC 1.1.1.417 it catalyses an oxidative decarboxylation that results in reduction of the 3β -hydroxy group at the C-3 carbon to an oxo group. As EC 1.1.1.270, 3β -hydroxysteroid 3-dehydrogenase, it reduces the 3-oxo group back to a 3β -hydroxyl. Since the remaining methyl group at C-4 is in an α orientation, it cannot serve as a substrate for a second round of demethylation by this system.

References: [2376]

[EC 1.1.1.417 created 2019]

EC 1.1.1.418

Accepted name: plant 3β-hydroxysteroid- 4α -carboxylate 3-dehydrogenase (decarboxylating) **Reaction:** a 3β-hydroxysteroid- 4α -carboxylate + NAD⁺ = a 3-oxosteroid + CO₂ + NADH

Other name(s): 3β-HSD/D1 (gene name); 3β-HSD/D2 (gene name); 3β-hydroxysteroid dehydrogenases/C-4 decar-

boxylase (ambiguous)

Systematic name: 3β -hydroxysteroid- 4α -carboxylate:NAD⁺ 3-oxidoreductase (decarboxylating)

Comments: The enzyme, found in plants, catalyses multiple reactions during plant sterol biosynthesis. Unlike

the fungal/animal enzyme EC 1.1.1.170, 3β-hydroxysteroid-4α-carboxylate 3-dehydrogenase (decar-

boxylating), the plant enzyme is specific for NAD⁺.

References: [3567, 3427, 3426]

[EC 1.1.1.418 created 2019]

EC 1.1.1.419

Accepted name: nepetalactol dehydrogenase

Reaction: (1) (+)-cis,cis-nepetalactol + NAD⁺ = (+)-cis,cis-nepetalactone + NADH + H⁺

(2) (+)-cis,trans-nepetalactol + NAD⁺ = (+)-cis,trans-nepetalactone + NADH + H⁺

Other name(s): NEPS1 (gene name)

Systematic name: nepetalactol:NAD⁺ 1-oxidoreductase

Comments: The enzyme, characterized from the plant *Nepeta mussinii*, binds an NAD⁺ cofactor. It also catalyses

the activity of EC 5.5.1.34, (+)-cis,trans-nepetalactol synthase.

References: [2476, 2477]

[EC 1.1.1.419 created 2019]

EC 1.1.1.420

Accepted name: D-apiose dehydrogenase

Reaction: D-apiofuranose + NAD $^+$ = D-apionolactone + NADH + H $^+$

Other name(s): apsD (gene name)

Systematic name: D-apiofuranose:NAD⁺ 1-oxidoreductase

Comments: The enzyme, characterized from several bacterial species, is involved in a catabolic pathway for D-

apiose.

References: [565]

[EC 1.1.1.420 created 2019]

EC 1.1.1.421

Accepted name: D-apionate oxidoisomerase

Reaction: D-apionate + NAD⁺ = 3-oxoisoapionate + NADH + H⁺

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

Systematic name: D-apionate:NAD⁺ oxidoreductase (isomerizing)

Comments: The enzyme, characterized from several bacterial species, participates in the degradation of D-

apionate. The reaction involves migration of a hydroxymethyl group from position 3 to position 2 and oxidation of the 3-hydroxyl group. Stereospecificity of the product, 3-oxoisoapionate, has not been

determined.

References: [565]

[EC 1.1.1.421 created 2019]

EC 1.1.1.422

Accepted name: pseudoephedrine dehydrogenase

Reaction: (+)-(1S,2S)-pseudoephedrine + NAD⁺ = (S)-2-(methylamino)-1-phenylpropan-1-one + NADH + H⁺

Other name(s): PseDH

Systematic name: (+)-(1S,2S)-pseudoephedrine:NAD $^+$ 1-oxidoreductase

Comments: The enzyme, characterized from the bacterium *Arthrobacter* sp. TS-15, acts on a broad range of dif-

ferent aryl-alkyl ketones, such as haloketones, ketoamines, diketones, and ketoesters. It accepts various types of aryl groups including phenyl-, pyridyl-, thienyl-, and furyl-rings, but the presence of an aromatic ring is essential for the activity. In addition, the presence of a functional group on the alkyl chain, such as an amine, a halogen, or a ketone, is also crucial. The enzyme exhibits a strict anti-Prelog enantioselectivity. When acting on diketones, it catalyses the reduction of only the keto group closest to the ring, with no further reduction to the diol. *cf.* EC 1.1.1.423, ephedrine dehydrogenase.

References: [3819, 3817, 3818]

[EC 1.1.1.422 created 2020]

EC 1.1.1.423

Accepted name: (1*R*,2*S*)-ephedrine 1-dehydrogenase

Reaction: (-)-(1R,2S)-ephedrine + NAD⁺ = (S)-2-(methylamino)-1-phenylpropan-1-one + NADH + H⁺

Other name(s): EDH; ephedrine dehydrogenase

Systematic name: (-)-(1R,2S)-ephedrine:NAD⁺ 1-oxidoreductase

Comments: The enzyme, characterized from the bacterium *Arthrobacter* sp. TS-15, acts on a broad range of dif-

ferent aryl-alkyl ketones, such as haloketones, ketoamines, diketones, and ketoesters. It exhibits a strict enantioselectivity and accepts various types of aryl groups including phenyl-, pyridyl-, thienyl-, and furyl-rings, but the presence of an aromatic ring is essential for the activity. In addition, the presence of a functional group on the alkyl chain, such as an amine, a halogen, or a ketone, is also crucial. When acting on diketones, it catalyses the reduction of only the keto group closest to the ring, with no further reduction to the diol. *cf.* EC 1.1.1.422, pseudoephedrine dehydrogenase and EC 1.5.1.18,

ephedrine dehydrogenase.

References: [3819, 3817]

[EC 1.1.1.423 created 2020, modified 2020]

EC 1.1.1.424

Accepted name: D-xylose 1-dehydrogenase (NADP⁺, D-xylono-1,4-lactone-forming)

Reaction: D-xylose + NADP $^+$ = D-xylono-1,4-lactone + NADPH + H $^+$

Other name(s): xacA (gene name); xdh (gene name)

Systematic name: D-xylose:NADP⁺ 1-oxidoreductase (D-xylono-1,4-lactone-forming)

Comments: The enzyme, which participates in the degradation of D-xylose, has been characterized from several

halophilic archaeal species. cf. EC 1.1.1.179, D-xylose 1-dehydrogenase (NADP⁺, D-xylono-1,5-

lactone-forming).

References: [1926, 1925, 4131]

[EC 1.1.1.424 created 2020]

Accepted name: levoglucosan dehydrogenase

Reaction: levoglucosan + NAD $^+$ = 3-dehydrolevoglucosan + NADH + H $^+$

Other name(s): 1,6-anhydro-β-D-glucose dehydrogenase

Systematic name: 1,6-anhydro-β-D-glucopyranose:NAD⁺ 3-oxidoreductase

Comments: Levoglucosan is formed from the pyrolysis of carbohydrates such as starch and cellulose and is an important molecular marker for pollution from biomass burning. This enzyme is present only in bacteria

portant molecular marker for pollution from biomass burning. This enzyme is present only in bacteria, and has been characterized from *Arthrobacter* sp. I-552 and *Pseudarthrobacter phenanthrenivorans*.

cf. EC 2.7.1.232, levoglucosan kinase.

References: [2975, 4102]

[EC 1.1.1.425 created 2021]

EC 1.1.1.426

Accepted name: UDP-*N*-acetyl-α-D-quinovosamine dehydrogenase

Reaction: UDP-*N*-acetyl- α -D-quinovosamine + NAD(P)⁺ = UDP-2-acetamido-2,6-dideoxy- α -D-xylohex-4-

ulose + $NAD(P)H + H^+$

Other name(s): wbpV (gene name); wreQ (gene name)

Systematic name: UDP-*N*-acetyl- α -D-quinovosamine:NAD(P)⁺ 4-dehydrogenase

Comments: The enzyme participates in the biosynthesis of N-acetyl- α -D-quinovosamine, a 6-deoxy sugar that

is present in the O antigens of many Gram-negative bacteria, including Pseudomonas aeruginosa

serotypes O6 and O10, Rhizobium etli, and Brucella abortus.

References: [277, 1147, 2458]

[EC 1.1.1.426 created 2021]

EC 1.1.1.427

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

Reaction: D-arabinofuranose + NADP⁺ = D-arabinono-1,4-lactone + NADPH + H⁺

Other name(s): AraDH; adh-4 (gene name)

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

Comments: The enzyme from the archaeon Saccharolobus solfataricus is tetrameric and contains zinc. L-fucose

also is a substrate. In contrast to EC 1.1.1.116 (D-arabinose 1-dehydrogenase (NAD⁺)) and EC 1.1.1.117 (D-arabinose 1-dehydrogenase [NAD(P)⁺]), this enzyme is specific for NADP⁺.

References: [455, 454]

[EC 1.1.1.427 created 2022]

EC 1.1.1.428

Accepted name: 4-methylthio 2-oxobutanoate reductase (NADH)

Reaction: (2R)-2-hydroxy-4-(methylsulfanyl)butanoate + NAD⁺ = 4-(methylsulfanyl)-2-oxobutanoate + NADH

 $+ H^+$

Other name(s): CTBP1 (gene name); *C*-terminal-binding protein 1; MTOB reductase; 4-methylthio 2-oxobutyrate

reductase; 4-methylthio 2-oxobutyric acid reductase

Systematic name: (2R)-2-hydroxy-4-(methylsulfanyl)butanoate:NAD⁺ 2-oxidoreductase

Comments: The substrate of this enzyme is formed as an intermediate during L-methionine salvage from S-

methyl-5'-thioadenosine, which is formed during the biosynthesis of polyamines. The human enzyme also functions as a transcriptional co-regulator that downregulates the expression of many tumor-suppressor genes, thus providing a link between gene repression and the methionine salvage pathway. A similar, but NADP-specific, enzyme is involved in dimethylsulfoniopropanoate biosynthesis in al-

gae and phytoplankton.

References: [2284, 7, 1650, 2236]

[EC 1.1.1.428 created 2022]

Accepted name: (2S)-[(R)-hydroxy(phenyl)methyl]succinyl-CoA dehydrogenase

Reaction: (2S)-[(R)-hydroxy(phenyl)methyl]succinyl-CoA + NAD⁺ = <math>(S)-2-benzoylsuccinyl-CoA + NADH +

 H^+

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

Systematic name: (2S)-[(R)-hydroxy(phenyl)methyl]succinyl-CoA:NAD⁺ oxidoreductase

Comments: The enzyme, purified from the bacterium *Thauera aromatica*, is involved in an anaerobic toluene

degradation pathway. It is specific for NAD⁺.

References: [4468]

[EC 1.1.1.429 created 2022]

EC 1.1.1.430

Accepted name: D-xylose reductase (NADH)

Reaction: $xylitol + NAD^+ = D-xylose + NADH + H^+$

Other name(s): XYL1 (gene name) (ambiguous)

Systematic name: xylitol:NAD+ oxidoreductase

Comments: Xylose reductases catalyse the reduction of xylose to xylitol, the initial reaction in the fungal D-xylose

degradation pathway. Most of the enzymes exhibit a strict requirement for NADPH (cf. EC 1.1.1.431, D-xylose reductase (NADPH)). Some D-xylose reductases have dual coenzyme specificity, though they still prefer NADPH to NADH (cf. EC 1.1.1.307, D-xylose reductase [NAD(P)H]). The enzyme from *Candida parapsilosis* is a rare example of a xylose reductase that significantly prefers NADH, with K_m and V_{max} values for NADH being 10-fold lower and 10-fold higher, respectively, than for

NADPH.

References: [2386]

[EC 1.1.1.430 created 2022]

EC 1.1.1.431

Accepted name: D-xylose reductase (NADPH)

Reaction: $xylitol + NADP^+ = D-xylose + NADPH + H^+$

Other name(s): XYL1 (gene name, ambiguous); xyl1 (gene name, ambiguous); xyrA (gene name); xyrB (gene name)

Systematic name: xylitol:NADP⁺ oxidoreductase

Comments: Xylose reductases catalyse the reduction of xylose to xylitol, the initial reaction in the fungal D-xylose

degradation pathway. Most of the enzymes exhibit a strict requirement for NADPH (e.g. the enzymes from *Saccharomyces cerevisiae*, *Aspergillus niger*, *Trichoderma reesei*, *Candida tropicalis*, *Saitozyma flava*, and *Candida intermedia*). Some D-xylose reductases have dual coenzyme specificity, though they still prefer NADPH to NADH (*cf.* EC 1.1.1.307, D-xylose reductase [NAD(P)H]). Very rarely the

enzyme prefers NADH (cf. EC 1.1.1.430, D-xylose reductase (NADH)).

References: [376, 4144, 3065, 2734, 3797, 1904, 686, 4245]

[EC 1.1.1.431 created 2022]

EC 1.1.1.432

Accepted name: 6-dehydroglucose reductase

Reaction: D-glucose + NADP $^+$ = 6-dehydro-D-glucose + NADPH + H $^+$ **Other name(s):** D-glucose 6-dehydrogenase; smoB (gene name); squF (gene name)

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

Comments: The enzyme, characterized from alphaproteobacteria, is involved in a D-sulfoquinovose degradation

pathway.

References: [3827, 2516]

[EC 1.1.1.432 created 2022]

Accepted name: sulfoacetaldehyde reductase (NADH)

Reaction: isethionate + NAD $^+$ = 2-sulfoacetaldehyde + NADH + H $^+$

Other name(s): sarD (gene name); tauF (gene name); sqwF (gene name); BkTauF

Systematic name: isethionate:NAD⁺ oxidoreductase

Comments: The enzymes from the bacteria *Bilophila wadsworthia* and *Clostridium* sp. MSTE9 catalyse the re-

action only in the reduction direction. In the bacterium *Bifidobacterium kashiwanohense* the optimal reaction pH for sulfoacetaldehyde reduction is 7.5, while that for isethionate oxidation is 10.0. *cf.* EC

1.1.1.313, sulfoacetaldehyde reductase (NADPH).

References: [3275, 4702, 4918, 2516]

[EC 1.1.1.433 created 2022]

EC 1.1.1.434

Accepted name: 2-dehydro-3-deoxy-L-fuconate 4-dehydrogenase

Reaction: 2-dehydro-3-deoxy-L-fuconate + NAD $^+$ = 2,4-didehydro-3-deoxy-L-fuconate + NADH + H $^+$

Systematic name: 2-dehydro-3-deoxy-L-fuconate:NAD⁺ 4-oxidoreductase

Comments: The enzyme, originally described from the bacterium Xanthomonas campestris pv. campestris, par-

ticipates in an L-fucose degradation pathway. It can also act on 2-dehydro-3-deoxy-L-galactonate and

2-dehydro-3-deoxy-D-pentonate.

References: [4789, 4556]

[EC 1.1.1.434 created 2022]

EC 1.1.1.435

Accepted name: L-fucose dehydrogenase

Reaction: β -L-fucopyranose + NADP⁺ = L-fucono-1,5-lactone + NADPH + H⁺

Systematic name: β-L-fucopyranose:NADP⁺ 1-oxidoreductase

Comments: The enzyme, characterized from the bacterium Burkholderia multivorans, participates in an L-fucose

degradation pathway. The enzyme catalyses the oxidation of β -L-fucopyranose to L-fucono-1,5-lactone, which is unstable and is rapidly converted to L-fucono-1,4-lactone. The α anomer is not recognized. The enzyme can also act on β -L-galactopyranose and D-arabinose with lower activity.

NADP⁺ is a better cosubstrate than NAD⁺.

References: [1677]

[EC 1.1.1.435 created 2022]

EC 1.1.1.436

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 confur-

cation to drive endergonic lactate oxidation with NAD+ as oxidant at the expense of simultaneous

exergonic electron flow from reduced ferredoxin to NAD+.

References: [4571]

[EC 1.1.1.436 created 2015 as EC 1.3.1.110, transferred 2022 to EC 1.1.1.436]

EC 1.1.1.437

Accepted name: 5-dehydrofumagillol 5-reductase

Reaction: fumagillol + NADP $^+$ = 5-dehydrofumagillol + NADPH + H $^+$

Other name(s): af490 (gene name); Fma-KR

Systematic name: fumagillol:NADP⁺ 5-oxidoreductase

Comments: The enzyme, characterized from the mold *Aspergillus fumigatus*, participates in the biosynthesis of

the meroterpenoid fumagillin. It is a partial polyketide synthase (PKS) consisting of only a dehy-

dratase (DH) and a ketoreductase (KR) domain.

References: [2489]

[EC 1.1.1.437 created 2022]

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 ferrocytochrome $c + 2 H^+$

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: [129, 667]

[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 ferrocytochrome c + 2 H⁺

Other name(s): lactic acid dehydrogenase; cytochrome b_2 (flavin-free derivative of flavocytochrome b_2); flavocy-

tochrome b_2 ; L-lactate cytochrome c reductase; L(+)-lactate:cytochrome c oxidoreductase; dehydrogenase, lactate (cytochrome); L-lactate cytochrome c oxidoreductase; lactate dehydrogenase (cy-

tochrome); lactic cytochrome c reductase

Systematic name: (S)-lactate:ferricytochrome-c 2-oxidoreductase

Comments: Identical with cytochrome b_2 ; a flavohemoprotein (FMN).

References: [120, 119, 171, 3120]

[EC 1.1.2.3 created 1961]

EC 1.1.2.4

Accepted name: D-lactate dehydrogenase (cytochrome)

Reaction: (R)-lactate + 2 ferricytochrome $c = \text{pyruvate} + 2 \text{ ferrocytochrome } c + 2 \text{ H}^+$

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:** [1403, 1404, 3119, 3120]

[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 ferrocytochrome 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: [3133]

[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 + ferrocytochrome 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: [3867, 3869, 2634, 1673, 1747, 2042]

[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 ferrocytochrome c_l + 2 H⁺

Other name(s): methanol dehydrogenase; MDH (ambiguous) 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: [108, 109, 980, 3647, 757, 347, 4694, 30, 107, 4634]

[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** ferrocytochrome c + **2** H⁺ 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 disul-

fide ring structure in close proximity to the PQQ.

References: [3605, 4319, 3739, 2058, 2049, 2770]

[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 ferrocytochrome 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 bu*-

tanivorans, 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: [4421, 4422, 4423]

[EC 1.1.2.9 created 2016]

EC 1.1.2.10

Accepted name: lanthanide-dependent methanol dehydrogenase

Reaction: methanol + 2 oxidized cytochrome c_l = formaldehyde + 2 reduced cytochrome c_l

Other name(s): XoxF; XoxF-MDH; Ce-MDH; La³⁺-dependent MDH; Ce³⁺-induced methanol dehydrogenase;

cerium dependent MDH

Systematic name: methanol:cytochrome c_l oxidoreductase

Comments: Isolated from the bacterium *Methylacidiphilum fumariolicum* and many *Methylobacterium* species.

Requires La³⁺, Ce³⁺, Pr³⁺ or Nd³⁺. The higher lanthanides show decreasing activity with Sm³⁺, Eu³⁺ and Gd³⁺. The lanthanide is coordinated by the enzyme and pyrroloquinoline quinone. Shows little activity with Ca²⁺, the required cofactor of EC 1.1.2.7, methanol dehydrogenase (cytochrome c).

References: [1638, 2974, 3344, 370, 3373, 2694]

[EC 1.1.2.10 created 2019]

EC 1.1.2.11

Accepted name: glucoside 3-dehydrogenase (cytochrome c)

Reaction: a D-glucoside + a ferric *c*-type cytochrome = a 3-dehydro-D-glucoside + a ferrous *c*-type cytochrome **Other name(s):** D-glucoside 3-dehydrogenase (ambiguous); D-aldohexopyranoside dehydrogenase (ambiguous); D-

aldohexoside:cytochrome c oxidoreductase; hexopyranoside-cytochrome c oxidoreductase

Systematic name: a D-glucoside:ferric c-type cytochrome 3-oxidoreductase

Comments: This bacterial enzyme acts on D-glucose, D-galactose, D-glucosides and D-galactosides, but the

best substrates are disaccharides with a glucose moiety at the non-reducing end. It consists of two subunits, a catalytic subunit that contains an FAD cofactor and an iron-sulfur cluster, and a "hitch-hiker" subunit containing a signal peptide for translocation into the periplasm. A dedicated *c*-type cytochrome protein serves as an electron acceptor, transferring the electrons from the catalytic subunit

to the cell's electron transfer chain. cf. EC 1.1.99.13, glucoside 3-dehydrogenase (acceptor).

References: [1576, 2979, 4184, 4183, 4340, 2207, 4877, 4876, 2843]

[EC 1.1.2.11 created 2022]

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 + O_2 = pyruvate + H_2O_2

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: [983, 2603, 1319, 4376, 1239, 4043]

[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 + O_2 = D-glucono-1,5-lactone + H_2O_2

Other name(s): glucose oxyhydrase; corylophyline; penatin; glucose aerodehydrogenase; microcid; β-D-glucose oxi-

dase; D-glucose oxidase; D-glucose-1-oxidase; β -D-glucose:quinone oxidoreductase; glucose oxyhy-

drase; deoxin-1; GOD

Systematic name: β -D-glucose:oxygen 1-oxidoreductase

Comments: A flavoprotein (FAD). **References:** [291, 750, 2055, 2056]

[EC 1.1.3.4 created 1961]

EC 1.1.3.5

Accepted name: hexose oxidase

Reaction: D-glucose + O_2 = D-glucono-1,5-lactone + H_2O_2

Systematic name: D-hexose:oxygen 1-oxidoreductase

Comments: A copper glycoprotein. Also oxidizes D-galactose, D-mannose, maltose, lactose and cellobiose.

References: [254, 255, 4111]

[EC 1.1.3.5 created 1961, modified 1976]

EC 1.1.3.6

Accepted name: cholesterol oxidase

Reaction: cholesterol + O_2 = cholest-5-en-3-one + H_2O_2

Other name(s): cholesterol- O_2 oxidoreductase; 3β -hydroxy steroid oxidoreductase; 3β -hydroxysteroid:oxygen oxi-

doreductase

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 Δ^5 position to Δ^6 position (*cf.* EC 5.3.3.1, steroid Δ -isomerase).

References: [3514, 3997, 2594, 4477]

[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 + O_2 = an aromatic aldehyde + H_2O_2 **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: [1092]

[EC 1.1.3.7 created 1965]

EC 1.1.3.8

Accepted name: L-gulonolactone oxidase

Reaction: L-gulono-1,4-lactone + O_2 = L-ascorbate + H_2O_2 (overall reaction)

(1a) L-gulono-1,4-lactone + O_2 = L-xylo-hex-2-ulono-1,4-lactone + H_2O_2

(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 asborbic acid, primates and guinea pigs cannot [3077].

References: [1826, 2141, 3077, 613]

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

EC 1.1.3.9

Accepted name: galactose oxidase

Reaction: D-galactose + O_2 = D-galacto-hexodialdose + H_2O_2

Other name(s): D-galactose oxidase; β-galactose oxidase Systematic name: D-galactose: oxygen 6-oxidoreductase

Comments: A copper protein.

References: [159]

[EC 1.1.3.9 created 1965]

EC 1.1.3.10

Accepted name: pyranose oxidase

Reaction: D-glucose + O_2 = 2-dehydro-D-glucose + H_2O_2

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: [1890, 2592, 3039, 3598]

[EC 1.1.3.10 created 1972]

EC 1.1.3.11

Accepted name: L-sorbose oxidase

Reaction: L-sorbose + O_2 = 5-dehydro-D-fructose + H_2O_2

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: [4728]

[EC 1.1.3.11 created 1972]

EC 1.1.3.12

Accepted name: pyridoxine 4-oxidase

Reaction: pyridoxine + O_2 = pyridoxal + H_2O_2 **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: [4122]

[EC 1.1.3.12 created 1972, modified 1976]

EC 1.1.3.13

Accepted name: alcohol oxidase

Reaction: a primary alcohol + O_2 = an aldehyde + H_2O_2 **Other name(s):** ethanol oxidase; alcohol:oxygen oxidoreductase **Systematic name:** alcohol:oxygen oxidoreductase (H_2O_2 -forming)

Comments: The enzymes from the fungi *Candida methanosorbosa* and several *Basidiomycetes* species contain an

FAD cofactor [1889, 4133]. The enzyme from the phytopathogenic fungi *Colletotrichum graminicola* and *Colletotrichum gloeosporioides* utilize a mononuclear copper-radical mechanism [4792]. The enzyme acts on primary alcohols and unsaturated alcohols, and has much lower activity with branched-

chain and secondary alcohols.

References: [1889, 3073, 4133, 4792]

[EC 1.1.3.13 created 1972]

EC 1.1.3.14

Accepted name: catechol oxidase (dimerizing)

Reaction: 4 catechol + $3 O_2 = 2$ dibenzo[1,4]dioxin-2,3-dione + $6 H_2O$

Systematic name: catechol:oxygen oxidoreductase (dimerizing)

References: [2970]

[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 + O_2 = a 2-oxo carboxylate + H_2O_2

Other name(s): hydroxy-acid oxidase A; hydroxy-acid oxidase B; glycolate oxidase; L-2-hydroxy acid oxidase; hy-

droxyacid 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: [353, 1189, 2287, 2990, 2992, 3315, 3759, 1944]

[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 + O_2 = 3-dehydroecdysone + H_2O_2

Other name(s): β -ecdysone oxidase

Systematic name: ecdysone:oxygen 3-oxidoreductase

Comments: 2,6-Dichloroindophenol can act as an acceptor.

References: [2228]

[EC 1.1.3.16 created 1976]

EC 1.1.3.17

Accepted name: choline oxidase

Reaction: choline + $2 O_2 + H_2O = betaine + <math>2 H_2O_2$ (overall reaction)

(1a) choline + O_2 = betaine aldehyde + H_2O_2 (1b) betaine aldehyde + O_2 + H_2O = betaine + H_2O_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) [4485]. 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: [1801, 3588, 3448, 1252, 1083, 4485, 1084, 1249]

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

EC 1.1.3.18

Accepted name: secondary-alcohol oxidase

Reaction: a secondary alcohol + O_2 = a ketone + H_2O_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: [2893, 3637, 4142, 4143]

[EC 1.1.3.18 created 1981]

EC 1.1.3.19

Accepted name: 4-hydroxymandelate oxidase (decarboxylating)

Reaction: (S)-4-hydroxymandelate + O_2 = 4-hydroxybenzaldehyde + CO_2 + H_2O_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 Mn²⁺. The enzyme from the bacterium *Pseudomonas putida* is in-

volved in the degradation of mandelate.

References: [325]

[EC 1.1.3.19 created 1984, modified 2014]

EC 1.1.3.20

Accepted name: long-chain-alcohol oxidase

Reaction: a long-chain alcohol + O_2 = a long-chain aldehyde + H_2O_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: [2880, 2881, 644, 4903, 645]

[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 + O_2 = glycerone phosphate + H_2O_2

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: [1268, 2183]

[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 + $2 O_2 + H_2 O =$ thiamine acetic acid + $2 H_2 O_2$

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: [1018, 1355, 3030]

[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 $+ O_2 = 2$ -oxophytanate $+ H_2O_2$ **Other name(s):** L-2-hydroxyphytanate:oxygen 2-oxidoreductase **Systematic name:** L-2-hydroxyphytanate:oxygen 2-oxidoreductase

References: [4395]

[EC 1.1.3.27 created 1990]

EC 1.1.3.28

Accepted name: nucleoside oxidase

Reaction: inosine + O_2 = 9-riburonosylhypoxanthine + H_2O

(1a) 2 inosine + O_2 = 2 5'-dehydroinosine + 2 H_2O

(1b) 2 5'-dehydroinosine + O_2 = 2 9-riburonosylhypoxanthine

Systematic name: nucleoside:oxygen 5'-oxidoreductase

Comments: Other purine and pyrimidine nucleosides (as well as 2'-deoxyribonucleosides) are substrates, but ri-

bose 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 (H_2O_2 -forming), as it produces water

rather than hydrogen peroxide.

References: [1839, 1838]

[EC 1.1.3.28 created 1992, modified 2001]

EC 1.1.3.29

Accepted name: *N*-acylhexosamine oxidase

Reaction: (1) N-acetyl-D-glucosamine + $O_2 + H_2O = N$ -acetyl-D-glucosaminate + H_2O_2 (overall reaction)

(1a) N-acetyl-D-glucosamine + $O_2 = N$ -acetyl-D-glucosamino-1,5-lactone + H_2O_2

(1b) N-acetyl-D-glucosamino-1,5-lactone + $H_2O = N$ -acetyl-D-glucosaminate (spontaneous) (2) N-acetyl-D-galactosamine + $O_2 + H_2O = N$ -acetyl-D-galacotsaminate + $O_2 + O_2 = N$ -acetyl-D-ga

(2a) N-acetyl-D-galactosamine + O_2 = N-acetyl-D-galactosamino-1,5-lactone + H_2O_2

(2b) N-acetyl-D-galactosamino-1,5-lactone + $H_2O = N$ -acetyl-D-galactosaminate (spontaneous)

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: The enzyme, found in bacteria, also acts more slowly on *N*-acetyl-D-mannosamine.

References: [1726, 3495]

[EC 1.1.3.29 created 1992, modified 2022]

EC 1.1.3.30

Accepted name: polyvinyl-alcohol oxidase

Reaction: polyvinyl alcohol + O_2 = oxidized polyvinyl alcohol + H_2O_2

Other name(s): dehydrogenase, polyvinyl alcohol; PVA oxidase
Systematic name: polyvinyl-alcohol:oxygen oxidoreductase

References: [3868, 3869]

[EC 1.1.3.30 created 1992]

[1.1.3.31 Deleted entry. methanol oxidase. Cannot be distingu

[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. berbamunine synthase. Now EC 1.14.21.3, berbamunine 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 + O_2 = dehydro-D-arabinono-1,4-lactone + H_2O_2

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 [1767]. With L-galactono-1,4-lactone as substrate, the product is L-ascorbate [2377]. 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 [1767].

References: [1767, 1768, 2377]

[EC 1.1.3.37 created 1999]

EC 1.1.3.38

Accepted name: vanillyl-alcohol oxidase

Reaction: vanillyl alcohol + O_2 = vanillin + H_2O_2 **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 aldehy-

des. The allyl group of 4-allylphenols is also converted into the -CH=CH-CH₂OH group.

References: [846, 1158]

[EC 1.1.3.38 created 1999]

EC 1.1.3.39

Accepted name: nucleoside oxidase (H₂O₂-forming)

Reaction: adenosine + $2 O_2 + H_2O = 9$ -riburonosyladenine + $2 H_2O_2$ (overall reaction)

(1a) adenosine + $O_2 = 5'$ -dehydroadenosine + H_2O_2

(1b) 5'-dehydroadenosine + O_2 + H_2O = 9-riburonosyladenine + H_2O_2

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: [2194]

[EC 1.1.3.39 created 2001]

EC 1.1.3.40

Accepted name: D-mannitol oxidase

Reaction: D-mannitol $+ O_2 = D$ -mannose $+ H_2O_2$ **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: [4473, 2630, 2352, 796]

[EC 1.1.3.40 created 2001]

EC 1.1.3.41

Accepted name: alditol oxidase

Reaction: an alditol + O_2 = an aldose + H_2O_2

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 oxi-

dase containing one molecule of FAD per molecule of protein [4752, 1633]. 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 [4752, 1633]. Belongs in the vanillyl-alcohol-oxidase family of en-

zymes [1633].

References: [4752, 1633, 1145]

[EC 1.1.3.41 created 2002, modified 2008]

EC 1.1.3.42

Accepted name: prosolanapyrone-II oxidase

Reaction: prosolanapyrone II + O_2 = prosolanapyrone III + H_2O_2

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 bi-

functional 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: [2003, 2013, 2012]

[EC 1.1.3.42 created 2011]

EC 1.1.3.43

Accepted name: paromamine 6'-oxidase

Reaction: paromamine + $O_2 = 6'$ -dehydroparomamine + H_2O_2

 $\textbf{Other name(s):} \quad \textit{btrQ} \text{ (gene name); } \textit{neoG} \text{ (gene name); } \textit{kanI} \text{ (gene name); } \textit{tacB} \text{ (gene name); } \textit{neoQ} \text{ (obsolete gene name); } \textit{tacB} \text{ (gene name); } \textit{neoQ} \text{ (obsolete gene name); } \textit{tacB} \text{ (gene name); } \textit{neoQ} \text{ (obsolete gene name); } \textit{tacB} \text{ (gene name$

name)

Systematic name: paromamine:oxygen 6'-oxidoreductase

Comments: Contains FAD. Involved in the biosynthetic pathways of several clinically important aminocycli-

tol 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: [1751, 4839, 700]

[EC 1.1.3.43 created 2012]

EC 1.1.3.44

Accepted name: 6'''-hydroxyneomycin C oxidase

Reaction: 6'''-deamino-6'''-hydroxyneomycin C + $O_2 = 6'''$ -deamino-6'''-oxoneomycin C + H_2O_2

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: [1751, 700]

[EC 1.1.3.44 created 2012]

EC 1.1.3.45

Accepted name: aclacinomycin-N oxidase

Reaction: aclacinomycin N + O_2 = aclacinomycin A + H_2O_2

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 in-

volved in the modification of the terminal sugar residues in the biosynthesis of aclacinomycins. The enzyme utilizes the same active site to catalyse the oxidation of the rhodinose moiety of aclacinomycin N to the cinerulose A moiety of aclacinomycin A and the oxidation of the latter to the L-

aculose moiety of aclacinomycin Y (cf. EC 1.3.3.14, aclacinomycin A oxidase).

References: [66, 4112]

[EC 1.1.3.45 created 2013]

EC 1.1.3.46

Accepted name: 4-hydroxymandelate oxidase

Reaction: (S)-4-hydroxymandelate + O_2 = 2-(4-hydroxyphenyl)-2-oxoacetate + H_2O_2

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: [1758, 2459]

[EC 1.1.3.46 created 2014]

EC 1.1.3.47

Accepted name: 5-(hydroxymethyl)furfural oxidase

Reaction: 5-(hydroxymethyl)furfural + $3 O_2 + 2 H_2O = \text{furan-2,5-dicarboxylate} + <math>3 H_2O_2 \text{ (overall reaction)}$

(1a) 5-(hydroxymethyl)furfural + O_2 = furan-2,5-dicarbaldehyde + H_2O_2

(1b) furan-2,5-dicarbaldehyde + H_2O = 5-(dihydroxymethyl)furan-2-carbaldehyde (spontaneous) (1c) 5-(dihydroxymethyl)furan-2-carbaldehyde + O_2 = 5-formylfuran-2-carboxylate + H_2O_2 (1d) 5-formylfuran-2-carboxylate + H_2O = 5-(dihydroxymethyl)furan-2-carboxylate (spontaneous)

(1e) 5-(dihydroxymethyl)furan-2-carboxylate + O_2 = furan-2,5-dicarboxylate + H_2O_2

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 [914]. The enzyme has

a broad substrate range that overlaps with EC 1.1.3.7, aryl-alcohol oxidase.

References: [2229, 913, 914]

[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 + $O_2 = 3.8$ -dideoxy-8-oxo- α -D-manno-octulosonate + $O_2 = 3.8$ -dideoxy-8-oxo- α -D-manno-octulosonate + $O_2 = 3.8$ -dideoxy-0-D-manno-octulosonate + $O_2 = 0.8$ -D-manno-octulosonate + O

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 lipopolysac-charides of members of the *Shewanella* genus. *cf.* EC 2.6.1.109, 8-amino-3,8-dideoxy-α-D-*manno*-

octulosonate transaminase.

References: [1280]

[EC 1.1.3.48 created 2015]

EC 1.1.3.49

Accepted name: (*R*)-mandelonitrile oxidase

Reaction: (*R*)-mandelonitrile + O_2 = benzoyl cyanide + H_2O_2

Other name(s): ChuaMOX (gene name)

Systematic name: (*R*)-mandelonitrile:oxygen oxidoreductase

Comments: Contains FAD. The enzyme, characterized from the millipede *Chamberlinius hualienensis*, is segre-

gated 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 produc-

tion of the defensive chemical benzoyl cyanide.

References: [1829]

[EC 1.1.3.49 created 2016]

EC 1.1.3.50

Accepted name: *C*-glycoside oxidase

Reaction: carminate + $O_2 = 3'$ -dehydrocarminate + H_2O_2

Other name(s): carA (gene name)

Systematic name: carminate:oxygen 3'-oxidoreductase (H₂O₂-forming)

Comments: A flavoprotein (FAD). This bacterial enzyme participates in degradation of certain *C*-glucosides

by catalysing the oxidation of the hydroxyl group at position 3 of the glycose moiety. The enzyme was found active with assorted C-glycosides, such as carminate, mangiferin, and C^6 -glycosylated

flavonoids, but not with D-glucose or C^8 -glycosylated flavonoids.

References: [2281]

[EC 1.1.3.50 created 2022]

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 de-

hydrogenase (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: [4726, 893, 981, 80, 760, 762, 1036, 1885, 1035, 2951]

[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-linked L-glycerol-3-phosphate dehydrogenase; FAD-linked L-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 (flavin-linked); glycerol-3-phosphate CoQ reductase; glycerol-3-phosphate 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:

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 [4509], while in eukaryotes it is tightly bound to the outer surface of the inner mitochondrial membrane [3747]. 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 [2589]. This shuttle plays a critical role in transferring reducing equivalents from cytosolic NADH into the mitochondrial matrix [106, 2359]. Insect flight muscle uses only CoQ $_{10}$ as the physiological quinone whereas hamster and rat mitochondria use

mainly CoQ₉ [3458]. The enzyme is activated by calcium [2589].

References: [3525, 3747, 2589, 3458, 3842, 4509, 106, 2359]

[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) oxi-

doreductase; 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: [1802, 1803, 3475, 2863, 2014]

[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 (C_2 to C_6), but not methanol, secondary alcohols and some aldehydes. It is assayed with phenazine methosulfate or with

ferricyanide.

References: [1354, 3884, 654, 1173, 2713, 2719, 2716, 2717, 761]

[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 [2872].

References: [2872]

[EC 1.1.5.7 created 2010]

EC 1.1.5.8

Accepted name: quinate/shikimate dehydrogenase (quinone)

Reaction: quinate + quinone = 3-dehydroquinate + quinol

Other name(s): NAD(P)⁺-independent quinate dehydrogenase; quinate:pyrroloquinoline-quinone 5-oxidoreductase;

quinate dehydrogenase (quinone)

Systematic name: quinate:quinol 3-oxidoreductase

Comments: The enzyme is membrane-bound. Does not use NAD(P)⁺ as acceptor. Contains pyrroloquinoline-

quinone. cf. EC 1.1.1.24, quinate/shikimate dehydrogenase (NAD+), EC 1.1.1.282, quinate/shikimate

dehydrogenase [NAD(P)⁺], and EC 1.1.1.25, shikimate dehydrogenase (NADP⁺).

References: [4411, 16, 4424]

[EC 1.1.5.8 created 1992 as EC 1.1.99.25, modified 2004, transferred 2010 to EC 1.1.5.8, modified 2021]

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: [189, 580, 2546, 1812, 4152, 4153]

[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 dehy-

drogenase (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: [4348, 4349, 536, 537]

[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 bu-

tanivorans, is involved in butane degradation. It contains a pyrroloquinoline quinone (PQQ) pros-

thetic group. cf. EC 1.1.2.9, 1-butanol dehydrogenase (cytochrome c).

References: [4422, 4423]

[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 respi-

ration. Electrons derived from D-lactate oxidation are transferred to the membrane soluble quinone

pool.

References: [2202, 1241, 2712, 3281, 997]

[EC 1.1.5.12 created 2017]

EC 1.1.5.13

Accepted name: (S)-2-hydroxyglutarate dehydrogenase

Reaction: (S)-2-hydroxyglutarate + a quinone = 2-oxoglutarate + a quinol

Other name(s): L-2-hydroxyglutarate dehydrogenase; *lhgO* (gene name); *ygaF* (gene name)

Systematic name: (S)-2-hydroxyglutarate:quinone oxidoreductase

Comments: The enzyme, characterized from the bacterium *Escherichia coli*, contains an FAD cofactor that is

not covalently attached. It is bound to the cytoplasmic membrane and is coupled to the membrane

quinone pool.

References: [1982, 2172]

[EC 1.1.5.13 created 2019]

EC 1.1.5.14

Accepted name: fructose 5-dehydrogenase

Reaction: D-fructose + a ubiquinone = 5-dehydro-D-fructose + a ubiquinol

Other name(s): fructose 5-dehydrogenase (acceptor); D-fructose dehydrogenase; D-fructose:(acceptor) 5-

oxidoreductase

Systematic name: D-fructose:ubiquinone 5-oxidoreductase

Comments: The enzyme, characterized from the bacterium Gluconobacter japonicus, is a heterotrimer composed

of an FAD-containing large subunit, a small subunit, and a heme *c*-containing subunit, which is responsible for anchoring the complex to the cytoplasmic membrane and for transferring the electrons

to ubiquinone.

References: [4727, 79, 2996, 2045]

 $[EC\ 1.1.5.14\ created\ 1972\ as\ EC\ 1.1.99.11,\ transferred\ 2021\ to\ EC\ 1.1.5.14]$

EC 1.1.7 With an iron-sulfur protein as acceptor

EC 1.1.7.1

Accepted name: 4-hydroxybenzoyl-CoA reductase

Reaction: benzoyl-CoA + oxidized ferredoxin + H_2O = 4-hydroxybenzoyl-CoA + reduced ferredoxin

Other name(s): 4-hydroxybenzoyl-CoA reductase (dehydroxylating); 4-hydroxybenzoyl-CoA:(acceptor) oxidoreduc-

tase; benzoyl-CoA:acceptor oxidoreductase

Systematic name: benzoyl-CoA:oxidized ferredoxin 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 [432].

References: [1344, 1605, 432, 417, 1606]

[EC 1.1.7.1 created 2000 as EC 1.3.99.20, transferred 2011 to EC 1.3.7.9, transferred 2020 to EC 1.1.7.1]

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 POO.

References: [1417, 847, 4319, 2720, 641, 3211]

[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 $F_{420} = 6$ -phospho-D-glucono-1,5-lactone + reduced

coenzyme F₄₂₀

 $\label{eq:other_name} \textbf{Other name}(s) : \quad \text{coenzyme } F_{420}\text{-dependent glucose-6-phosphate dehydrogenase}; \\ F_{420}\text{-dependent glucose-6-phosphate}; \\ F_{420}\text{-dependent glucose-6-phosphate};$

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 [3396].

References: [3396, 231, 3397]

[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 poly-

mers.

References: [3512, 4326]

[EC 1.1.98.3 created 2012, modified 2014]

EC 1.1.98.4

Accepted name: $F_{420}H_2$:quinone oxidoreductase

Reaction: a quinol + oxidized coenzyme F_{420} = a quinone + reduced coenzyme F_{420}

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: [467, 2293, 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 $F_{420} = R$ -CO-R' + reduced coenzyme F_{420}

Other name(s): F_{420} -dependent alcohol dehydrogenase; secondary alcohol: F_{420} -dependent sec-

ondary alcohol dehydrogenase

Systematic name: secondary-alcohol:coenzyme F₄₂₀ oxidoreductase

Comments: The enzyme isolated from the methanogenic archaea *Methanogenium liminatans* catalyses the re-

versible oxidation of various secondary and cyclic alcohols to the corresponding ketones.

References: [359, 154]

[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 + $CO_2 + H_2O$ **Other name(s):** nrdD (gene name); class III ribonucleoside-triphosphate reductase; anaerobic ribonucleotide reduc-

tase; 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, con-

tains an iron sulfur center. The active form of the enzyme contains an oxygen-sensitive glycyl (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 glycyl 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 ($1\lambda^4$ -disulfan-1-yl) radical bridge between methionine and cysteine residues. Oxidation of formate by the thiosulfuranyl radical results in the release of CO_2 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: [1037, 2930, 2931, 3172, 4574]

[EC 1.1.98.6 created 2017]

EC 1.1.98.7

Accepted name: serine-type anaerobic sulfatase-maturating enzyme

Reaction: S-adenosyl-L-methionine + a [sulfatase]-L-serine = a [sulfatase]-3-oxo-L-alanine + 5'-deoxyadenosine

+ L-methionine

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

Systematic name: [sulfatase]-L-serine: S-adenosyl-L-methionine oxidoreductase (3-oxo-L-alanine-forming)

Comments: A bacterial radical S-adenosyl-L-methionine (AdoMet) enzyme that contains three [4Fe-4S] clusters.

The enzyme, found in some bacteria, activates a type I sulfatase enzyme (EC 3.1.6.1) by converting a conserved L-serine residue in the active site to a unique 3-oxo-L-alanine residue that is essential for the sulfatase activity. While the enzyme from *Klebsiella pneumoniae* is specific for L-serine, the enzyme from *Clostridium perfringens* can also act on L-cysteine, see EC 1.8.98.7, cysteine-type anaero-

bic sulfatase-maturating enzyme.

References: [4155, 1087, 1431]

[EC 1.1.98.7 created 2020]

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) [4485]. 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: [83, 1010, 1251, 4485]

[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

 $\textbf{Other name}(s) \textbf{:} \quad \alpha\text{-ketoglutarate reductase}; \ \alpha\text{-hydroxyglutarate dehydrogenase}; \ L\text{-}\alpha\text{-hydroxyglutarate dehydrogenase}; \ L\text{-}\alpha\text{-hydr$

hydrogenase; 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: [4575]

[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: [2715, 3443]

[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:** [831, 3882]

[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⁺, cy-

tochrome 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: [3477]

[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: [69, 70]

[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 de-

hydrogenase; pyridoxine 5'-dehydrogenase; pyridoxine:(acceptor) 5-oxidoreductase

Systematic name: pyridoxine:acceptor 5-oxidoreductase

Comments: A flavoprotein (FAD).

References: [4122]

[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]

[1.1.99.11 Transferred entry, fructose 5-dehydrogenase, now classified as EC 1.1.5.14, fructose 5-dehydrogenase.]

[EC 1.1.99.11 created 1972, deleted 2021.]

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: [3668]

[EC 1.1.99.12 created 1972]

EC 1.1.99.13

Accepted name: glucoside 3-dehydrogenase (acceptor)

Reaction: sucrose + acceptor = 3-dehydro- α -D-glucosyl- β -D-fructofuranoside + reduced acceptor

Other name(s): D-glucoside 3-dehydrogenase (ambiguous); D-aldohexopyranoside dehydrogenase (ambiguous);

D-aldohexoside:(acceptor) 3-oxidoreductase; thuA (gene name); thuB (gene name); glucoside 3-

dehydrogenase

Systematic name: D-aldohexoside:acceptor 3-oxidoreductase

Comments: The enzymes from members of the *Rhizobiaceae* family (such as *Agrobacterium tumefaciens*) act on

disaccharides that contain a glucose moiety at the non-reducing end, such as sucrose, trehalose, leucrose, palatinose, trehalulose, and maltitol, forming the respective 3'-keto derivatives. cf. EC 1.1.2.11,

glucoside 3-dehydrogenase (cytochrome c).

References: [1902, 86, 87]

[EC 1.1.99.13 created 1972, modified 2022]

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: [2539]

[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; cel-

lobiose:(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, benzo-quinones, and molecular oxygen, and one-electron oxidants, including semiquinone species, iron(II) complexes, and the model acceptor cytochrome c [2683]. 2,6-Dichloroindophenol can act as acceptor

in vitro.

References: [748, 867, 868, 1463, 205, 1484, 166, 167, 2683]

[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: [2043, 2044]

[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: [3883]

[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: [84]

[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: [2034]

[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: [823]

[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: [2011]

[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 sub-

strates, 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: [4852, 1531, 1988]

[EC 1.1.99.28 created 1999]

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) + re-

duced 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;

nase; 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 O_2 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 $1\rightarrow 4-\alpha$ - and $1\rightarrow 4-\beta$ -glucooligosaccharides, 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: [4462, 4464, 4465, 4461, 4463]

[EC 1.1.99.29 created 2004]

EC 1.1.99.30

Accepted name: 2-oxo-acid reductase

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

Systematic name: (2R)-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: [4324, 3050]

[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 (ambiguous)

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

Comments: This enzyme is a member of the FMN-dependent α -hydroxy-acid oxidase/dehydrogenase family

[2408]. 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 [2408, 895]. 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 [895]. The enzyme has a large active-site pocket and preferentially binds substrates with longer sidechains, e.g. 2-hydroxyoctanoate rather than 2-hydroxybutyrate [2408]. It also prefers substrates that, like (S)-mandelate, have β unsaturation, e.g. (indol-3-yl)glycolate compared with (indol-3-yl)lactate [2408]. Esters of mandelate, such as

methyl (S)-mandelate, are also substrates [894].

References: [2408, 895, 894]

[EC 1.1.99.31 created 2006]

Accepted name: L-sorbose 1-dehydrogenase

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

Other name(s): SDH (ambiguous)

Systematic name: L-sorbose:acceptor 1-oxidoreductase

Comments: The product, L-sorbosone, is an intermediate in bacterial 2-keto-L-gulonic-acid formation. The activ-

ity of this membrane-bound enzyme is stimulated by Fe(III) or Co^{2+} but is inhibited by Cu^{2+} . 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: [4100]

[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- F_{420}). As the acceptor is now known, the enzyme has been transferred to EC 1.1.98.2, glucose-6-phosphate dehydrogenase (coenzyme- F_{420})]

[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: [1296, 938, 701, 2714, 3210, 2718]

[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 Zn^{2+} . Nicotinoprotein alcohol dehydrogenases are unique medium-chain dehydrogenases.

nases/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 ac-

cept many primary alcohols as substrates, including benzylalcohol [3188].

References: [3188, 3322, 3710, 3321, 3108]

[EC 1.1.99.36 created 2010]

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 Grampositive methylotrophic bacteria, including *Amycolatopsis methanolica*, *Rhodococcus rhodochrous* and *Rhodococcus erythropolis* [4472, 3188, 514]. These enzymes are decameric, and possess a 5-fold symmetry [1616]. Some of the enzymes can also dismutate formaldehyde to methanol and formate

[3239].

References: [4472, 3188, 514, 1616, 3239]

[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: [4795, 4796]

[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 Zn^{2+} , Co^{2+}

and Mn^{2+} .

References: [1050, 8]

[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: [263]

[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: [3407]

[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, par-

ticipates 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: [4721, 1291]

[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 phosphory-lated 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. Subsubclasses 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⁺ + H_2O = a carboxylate + NADH + H^+

Other name(s): CoA-independent aldehyde dehydrogenase; *m*-methylbenzaldehyde dehydrogenase; NAD-aldehyde

dehydrogenase; NAD-dependent 4-hydroxynonenal dehydrogenase; NAD-dependent aldehyde dehydrogenase; NAD-linked aldehyde dehydrogenase; propionaldehyde dehydrogenase; aldehyde aldehyde dehydrogenase; aldehyde aldehyde

drogenase (NAD)

Systematic name: aldehyde:NAD⁺ oxidoreductase

Comments: Wide specificity, including oxidation of D-glucuronolactone to D-glucarate.

References: [1880, 3419]

[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⁺ + H_2O = a carboxylate + NADPH + H^+

Other name(s): NADP-acetaldehyde dehydrogenase; NADP-dependent aldehyde dehydrogenase; aldehyde dehydrogenase;

genase (NADP)

Systematic name: aldehyde:NADP⁺ oxidoreductase

References: [15, 1880, 2999, 3781]

[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:** [343, 1880, 2121, 4020, 4198]

[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: [1443, 3994]

[EC 1.2.1.7 created 1961]

EC 1.2.1.8

Accepted name: betaine-aldehyde dehydrogenase

Reaction: betaine aldehyde + NAD⁺ + H_2O = betaine + NADH + $2H^+$

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) [4485]. 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: [3580, 2527, 3113, 1923, 4485]

[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 (ambiguous); glyceraldehyde phosphate dehydrogenase (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

Systematic name: D-glyceraldehyde-3-phosphate:NADP⁺ oxidoreductase

References: [3575]

[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 dehyrogenase; 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 [3364].

References: [507, 3936, 3364, 196, 195]

[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 $^+$ aspartate semialdehyde dehydrogenase; aspartic semialdehyde dehydrogenase; L-aspartate- β -

semialdehyde:NADP⁺ oxidoreductase (phosphorylating); aspartic β-semialdehyde dehydrogenase;

ASA dehydrogenase

 $\textbf{Systematic name:} \quad \text{L-aspartate-4-semialdehyde:} NADP^+ \ oxidoreductase \ (phosphorylating)$

References: [345, 1880]

[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 (ambiguous); glyceraldehyde phosphate dehydrogenase; phos-

phoglyceraldehyde dehydrogenase; 3-phosphoglyceraldehyde dehydrogenase; NAD^+ -dependent glyceraldehyde phosphate dehydrogenase; glyceraldehyde phosphate dehydrogenase (NAD^+); glyceraldehyde-3-phosphate dehydrogenase (NAD^+); NADH-glyceraldehyde phosphate dehydrogenase (NAD^+);

genase; 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: [548, 736, 1472, 4429, 4541, 3615]

[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⁺-dependent glyceraldehyde phosphate dehydrogenase; NADP⁺-triose phosphate dehydrogenase; glyceraldehyde-3-phosphate dehydrogenase; phosphate dehydrogenase; p

hydrogenase (NADP⁺) (phosphorylating); GAPDH

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

References: [438, 1318, 3575]

[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: [2978]

[EC 1.2.1.15 created 1965]

EC 1.2.1.16

Accepted name: succinate-semialdehyde dehydrogenase $[NAD(P)^+]$

Reaction: succinate semialdehyde + NAD(P)⁺ + H_2O = succinate + NAD(P)H + $\mathbf{2}$ H⁺

Other name(s): succinate semialdehyde dehydrogenase (nicotinamide adenine dinucleotide (phosphate)); succinate-

semialdehyde dehydrogenase [NAD(P)]

 $\textbf{Systematic name:} \quad \text{succinate-semialdehyde:} NAD(P)^{+} \text{ oxidoreductase}$

References: [1880, 1883, 3072]

[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: [3413]

[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: [1573, 1880, 4722]

[EC 1.2.1.18 created 1965]

EC 1.2.1.19

Accepted name: aminobutyraldehyde dehydrogenase

Reaction: 4-aminobutanal + NAD⁺ + H_2O = 4-aminobutanoate + NADH + $\mathbf{2}$ H⁺

Other name(s): γ-guanidinobutyraldehyde dehydrogenase (ambiguous); ABAL dehydrogenase; 4-

aminobutyraldehyde dehydrogenase; 4-aminobutanal dehydrogenase; γ-aminobutyraldehyde dehy-

droganase; 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 [1433]. 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 [3650] and belongs in

the aldehyde dehydrogenase superfamily [1433].

References: [529, 1880, 1881, 2698, 4803, 3383, 3382, 3650, 1433]

[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 + NADP $^+$ + H $_2$ O = glutarate + NADPH + H $^+$ **Other name(s):** glutarate semialdehyde dehydrogenase; davD (gene name)

Systematic name: glutarate-semialdehyde:NADP⁺ oxidoreductase

Comments: The enzyme, characterized from multiple *Pseudomonas* strains, participates in L-lysine degradation.

Unlike earlier claims, it prefers NADP⁺ to NAD⁺.

References: [1787, 602, 1152, 603, 4749]

[EC 1.2.1.20 created 1965, modified 2021]

EC 1.2.1.21

Accepted name: glycolaldehyde dehydrogenase

Reaction: glycolaldehyde + NAD⁺ + H_2O = glycolate + NADH + $\mathbf{2}$ H⁺

Other name(s): glycol aldehyde dehydrogenase Systematic name: glycolaldehyde:NAD⁺ oxidoreductase

References: [840]

[EC 1.2.1.21 created 1972]

EC 1.2.1.22

Accepted name: lactaldehyde dehydrogenase

Reaction: (S)-lactaldehyde + NAD⁺ + $H_2O = (S)$ -lactate + NADH + $\mathbf{2}$ H⁺

Other name(s): L-lactaldehyde:NAD oxidoreductase; nicotinamide adenine dinucleotide (NAD)-linked dehydroge-

nase

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

References: [3496, 3992]

[EC 1.2.1.22 created 1972]

EC 1.2.1.23

Accepted name: 2-oxoaldehyde dehydrogenase (NAD⁺)

Reaction: a 2-oxoaldehyde + NAD⁺ + H_2O = a 2-oxo carboxylate + NADH + H^+

Other name(s): α -ketoaldehyde dehydrogenase; methylglyoxal dehydrogenase; NAD⁺-linked α -ketoaldehyde dehydrogenase;

drogenase; 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: [2866, 3465, 3467]

[EC 1.2.1.23 created 1972, modified 1986]

EC 1.2.1.24

Accepted name: succinate-semialdehyde dehydrogenase (NAD⁺)

Reaction: succinate semialdehyde + NAD⁺ + H_2O = succinate + NADH + $2H^+$

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: [58, 3616, 508]

[EC 1.2.1.24 created 1972, modified 2010]

EC 1.2.1.25

Accepted name: branched-chain α-keto acid dehydrogenase system

Reaction: 3-methyl-2-oxobutanoate + CoA + NAD⁺ = 2-methylpropanoyl-CoA + CO₂ + NADH **Other name(s):** branched-chain α -keto acid dehydrogenase complex; 2-oxoisovalerate dehydrogenase; α -

ketoisovalerate dehydrogenase; 2-oxoisovalerate dehydrogenase (acylating)

Systematic name: 3-methyl-2-oxobutanoate:NAD⁺ 2-oxidoreductase (CoA-methylpropanoylating)

Comments: This enzyme system catalyses the oxidative decarboxylation of branched-chain α-

This enzyme system catalyses the oxidative decarboxylation of branched-chain α -keto acids derived from L-leucine, L-isoleucine, and L-valine to branched-chain acyl-CoAs. It belongs to the 2-oxoacid dehydrogenase system family, which also includes EC 1.2.1.104, pyruvate dehydrogenase system, EC 1.2.1.105, 2-oxoglutarate dehydrogenase system, EC 1.4.1.27, glycine cleavage system, and EC 2.3.1.190, acetoin dehydrogenase system. With the exception of the glycine cleavage system, which contains 4 components, the 2-oxoacid dehydrogenase systems share a common structure, consisting of three main components, namely a 2-oxoacid dehydrogenase (E1), a dihydrolipoamide acyltransferase (E2), and dihydrolipoamide dehydrogenase (E3). The reaction catalysed by this system is the sum of three activities: EC 1.2.4.4, 3-methyl-2-oxobutanoate dehydrogenase (2-methylpropanoyl-transferring), EC 2.3.1.168, dihydrolipoyllysine-residue (2-methylpropanoyl)transferase, and EC 1.8.1.4, dihydrolipoyl dehydrogenase. The system also acts on (S)-3-methyl-2-oxopentanoate and

4-methyl-2-oxopentanoate.

References: [3005, 3309, 1538, 1071, 3478]

[EC 1.2.1.25 created 1972, modified 2019, modified 2020]

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: [25]

[EC 1.2.1.26 created 1972]

EC 1.2.1.27

Accepted name: methylmalonate-semialdehyde dehydrogenase (CoA-acylating)

Reaction: 2-methyl-3-oxopropanoate + $CoA + H_2O + NAD^+$ = propanoyl- $CoA + HCO_3^- + NADH$

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 [4034]. The reaction occurs in two steps with the

decarboxylation process preceding CoA-binding [4034]. Bicarbonate rather than CO₂ is released as a

final product [4034].

References: [3954, 977, 4034]

[EC 1.2.1.27 created 1972, modified 2014]

EC 1.2.1.28

Accepted name: benzaldehyde dehydrogenase (NAD⁺)

Reaction: benzaldehyde + NAD⁺ + H_2O = benzoate + NADH + $\mathbf{2}$ H⁺

Other name(s): benzaldehyde (NAD) dehydrogenase; benzaldehyde dehydrogenase (NAD)

Systematic name: benzaldehyde:NAD⁺ oxidoreductase

References: [1443]

[EC 1.2.1.28 created 1972]

EC 1.2.1.29

Accepted name: aryl-aldehyde dehydrogenase

Reaction: an aromatic aldehyde + NAD⁺ + H_2O = an aromatic acid + NADH + H^+

Systematic name: aryl-aldehyde:NAD⁺ oxidoreductase

Comments: Oxidizes a number of aromatic aldehydes, but not aliphatic aldehydes.

References: [3434]

[EC 1.2.1.29 created 1972]

EC 1.2.1.30

Accepted name: carboxylate reductase (NADP⁺)

Reaction: an aromatic aldehyde + NADP $^+$ + AMP + diphosphate = an aromatic acid + NADPH + H $^+$ + ATP

Other name(s): aromatic acid reductase; aryl-aldehyde dehydrogenase (NADP⁺)

Systematic name: aryl-aldehyde:NADP⁺ oxidoreductase (ATP-forming)

Comments: The enzyme contains an adenylation domain, a phosphopantetheinyl binding 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 phosphopantetheinyl binding domain. The resulting thioester is subsequently transferred to the reductase domain, where it is reduced to an

aldehyde and released.

References: [1425, 1423, 4434, 4046]

[EC 1.2.1.30 created 1972, modified 2019]

EC 1.2.1.31

Accepted name: L-aminoadipate-semialdehyde dehydrogenase

Reaction: (S)-2-amino-6-oxohexanoate + NAD(P)⁺ + $H_2O = L$ -2-aminoadipate + NAD(P)H + H⁺ (overall reac-

tion)

(1a) (*S*)-2-amino-6-oxohexanoate = (*S*)-2,3,4,5-tetrahydropyridine-2-carboxylate + H_2O (spontaneous) (1b) (*S*)-2,3,4,5-tetrahydropyridine-2-carboxylate + $NAD(P)^+$ + **2** H_2O = 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 din-

ucleotide 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: [530, 3550, 849, 1204]

[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^+ + H_2O = 2-aminomuconate + NADH + **2** H^+

Other name(s): 2-aminomuconate semialdehyde dehydrogenase; 2-hydroxymuconic acid semialdehyde dehydroge-

nase; 2-hydroxymuconate semialdehyde dehydrogenase; α -aminomuconic ϵ -semialdehyde dehydrogenase; α -hydroxymuconic ϵ -semialdehyde dehydrogenase; 2-hydroxymuconic semialdehyde dehydrogenase; α -hydroxymuconic semialdehyde dehydroxymuconic semialdehyde semialdehyde semialdehyde semialdehyde se

drogenase

Systematic name: 2-aminomuconate-6-semialdehyde:NAD⁺ 6-oxidoreductase

Comments: Also acts on 2-hydroxymuconate semialdehyde.

References: [1788]

[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: [2607]

[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⁺ + H_2O = retinoate + NADH + $2H^+$

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: [2856]

[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⁺ oxi-

doreductase (phosphorylating)

Systematic name: *N*-acetyl-L-glutamate-5-semialdehyde:NADP⁺ 5-oxidoreductase (phosphorylating)

References: [181, 1338]

[EC 1.2.1.38 created 1972]

EC 1.2.1.39

Accepted name: phenylacetaldehyde dehydrogenase

Reaction: phenylacetaldehyde + NAD⁺ + H_2O = phenylacetate + NADH + $\mathbf{2}$ H⁺

Systematic name: phenylacetaldehyde:NAD⁺ oxidoreductase

References: [1205]

[EC 1.2.1.39 created 1976]

[1.2.1.40 Deleted entry. 3\alpha,7\alpha,12\alpha-trihydroxycholestan-26-al 26-oxidoreductase. The activity is part of EC 1.14.13.15, cholestanetriol 26-monooxygenase]

[EC 1.2.1.40 created 1976, deleted 2012]

EC 1.2.1.41

Accepted name: glutamate-5-semialdehyde dehydrogenase

 $\label{eq:Reaction: Possible Possible$

glutamate semialdehyde dehydrogenase; glutamate-γ-semialdehyde dehydrogenase

Systematic name: L-glutamate-5-semialdehyde:NADP⁺ 5-oxidoreductase (phosphorylating)

References: [180]

[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: [1937]

[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: [1424, 3665, 4587]

[EC 1.2.1.44 created 1978]

[1.2.1.45 Transferred entry. 4-carboxy-2-hydroxymuconate-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⁺ + H_2O = formate + NADH + $2H^+$

Other name(s): NAD-linked formaldehyde dehydrogenase; NAD-dependent formaldehyde dehydrogenase

Systematic name: formaldehyde:NAD⁺ oxidoreductase

References: [1688]

[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: [3469]

[EC 1.2.1.47 created 1983]

EC 1.2.1.48

Accepted name: long-chain-aldehyde dehydrogenase

Reaction: a long-chain aldehyde + NAD⁺ + H_2O = a long-chain carboxylate + NADH + $\mathbf{2}$ H⁺

Other name(s): long-chain aliphatic aldehyde dehydrogenase; long-chain fatty aldehyde dehydrogenase; fatty

 $aldehyde: NAD^+\ oxidoreduct as e$

Systematic name: long-chain-aldehyde:NAD⁺ oxidoreductase
Comments: The best substrate is dodecylaldehyde.

References: [260, 2880, 2881]

[EC 1.2.1.48 created 1984]

EC 1.2.1.49

Accepted name: 2-oxoaldehyde dehydrogenase (NADP⁺)

Reaction: a 2-oxoaldehyde + NADP⁺ + H_2O = a 2-oxo carboxylate + NADPH + H^+

Other name(s): α -ketoaldehyde dehydrogenase; methylglyoxal dehydrogenase; NADP⁺-linked α -ketoaldehyde dehydrogenase;

drogenase; 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: [3465, 3467]

[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: [3520, 4500, 2491]

[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 + CO $_2$ + NADPH **Systematic name:** pyruvate:NADP $^+$ 2-oxidoreductase (CoA-acetylating)

Comments: The *Euglena* enzyme can also use FAD or methyl viologen as acceptor, more slowly. The enzyme is

inhibited by oxygen.

References: [1820, 1821]

[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: [1820]

[EC 1.2.1.52 created 1989]

EC 1.2.1.53

Accepted name: 4-hydroxyphenylacetaldehyde dehydrogenase

Reaction: 4-hydroxyphenylacetaldehyde + NAD⁺ + H_2O = 4-hydroxyphenylacetate + NADH + $\mathbf{2}$ 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 *Pseu-*

domonas.

References: [790]

[EC 1.2.1.53 created 1989]

EC 1.2.1.54

Accepted name: γ-guanidinobutyraldehyde dehydrogenase

Reaction: 4-guanidinobutanal + NAD⁺ + H_2O = 4-guanidinobutanoate + NADH + $2H^+$

Other name(s): \(\alpha\)-guanidinobutyraldehyde dehydrogenase; 4-guanidinobutyraldehyde dehydrogenase; GBAL dehy-

drogenase

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: [4803]

[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 dehydro-

genase]

[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 dehydro-

genase]

[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: [3225]

[EC 1.2.1.57 created 1992]

EC 1.2.1.58

Accepted name: phenylglyoxylate dehydrogenase (acylating)

Reaction: phenylglyoxylate + NAD^+ + CoA = benzoyl-S-CoA + CO_2 + 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 phenyl-

glyoxylate. Also reduces viologen dyes. Contains iron-sulfur centres and FAD.

References: [1674]

[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: [4393, 4394]

[EC 1.2.1.59 created 1999]

EC 1.2.1.60

Accepted name: 5-carboxymethyl-2-hydroxymuconic-semialdehyde dehydrogenase

Reaction: 5-carboxymethyl-2-hydroxymuconate semialdehyde + $H_2O + NAD^+ = 5$ -carboxymethyl-2-

hydroxymuconate + NADH + 2 H⁺

Other name(s): carboxymethylhydroxymuconic semialdehyde dehydrogenase

Systematic name: 5-carboxymethyl-2-hydroxymuconic-semialdehyde:NAD⁺ oxidoreductase

Comments: Involved in the tyrosine degradation pathway in *Arthrobacter* sp.

References: [349, 73, 730, 1277]

[EC 1.2.1.60 created 2000]

EC 1.2.1.61

Accepted name: 4-hydroxymuconic-semialdehyde dehydrogenase

Reaction: 4-hydroxymuconic semialdehyde + NAD⁺ + H_2O = maleylacetate + NADH + $2H^+$

Systematic name: 4-hydroxymuconic-semialdehyde:NAD⁺ oxidoreductase **Comments:** Involved in the 4-nitrophenol degradation pathway.

References: [3971]

[EC 1.2.1.61 created 2000]

EC 1.2.1.62

Accepted name: 4-formylbenzenesulfonate dehydrogenase

Reaction: 4-formylbenzenesulfonate + NAD⁺ + H_2O = 4-sulfobenzoate + NADH + 2 H⁺

 $\textbf{Systematic name:} \quad \text{4-formylbenzene sulfonate: NAD}^+ \ oxidored uctase$

Comments: Involved in the toluene-4-sulfonate degradation pathway.

References: [1965, 1963]

[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: [837, 951]

[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 (am-

biguous)

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: [401, 3916]

[EC 1.2.1.64 created 2000, modified 2015]

EC 1.2.1.65

Accepted name: salicylaldehyde dehydrogenase

Reaction: salicylaldehyde + NAD⁺ + H_2O = salicylate + NADH + $\mathbf{2}$ H⁺

Systematic name: salicylaldehyde:NAD⁺ oxidoreductase

Comments: Involved in the naphthalene degradation pathway in some bacteria.

References: [1006]

[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⁺ + H_2O = vanillate + NADH + $2H^+$

Systematic name: vanillin:NAD⁺ oxidoreductase

References: [3351]

[EC 1.2.1.67 created 2000]

EC 1.2.1.68

Accepted name: coniferyl-aldehyde dehydrogenase

Reaction: coniferyl aldehyde + $H_2O + NAD(P)^+$ = ferulate + $NAD(P)H + 2H^+$

Systematic name: coniferyl aldehyde:NAD(P)⁺ oxidoreductase

Comments: Also oxidizes other aromatic aldehydes, but not aliphatic aldehydes.

References: [10]

[EC 1.2.1.68 created 2000]

EC 1.2.1.69

Accepted name: fluoroacetaldehyde dehydrogenase

Reaction: fluoroacetaldehyde + NAD⁺ + H_2O = 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: [2944, 2945]

[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-aminolevulinate from glutamate,

known as the C5 pathway. The route shown in the diagram is used in most eubacteria, and in all archaebacteria, algae and plants. However, in the α -proteobacteria, EC 2.3.1.37, 5-aminolevulinate synthase, is used in an alternative route to produce the product 5-aminolevulinate 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: [4471, 3352, 3705]

[EC 1.2.1.70 created 2004]

EC 1.2.1.71

Accepted name: succinvlglutamate-semialdehyde dehydrogenase

Reaction: *N*-succinyl-L-glutamate 5-semialdehyde + NAD⁺ + $H_2O = N$ -succinyl-L-glutamate + NADH + $\mathbf{2}$ H⁺ **Other name(s):** succinylglutamic semialdehyde dehydrogenase; *N*-succinylglutamate 5-semialdehyde dehydrogenase;

SGSD; 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 [4563]. 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)

[4329, 782].

References: [4563, 4564, 4329, 1851, 3732, 782, 783]

[EC 1.2.1.71 created 2006]

EC 1.2.1.72

Accepted name: erythrose-4-phosphate dehydrogenase

Reaction: D-erythrose 4-phosphate + NAD⁺ + H_2O = 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

[4899, 398]. 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 (pyridox-

ine 5'-phosphate synthase) and EC 1.4.3.5 (pyridoxamine-phosphate oxidase).

References: [4899, 398, 4771]

[EC 1.2.1.72 created 2006]

EC 1.2.1.73

Accepted name: sulfoacetaldehyde dehydrogenase

Reaction: 2-sulfoacetaldehyde + H_2O + 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, glycoylate, glycolaldehyde and 2-oxobutyrate are not sub-

strates.

References: [2260]

[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 + H_2O + 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 [1230]. The enzyme is expressed constitutively at a high level, and is not inducible by wounding of

the plant tissue [1232].

References: [1230, 1232]

[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 [4056, 296]. The enzyme from *Sulfolobus tokodaii* has been purified, and found to contain one RNA molecule per two subunits [57]. 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⁺)] [1764].

References: [4056, 296, 57, 1764]

[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 [3952], and in *Metallosphaera sedula*, where it participates in the 3-hydroxypropanonate/4-hydroxybutanoate cycle, an autotrophic CO₂ fixation pathway found in some thermoacidophilic archaea [57, 296].

References: [3952, 57, 296]

[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+ + $H_2O = 3,4$ -didehydroadipyl-CoA + NADPH +

 H^+

Other name(s): BoxD; 3,4-dehydroadipyl-CoA semialdehyde dehydrogenase 3,4-didehydroadipyl-CoA semialdehyde:NADP⁺ oxidoreductase

Comments: This enzyme catalyses a step in the aerobic benzoyl-coenzyme A catabolic pathway in *Azoarcus evan*-

sii and Burkholderia xenovorans.

References: [1307, 185]

[EC 1.2.1.77 created 2010]

EC 1.2.1.78

Accepted name: 2-formylbenzoate dehydrogenase

Reaction: 2-formylbenzoate + NAD^+ + $H_2O = o$ -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: [1857, 2145]

[EC 1.2.1.78 created 2010]

EC 1.2.1.79

Accepted name: succinate-semialdehyde dehydrogenase (NADP⁺)

Reaction: succinate semialdehyde + NADP⁺ + H_2O = succinate + NADPH + $\mathbf{2}$ H⁺

Other name(s): succinic semialdehyde dehydrogenase (NADP⁺); succinyl semialdehyde dehydrogenase (NADP⁺);

succinate semialdehyde:NADP+ oxidoreductase; NADP-dependent succinate-semialdehyde dehydro-

genase; 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⁺ [1875].

References: [229, 1875]

[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 pro-

tein] + $NAD(P)H + H^+$

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 *Syne*-

chococcus 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 decarbony-lase, it is involved in alkane biosynthesis. The natural substrates of the enzyme are C_{16} and C_{18} acti-

vated fatty acids. Requires Mg²⁺.

References: [3717]

[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-acetylating)

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: [4577]

[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: [1067, 901]

[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: [3402]

[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: [2782]

[EC 1.2.1.84 created 2012]

EC 1.2.1.85

Accepted name: 2-hydroxymuconate-6-semialdehyde dehydrogenase

Reaction: 2-hydroxymuconate-6-semialdehyde + NAD⁺ + $H_2O = (2Z,4E)$ -2-hydroxyhexa-2,4-dienedioate +

 $NADH + 2H^{+}$

Other name(s): *xylG* (gene name); *praB* (gene name)

Systematic name: 2-hydroxymuconate-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 [1815]. Activity with NAD $^+$ is more than 10-fold higher than

with NADP⁺ [2005]. cf. EC 1.2.1.32, aminomuconate-semialdehyde dehydrogenase.

References: [1815, 3191, 2005]

[EC 1.2.1.85 created 2012]

EC 1.2.1.86

Accepted name: geranial dehydrogenase

Reaction: geranial + H_2O + NAD^+ = geranate + NADH + H^+

Other name(s): GaDH; *geoB* (gene name)

Systematic name: geranial:NAD⁺ oxidoreductase

Comments: Does not act on neral.

References: [4658, 2556]

[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 (acetylat-

ing). NADP⁺ can replace NAD⁺ with a much slower rate [195].

References: [196, 555, 195]

[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⁺ + $H_2O = L$ -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-carboxylate 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 [1141, 458]. 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 [1808].

References: [24, 4058, 1141, 458, 1808]

[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⁺ + H_2O = 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: [1960, 3486]

[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)⁺ + $H_2O = 3$ -phospho-D-glycerate + NAD(P)H + $\mathbf{2}$ H⁺

Other name(s): non-phosphorylating glyceraldehyde-3-phosphate dehydrogenase (ambiguous); 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 *Thermopro-*

teus tenax. cf. EC 1.2.1.9 [glyceraldehyde-3-phosphate dehydrogenase (NADP⁺)].

References: [476, 477, 3340, 2540]

[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: [1107, 1836, 4250]

[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-oxidoredutase

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: [4846]

[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: Invoved in juvenile hormone production in insects. The enzyme was described from the corpora al-

lata of Drosophila melanogaster (fruit fly), Manduca sexta (tobacco hornworm) and Aedes aegypti

(dengue mosquito).

References: [2601, 193, 3530]

[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: [1025]

[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-xylenol by sev-

eral Pseudomonas strains. The enzyme is also active with 4-hydroxy-3-methylbenzaldehyde. cf. EC

1.2.1.64, 4-hydroxybenzaldehyde dehydrogenase (NAD⁺).

References: [4605, 639]

[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 sulfo-

quinovose degradation pathway. Also acts on succinate semialdehyde.

References: [1098]

[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⁺ + $H_2O = 2$ -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: [1110]

[EC 1.2.1.98 created 2016]

EC 1.2.1.99

Accepted name: 4- $(\gamma$ -glutamylamino)butanal dehydrogenase

Reaction: $4-(\gamma-L-glutamylamino)butanal + NAD(P)^+ + H_2O = 4-(\gamma-L-glutamylamino)butanoate + NAD(P)H +$

 H^{+}

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

Systematic name: $4-(\gamma-L-glutamylamino)butanal:NAD(P)^+$ 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: [2301, 1920, 3733]

[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^+ + $H_2O = 3$ -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, partici-

pates in the degradation of pyridoxine (vitamin B_6).

References: [2401, 4794, 2916]

[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): lnaA (gene name); lnbA (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: [1149]

[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 $^+$ 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: [2401]

[EC 1.2.1.102 created 2018]

EC 1.2.1.103

Accepted name: [amino-group carrier protein]-6-phospho-L-2-aminoadipate reductase

Reaction: an [amino-group carrier protein]-C-terminal-[N-(1-carboxy-5-oxopentyl)-L-glutamine] + phosphate +

 $NADP^+$ = an [amino-group carrier protein]-C-terminal-[N-(1-carboxy-5-phosphooxy-5-oxopentyl)-L-

glutamine] + NADPH + H+

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

Systematic name: [amino-group carrier protein]-*C*-terminal-[*N*-(1-carboxy-5-oxopentyl)-L-glutamine]:NADP⁺ 5-

oxidoreductase (phosphorylating)

Comments: The enzyme participates in an L-lysine biosynthesis in certain species of archaea and bacteria.

References: [3074, 1722, 3873]

[EC 1.2.1.103 created 2019]

EC 1.2.1.104

Accepted name: pyruvate dehydrogenase system

Reaction: pyruvate + CoA + NAD⁺ = acetyl-CoA + CO₂ + NADH

Other name(s): pyruvate dehydrogenase complex; PDH

Systematic name: pyruvate:NAD⁺ 2-oxidoreductase (CoA-acetylating)

Comments: The pyruvate dehydrogenase system (PDH) is a large enzyme complex that belongs to the 2-oxoacid

dehydrogenase system family, which also includes EC 1.2.1.25, branched-chain α-keto acid dehydrogenase system, EC 1.2.1.105, 2-oxoglutarate dehydrogenase system, EC 1.4.1.27, glycine cleavage system, and EC 2.3.1.190, acetoin dehydrogenase system. With the exception of the glycine cleavage system, which contains 4 components, the 2-oxoacid dehydrogenase systems share a common structure, consisting of three main components, namely a 2-oxoacid dehydrogenase (E1), a dihydrolipoamide acyltransferase (E2), and a dihydrolipoamide dehydrogenase (E3). The reaction catalysed by this system is the sum of three activities: EC 1.2.4.1, pyruvate dehydrogenase (acetyltransferring) (E1), EC 2.3.1.12, dihydrolipoyllysine-residue acetyltransferase (E2), and EC 1.8.1.4, dihydrolipoyl dehydrogenase (E3). The mammalian system also includes E3 binding protein, which is

involved in the interaction between the E2 and E3 subunits.

References: [3479, 236, 4002, 4764, 3256]

[EC 1.2.1.104 created 2020]

EC 1.2.1.105

Accepted name: 2-oxoglutarate dehydrogenase system

Reaction: 2-oxoglutarate + CoA + NAD⁺ = succinyl-CoA + CO₂ + NADH

Other name(s): 2-oxoglutarate dehydrogenase complex

Systematic name: 2-oxoglutarate:NAD⁺ 2-oxidoreductase (CoA-succinylating)

Comments: The 2-oxoglutarate dehydrogenase system is a large enzyme complex that belongs to the 2-oxoacid

dehydrogenase system family, which also includes EC 1.2.1.25, branched-chain α -keto acid dehydrogenase system, EC 1.2.1.104, pyruvate dehydrogenase system, EC 1.4.1.27, glycine cleavage system, and EC 2.3.1.190, acetoin dehydrogenase system. With the exception of the glycine cleavage system, which contains 4 components, the 2-oxoacid dehydrogenase systems share a common structure, consisting of three main components, namely a 2-oxoacid dehydrogenase (E1), a dihydrolipoamide acyltransferase (E2), and a dihydrolipoamide dehydrogenase (E3). This enzyme system converts 2-oxoglutarate to succinyl-CoA and produces NADH and CO₂ in a complicated series of irreversible reactions. The reaction catalysed by this system is the sum of three activities: EC 1.2.4.2, oxoglutarate dehydrogenase (succinyl-transferring) (E1), EC 2.3.1.61, dihydrolipoyllysine-residue succinyltrans-

ferase (E2) and EC 1.8.1.4, dihydrolipoyl dehydrogenase (E3).

References: [3539, 2164, 3478, 2946, 1165, 494, 795]

[EC 1.2.1.105 created 2020]

EC 1.2.1.106

Accepted name: [amino-group carrier protein]-5-phospho-L-glutamate reductase

 $\textbf{Reaction:} \quad \text{an [amino-group carrier protein]-C-terminal-} \\ \gamma\text{-}(\text{L-glutamate 5-semialdehyde-2-yl})\text{-L-glutamate +} \\ \quad \text{an [amino-group carrier protein]-C-terminal-} \\ \gamma\text{-}(\text{L-glutamate 5-semialdehyde-2-yl})\text{-L-glutamate +} \\ \quad \text{an [amino-group carrier protein]-C-terminal-} \\ \gamma\text{-}(\text{L-glutamate 5-semialdehyde-2-yl})\text{-L-glutamate +} \\ \quad \text{an [amino-group carrier protein]-} \\ \quad \text{an [ami$

phosphate + NADP⁺ = an [amino-group carrier protein]-C-terminal-γ-(5-phospho-L-glutamyl)-L-

glutamate + NADPH + H⁺

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

Systematic name: [amino-group carrier protein]-*C*-terminal-γ-(L-glutamate 5-semialdehyde-2-yl)-L-glutamate:NADP⁺

5-oxidoreductase (phosphorylating)

Comments: The enzyme participates in an L-arginine biosynthesis pathway in certain species of archaea and bac-

teria. In some organisms the enzyme is bifunctional and also catalyses the activity of EC 1.2.1.103,

[amino-group carrier protein]-6-phospho-L-2-aminoadipate reductase.

References: [3213, 4806]

[EC 1.2.1.106 created 2021]

EC 1.2.1.107

Accepted name: glyceraldehyde-3-phosphate dehydrogenase (arsenate-transferring)

Reaction: D-glyceraldehyde 3-phosphate + arsenate + NAD^+ = 1-arsono-3-phospho-D-glycerate + $NADH + H^+$

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

Comments: The enzyme, discovered in bacteria, is very similar to EC 1.2.1.12, glyceraldehyde-3-phosphate dehy-

drogenase (phosphorylating). However, the gene encoding it is located in arsenic resistance islands in the chromosome, next to a gene (*arsJ*) that encodes a transporter that removes the product, 1-arsono-3-phosphoglycerate, from the cell. Together the two proteins form an arsenic detoxification system.

References: [631, 4677]

[EC 1.2.1.107 created 2021]

EC 1.2.2 With a cytochrome as acceptor

EC 1.2.2.1

Accepted name: formate dehydrogenase (cytochrome)

Reaction: formate + 2 ferricytochrome $b_1 = CO_2 + 2$ ferrocytochrome $b_1 + 2$ H⁺ **Other name(s):** formate dehydrogenase; formate:cytochrome b_1 oxidoreductase

Systematic name: formate:ferricytochrome- b_1 oxidoreductase

References: [1257]

[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]

[1.2.2.4 Deleted entry. carbon-monoxide dehydrogenase (cytochrome b-561). Now classified as EC 1.2.5.3, aerobic carbon monoxide dehydrogenase]

[EC 1.2.2.4 created 1999 (EC 1.2.3.10 created 1990, incorporated 2003), modified 2003, deleted 2020]

EC 1.2.3 With oxygen as acceptor

EC 1.2.3.1

Accepted name: aldehyde oxidase

Reaction: an aldehyde + $H_2O + O_2$ = a carboxylate + H_2O_2

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 sub-

strate 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 [2261, 4815]. 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) [4303, 1750].

References: [1366, 2173, 2615, 2261, 4303, 4815, 1750, 4359]

[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 + O_2 = acetyl phosphate + CO_2 + H_2O_2 **Other name(s):** pyruvic oxidase; phosphate-dependent pyruvate oxidase 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. FADH $_2$ is reoxidized by O $_2$ to yield H $_2$ O $_2$ and FAD and AcThDP is cleaved phosphorolytically to acetyl phosphate and

thiamine diphosphate [4297].

References: [4632, 4297]

[EC 1.2.3.3 created 1961]

EC 1.2.3.4

Accepted name: oxalate oxidase

Reaction: oxalate + O_2 + **2** H⁺ = **2** CO₂ + H₂O₂

Other name(s): aero-oxalo dehydrogenase; oxalic acid oxidase

Systematic name: oxalate:oxygen oxidoreductase

Comments: Contains Mn^{2+} as a cofactor. The enzyme is not a flavoprotein as had been thought [3502].

References: [832, 2247, 3502]

[EC 1.2.3.4 created 1961]

EC 1.2.3.5

Accepted name: glyoxylate oxidase

Reaction: glyoxylate + $H_2O + O_2$ = oxalate + H_2O_2

Systematic name: glyoxylate:oxygen oxidoreductase

References: [2006]

[EC 1.2.3.5 created 1972]

EC 1.2.3.6

Accepted name: pyruvate oxidase (CoA-acetylating)

Reaction: pyruvate + $CoA + O_2$ = acetyl- $CoA + CO_2 + H_2O_2$ **Systematic name:** pyruvate:oxygen 2-oxidoreductase (CoA-acetylating)

Comments: A flavoprotein (FAD). May be identical with EC 1.2.7.1 pyruvate synthase.

References: [3485, 4185]

[EC 1.2.3.6 created 1976]

EC 1.2.3.7

Accepted name: indole-3-acetaldehyde oxidase

Reaction: (indol-3-yl)acetaldehyde + $H_2O + O_2$ = (indol-3-yl)acetate + H_2O_2

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 [3793, 3798]. 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* [3798]. While (indol-3-yl)acetaldehyde is the preferred substrate, it also oxidizes indole-3-carbaldehyde and acetaldehyde, but more slowly. The enzyme from maize con-

tains FAD, iron and molybdenum [2238].

References: [411, 2840, 3435, 2238, 2237, 3793, 3798]

[EC 1.2.3.7 created 1984, modified 2004, modified 2006]

EC 1.2.3.8

Accepted name: pyridoxal oxidase

Reaction: pyridoxal + $H_2O + O_2 = 4$ -pyridoxate + (?)

Systematic name: pyridoxal:oxygen 4-oxidoreductase

Comments: A molybdenum protein.

References: [1507, 4549]

[EC 1.2.3.8 created 1984]

EC 1.2.3.9

Accepted name: aryl-aldehyde oxidase

Reaction: an aromatic aldehyde + O_2 + H_2O = an aromatic carboxylate + H_2O_2

Systematic name: aryl-aldehyde:oxygen oxidoreductase

Comments: Acts on benzaldehyde, vanillin and a number of other aromatic aldehydes, but not on aliphatic aldehy-

des or sugars.

References: [769]

[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 + O_2 = 2 4-hydroxyphenylacetate + 2 CO_2 **Systematic name:** 4-hydroxyphenylpyruvate:oxygen oxidoreductase (decarboxylating)

Comments: Involved in tyrosine degradation pathway in *Arthrobacter sp.*

References: [349]

[EC 1.2.3.13 created 2000]

EC 1.2.3.14

Accepted name: abscisic-aldehyde oxidase

Reaction: abscisic aldehyde + $H_2O + O_2$ = abscisate + H_2O_2 **Other name(s):** abscisic aldehyde oxidase; AAO3; AOd; AO δ **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 [3799].

References: [3629, 3800, 3799]

[EC 1.2.3.14 created 2005]

EC 1.2.3.15

Accepted name: (methyl)glyoxal oxidase

Reaction: (1) glyoxal + $H_2O + O_2$ = glyoxylate + H_2O_2

(2) 2-oxopropanal + $H_2O + O_2$ = pyruvate + H_2O_2

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*, uti-

lizes a free radical-coupled copper complex for catalysis.

References: [2069, 2068, 2071, 4611]

[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): pyruvate decarboxylase (ambiguous); pyruvate dehydrogenase (ambiguous); pyruvate dehydrogenase

(lipoamide); pyruvate:lipoamide 2-oxidoreductase (decarboxylating and acceptor-acetylating); pyru-

vic acid dehydrogenase; pyruvic dehydrogenase (ambiguous)

Systematic name: pyruvate:[dihydrolipoyllysine-residue acetyltransferase]-lipoyllysine 2-oxidoreductase (decarboxylat-

ing, acceptor-acetylating)

Comments: Contains thiamine diphosphate. It is a component (in multiple copies) of the multienzyme pyruvate

dehydrogenase complex, EC 1.2.1.104, 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: [3129, 3775, 3293]

[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 oxidoreduc-

tase; 2-oxoglutarate:lipoamide 2-oxidoreductase (decarboxylating and acceptor-succinylating); α -ketoglutarate dehydrogenase; alphaketoglutaric acid dehydrogenase; α -ketoglutaric dehydrogenase; α -oxoglutarate dehydrogenase; AKGDH; OGDC; ketoglutaric dehydrogenase; oxoglutarate decarboxylase (misleading); oxoglutarate dehydrogenase; oxoglutarate dehydrogenase (lipoamide)

Systematic name: 2-oxoglutarate:[dihydrolipoyllysine-residue succinyltransferase]-lipoyllysine 2-oxidoreductase (decar-

boxylating, acceptor-succinylating)

Comments: Contains thiamine diphosphate. It is a component of the multienzyme 2-oxoglutarate dehydroge-

nase complex, EC 1.2.1.105, 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: [2684, 3129, 3651, 3293]

[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 (ambiguous); 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 -oxo acid dehydrogenase; branched-chain keto acid dehydrogenase; branched-chain keto acid dehydrogenase; branched-chain keto acid 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-oxobutanaoate, 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: [410, 721, 827, 3309, 3293]

[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 + H_2O = acetate + CO_2 + ubiquinol

Other name(s): pyruvate dehydrogenase (ambiguous); pyruvic dehydrogenase (ambiguous); pyruvic (cytochrome b_1)

dehydrogenase (incorrect); pyruvate:ubiquinone-8-oxidoreductase; pyruvate oxidase (ambiguous);

pyruvate dehydrogenase (cytochrome) (incorrect)

Systematic name: pyruvate:ubiquinone oxidoreductase

Comments: Flavoprotein (FAD) [3470]. This bacterial enzyme is located on the inner surface of the cytoplas-

mic membrane and coupled to the respiratory chain via ubiquinone [785, 2209]. Does not accept menaquinone. Activity is greatly enhanced by lipids [4,5,6]. Requires thiamine diphosphate [3128].

The enzyme can also form acetoin [308].

References: [3470, 785, 2209, 515, 4511, 4848, 3128, 308]

[EC 1.2.5.1 created 2010]

EC 1.2.5.2

Accepted name: aldehyde dehydrogenase (quinone)

Reaction: an aldehyde + a quinone + H_2O = 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 C_{10} , aromatic aldehydes, glyoxylate and glyc-

eraldehyde. The enzymes contains a PQQ cofactor and multiple hemes that deliver the electrons to the

membrane quinone pool.

References: [78, 82, 3257, 1353]

[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 $+ H_2O = CO_2 + a$ quinol

Other name(s): MoCu-CODH; coxSML (gene names); molybdoenzyme carbon monoxide dehydrogenase

Systematic name: carbon-monoxide, water: quinone oxidoreductase

Comments: This enzyme, found in carboxydotrophic 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 molyb-dopterin 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 [4626]. *cf.* EC 1.2.7.4, anaerobic

carbon monoxide dehydrogenase.

References: [1406, 933, 1347, 3503, 4626, 3286, 1655]

[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; pyruvate synthase; α -ketobutyrate-ferredoxin oxidoreductase;

Terredoxin oxidoreductase; 2-oxobutyrate synthase; α -ketobutyrate-ferredoxin oxidoreductase; 2-ketobutyrate synthase; α -ketobutyrate synthase; 2-oxobutyrate-ferredoxin oxidoreductase; 2-oxobutanoate:ferredoxin 2-oxobutano

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: [1070, 1295, 4382, 4383, 610]

[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-

succinvlating)

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: [485, 1295, 952, 2620, 3763]

EC 1.2.7.4

Accepted name: anaerobic carbon monoxide dehydrogenase

Reaction: CO + H₂O + 2 oxidized ferredoxin = CO_2 + 2 reduced ferredoxin + 2 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 CO₂ to CO. The electrons are trans-

ferred to redox proteins such as ferredoxin. In purple sulfur bacteria and methanogenic archaea it catalyses the oxidation of CO to CO₂, which is incorporated by the Calvin-Benson-Basham cycle or released, respectively. In acetogenic and sulfate-reducing microbes it catalyses the reduction of CO₂ 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: $CO + H_2O = CO_2 + H_2$. cf. EC 1.2.5.3, aerobic carbon monoxide dehydrogenase.

References: [3424, 907, 381, 964, 934, 959, 542]

[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 + H_2O + 2 oxidized ferredoxin = a carboxylate + 2 H⁺ + 2 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 clus-

ters. 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 ferre-

doxin or methyl viologen but not NAD(P)⁺ as electron acceptor.

References: [2920, 1934, 593, 3585]

[EC 1.2.7.5 created 2003]

EC 1.2.7.6

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

Reaction: D-glyceraldehyde-3-phosphate + $H_2O + 2$ oxidized ferredoxin = 3-phospho-D-glycerate + $2H^+ + 2$

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* [2921]. It is specific for

glyceraldehyde-3-phosphate.

References: [2921, 3585]

[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)- $CoA + CO_2 + 2$

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. Preferen-

tially 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 oxi-doreductases, 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: [483, 1607, 4248, 3763]

[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- $CoA + CO_2 + 2$ 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 (ferre-

doxin).

References: [2621, 3898, 4248, 3763]

[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 CO_2 + 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: [825, 3319]

[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 + CO_2 + 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 [4884]. 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: [2066, 4884, 1219, 1220, 3088, 3240]

[EC 1.2.7.11 created 2013]

EC 1.2.7.12

Accepted name: formylmethanofuran dehydrogenase

Reaction: a formylmethanofuran + $H_2O + 2$ oxidized ferredoxin [iron-sulfur] cluster = $CO_2 + a$ 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 and numerous [4Fe-4S] clusters. 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 CO_2 as well as the oxidation of coenzyme M to CO_2 . The reaction is endergonic, and is driven by coupling

with the soluble CoB-CoM heterodisulfide reductase via electron bifurcation.

References: [1999, 316, 315, 4474, 2783, 2007, 4489]

[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 other, known, physiological acceptors

EC 1.2.98.1

Accepted name: formaldehyde dismutase

Reaction: 2 formaldehyde + H_2O = 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 Zn^{2+} 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) [3239]. Formaldehyde and acetaldehyde can act as donors; formaldehyde, acetaldehyde and propanal can act as acceptors

[2018, 2021].

References: [2018, 2021, 3239]

[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 + H_2O = a carboxylate + reduced acceptor

Other name(s): aldehyde:(acceptor) oxidoreductase

Systematic name: aldehyde:acceptor oxidoreductase

Comments: A tungsten protein. Methyl viologen 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: [4603]

[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: [4359, 975, 97, 3565]

[EC 1.2.99.7 created 2004]

EC 1.2.99.8

Accepted name: glyceraldehyde dehydrogenase (FAD-containing)

Reaction: D-glyceraldehyde + H_2O + 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: [1993]

[EC 1.2.99.8 created 2013]

[1.2.99.9 Transferred entry. formate dehydrogenase (coenzyme F_{420}). Now EC 1.17.98.3, formate dehydrogenase (coenzyme F_{420})]

[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 + H_2O + acceptor = 4,4'-diapolycopen-4-oate + reduced acceptor

(2) 4,4'-diapolycopene-4,4'-dial + 2 H₂O + 2 acceptor = 4,4'-diapolycopene-4,4'-dioate + 2 reduced

acceptor

Other name(s): *crtNc*; 4,4′-diapolycopenealdehyde 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: [4215, 4016]

[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 bac-

terium, *Clostridium uracilicum*, which utilizes uracil and thymine as nitrogen and carbon sources for growth [540]. Since then the enzyme was found in additional organisms including *Alcaligenes eutro*-

phus [3730], Pseudomonas strains [2104, 4594] and Escherichia coli [4593, 1642].

References: [540, 3730, 2104, 4594, 4593, 1642]

[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: oxi-

doreductase; DPD; DHPDH; dehydrogenase, dihydrouracil (nicotinamide adenine dinucleotide phosphate); DHU dehydrogenase; hydropyrimidine dehydrogenase; dihydropyrimidine dehydrogenase

(NADP)

Systematic name: 5,6-dihydrouracil:NADP⁺ 5-oxidoreductase

Comments: Also acts on dihydrothymine.

References: [1192, 3888]

[EC 1.3.1.2 created 1961, modified 1986]

EC 1.3.1.3

Accepted name: Δ^4 -3-oxosteroid 5 β -reductase

Reaction: a 3-oxo-5 β -steroid + NADP⁺ = a 3-oxo-Delta⁴-steroid + NADPH + H⁺

Other name(s): 3-oxo-Delta⁴-steroid 5β-reductase; 5β-reductase; androstenedione 5β-reductase; cholestenone

5β-reductase; cortisone 5β-reductase; cortisone β-reductase; cortisone Δ^4 -5β-reductase; steroid 5β-reductase; testosterone 5β-reductase; Δ^4 -3-ketosteroid 5β-reductase; Δ^4 -5β-reductase; Δ^4 -hydrogenase; 4,5β-dihydrocortisone:NADP+ Δ^4 -oxidoreductase; 3-oxo-5β-steroid:NADP+ Δ^4 -

oxidoreductase

Systematic name: 3-oxo-5 β -steroid:NADP⁺ 4,5-oxidoreductase

Comments: The enzyme from human efficiently catalyses the reduction of progesterone, androstenedione, 17α-

hydroxyprogesterone and testosterone to 5β -reduced metabolites; it can also act on aldosterone, corticosterone and cortisol, but to a lesser extent [605]. The bile acid intermediates 7α , 12α -dihydroxy-4-

cholesten-3-one and 7α -hydroxy-4-cholesten-3-one can also act as substrates [2219].

References: [1138, 463, 2434, 4305, 4098, 1236, 3163, 605, 2219]

[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 Mn^{2+} . Fe²⁺ or Zn^{2+} can replace Mn^{2+} to some extent.

References: [3692, 3694]

[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: [1712]

[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: [2199]

[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 phos-

phate); 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: [945, 3806]

[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 reduc-

tase; 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 [4838]. The FAS-I enzyme from the bacterium *Mycobacterium tuberculosis* prefers substrates with carbon chain

length from 12 to 24 carbons.

References: [3866, 4569, 4838]

[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]

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 (As-

comycota 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: [3813]

[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: [2433]

[EC 1.3.1.11 created 1972]

Accepted name: prephenate dehydrogenase

Reaction: prephenate + NAD⁺ = 4-hydroxyphenylpyruvate + CO_2 + 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: [2179]

[EC 1.3.1.12 created 1972]

EC 1.3.1.13

Accepted name: prephenate dehydrogenase (NADP⁺)

Reaction: prephenate + NADP $^+$ = 4-hydroxyphenylpyruvate + CO $_2$ + NADPH

Other name(s): prephenate dehydrogenase (ambiguous); prephenate (nicotinamide adenine dinucleotide phosphate)

dehydrogenase; prephenate dehydrogenase (NADP)

Systematic name: prephenate:NADP⁺ oxidoreductase (decarboxylating)

References: [1267]

[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 (ambigu-

ous); 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 cat-

alytic subunit and a FAD and iron-sulfur binding electron transfer subunit [3067]. 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: [1185, 1186, 2481, 3067, 3583, 1976, 2646]

[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; oro-

tate reductase (NADPH)

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

Comments: Binds FMN and FAD [4361]. 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: [4229, 4361]

[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: [3836]

[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: [2912]

[EC 1.3.1.17 created 1972]

EC 1.3.1.18

Accepted name: kynurenate-7,8-dihydrodiol dehydrogenase

Reaction: 7,8-dihydro $xykynurenate + NAD^+ = 7,8$ -dihydro $xykynurenate + NADH + H^+$

Other name(s): 7,8-dihydro-7,8-dihydroxykynurenate dehydrogenase; 7,8-dihydroxykynurenic acid 7,8-diol dehydro-

genase

Systematic name: 7,8-dihydro-7,8-dihydroxykynurenate:NAD⁺ oxidoreductase

References: [4210]

[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 dinu-

cleotide) oxidoreductase;

Systematic name: *cis*-1,2-dihydrobenzene-1,2-diol:NAD⁺ oxidoreductase

References: [163, 1321]

[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: [165]

[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: [876, 2855]

[EC 1.3.1.21 created 1972, modified 2013]

EC 1.3.1.22

Accepted name: 3-oxo-5α-steroid 4-dehydrogenase (NADP⁺)

Reaction: a 3-oxo-5 α -steroid + NADP⁺ = a 3-oxo- Δ ⁴-steroid + NADPH + H⁺

Other name(s): cholestenone 5α -reductase; testosterone Δ^4 - 5α -reductase; steroid 5α -reductase; 3-oxosteroid

 Δ^4 -dehydrogenase; 5α -reductase; steroid 5α -hydrogenase; 3-oxosteroid 5α -reductase; testosterone Δ^4 -hydrogenase; 4-ene-3-oxosteroid 5α -reductase; reduced nicotinamide adenine dinucleotide phosphate: Δ^4 -3-ketosteroid 5α -oxidoreductase; 4-ene- 5α -reductase; Δ^4 -3-ketosteroid 5α -oxidoreductase; testosterone 5α -reductase; 3-oxo- 5α -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 5α 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 (22α) -hydroxy-

campest-4-en-3-one. cf. EC 1.3.99.5, 3-oxo-5α-steroid 4-dehydrogenase (acceptor).

References: [2435, 3837, 646, 3664, 3416, 3345, 2444, 3571]

[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, $\Delta 4$ -3-oxosteroid 5β -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: [3914]

[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; DHBDH; 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: (1*R*,6*S*)-1,6-dihydroxycyclohexa-2,4-diene-1-carboxylate:NAD⁺ oxidoreductase (decarboxylating)

References: [3490, 3038]

[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 $^+$ Δ^2 -oxidoreductase

Comments: Specific for long chain 2-trans- and 2-cis-alkenals, with chain length optimum around 14 to 16 carbon

atoms.

References: [4037]

[EC 1.3.1.27 created 1976]

EC 1.3.1.28

Accepted name: 2,3-dihydro-2,3-dihydroxybenzoate dehydrogenase

Reaction: (2S,3S)-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: [4828]

[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: (1R,2S)-1,2-dihydronaphthalene-1,2-diol + NAD⁺ = naphthalene-1,2-diol + NADH + H⁺ **Other name(s):** (+)-cis-naphthalene dihydrodiol dehydrogenase; cis-

dihydrodiol naphthalene dehydrogenase; *cis*-1,2-dihydronaphthalene-1,2-diol:NAD⁺ 1,2-

oxidoreductase

Systematic name: (1R,2S)-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: [3259]

[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⁺ Δ^2 -oxidoreductase

Comments: An iron-sulfur-flavoprotein (FAD). Acts (in the reverse direction) on a wide range of alkyl and aryl

 $\alpha\beta\text{-unsaturated}$ carboxylate ions; but-2-enoate was the best substrate tested.

References: [4295]

[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: [1242, 1243]

[EC 1.3.1.32 created 1983]

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); pro-

tochlorophyllide 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 (7S,8S)-configuration.

References: [117, 1410]

[EC 1.3.1.33 created 1984]

EC 1.3.1.34

Accepted name: 2,4-dienoyl-CoA reductase [(2E)-enoyl-CoA-producing]

Reaction: (1) a (2E)-2-enoyl-CoA + NADP⁺ = a (2E,4E)-2,4-dienoyl-CoA + NADPH + H⁺

(2) a (2E)-2-enoyl-CoA + NADP⁺ = a (2E,4Z)-2,4-dienoyl-CoA + NADPH + H⁺

Other name(s): fadH (gene name); 4-enoyl-CoA reductase (NADPH) (ambiguous); 4-enoyl coenzyme A (reduced

nicotinamide adenine dinucleotide phosphate) reductase (ambiguous); 4-enoyl-CoA reductase (ambiguous); 2,4-dienoyl-CoA reductase (NADPH) (ambiguous); *trans*-2,3-didehydroacyl-CoA:NADP+

4-oxidoreductase

Systematic name: (2E)-2-enoyl-CoA:NADP⁺ 4-oxidoreductase

Comments: This bacterial enzyme catalyses the reduction of either (2E,4E)-2,4-dienoyl-CoA or (2E,4Z)-2,4-

dienoyl-CoA to (2E)-2-enoyl-CoA. The enzyme from *Escherichia coli* contains FAD, FMN, and an [4Fe-4S] iron sulfur cluster. cf. EC 1.3.1.124, 2,4-dienoyl-CoA reductase [(3E)-enoyl-CoA-

producing].

References: [945, 944, 4821, 1592, 2471, 1759, 4347]

[EC 1.3.1.34 created 1984, modified 1986, modified 2020]

[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: [3311]

[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 de-

hydrogenase (NADP⁺)].

References: [2848]

[EC 1.3.1.37 created 1986]

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 dehy-

drogenase (NADP⁺)].

References: [2848]

[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: [978, 558]

[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 $^+$ Δ^2 -oxidoreductase

Comments: Broad specificity; reduces a number of compounds produced by *Pseudomonas* from aromatic hydro-

carbons by ring fission.

References: [3179]

[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: [3661]

[EC 1.3.1.41 created 1989]

Accepted name: 12-oxophytodienoate reductase

Reaction: (9S,13S)-10,11-dihydro-12-oxo-15-phytoenoate + NADP⁺ = (15Z)-12-oxophyto-10,15-dienoate +

 $NADPH + H^{+}$

Other name(s): 12-oxo-phytodienoic acid reductase; 8-[(1R,2R)-3-oxo-2-(Z)-pent-2-

enylcyclopentyl]octanoate:NADP+ 4-oxidoreductase

Systematic name: (9S,13S)-10,11-dihydro-12-oxo-15-phytoenoate:NADP⁺ 4-oxidoreductase

Comments: Involved in the conversion of linolenate into jasmonate in *Zea mays*.

References: [4444]

[EC 1.3.1.42 created 1989]

EC 1.3.1.43

Accepted name: arogenate dehydrogenase

Reaction: L-arogenate + NAD⁺ = L-tyrosine + NADH + CO_2

Other name(s): arogenic dehydrogenase (ambiguous); cyclohexadienyl dehydrogenase (ambiguous); pretyrosine de-

hydrogenase (ambiguous); L-arogenate:NAD⁺ oxidoreductase; arogenate dehydrogenase (NAD⁺)

Systematic name: L-arogenate:NAD⁺ 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). NAD⁺-specific enzymes have been reported from some bacteria [513] and plants [512].

Some enzymes also possess the activity of EC 1.3.1.12, prephenate dehydrogenase.

References: [4023, 513, 512, 2730, 2503, 4859]

[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: [1819]

[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: [4288]

[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⁺ Δ^2 -oxidoreductase

Comments: Some other isoflavones are reduced to the corresponding isoflavanones.

References: [4288]

[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: [2967]

[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- Δ^{13} -prostaglandin reductase; Δ^{13} -15-ketoprostaglandin reductase; 15-ketoprostaglandin

 Δ^{13} -reductase; prostaglandin Δ^{13} -reductase; prostaglandin 13-reductase; (5Z)-(15S)-11 α -hydroxy-9,15-dioxoprostanoate:NAD(P)⁺ Δ^{13} -oxidoreductase; (5Z)-11 α -hydroxy-9,15-dioxoprost-5-

enoate:NAD(P) $^+$ Δ^{13} -oxidoreductase

Systematic name: 11α -hydroxy-9,15-dioxoprostanoate:NAD(P)⁺ Δ^{13} -oxidoreductase

Comments: Reduces 13,14-dehydro-15-oxoprostaglandins to 13,14-dihydro derivatives. The enzyme from pla-

centa is specific for NAD⁺.

References: [1512, 1891]

[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: [2961]

[EC 1.3.1.49 created 1992]

[1.3.1.50 Deleted entry. tetrahydroxynaphthalene reductase] Deleted entry. 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: [1124]

[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: (3S,4R)-3,4-dihydroxycyclohexa-1,5-diene-1,4-dicarboxylate dehydrogenase

Reaction: (3S,4R)-3,4-dihydroxycyclohexa-1,5-diene-1,4-dicarboxylate + NAD⁺ = 3,4-dihydroxybenzoate +

 $CO_2 + NADH$

Other name(s): (1R,2S)-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+ ox-

idoreductase (decarboxylating)

Systematic name: (3S,4R)-3,4-dihydroxycyclohexa-1,5-diene-1,4-dicarboxylate:NAD⁺ oxidoreductase

Comments: Requires Fe^{II}. Involved in the terephthalate degradation pathway in bacteria [4539].

References: [3648, 4539]

[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; CobK

Systematic name: precorrin-6B:NADP⁺ oxidoreductase

Comments: The enzyme, which participates in the aerobic (late cobalt insertion) pathway of adenosylcobalamin

biosynthesis, catalyses the reduction of the double bond between C-18 and C-19 of precorrin-6A. See EC 1.3.1.106, cobalt-precorrin-6A reductase, for the corresponding enzyme that participates in the

anaerobic cobalamin biosynthesis pathway.

References: [354, 4550]

[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: [4154, 1223, 1685]

[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: [1465]

[EC 1.3.1.57 created 2000]

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: [1007]

[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: [2323, 883]

[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, (3S,4R)-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: [1262]

[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: [237]

[EC 1.3.1.64 created 2000]

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: [3695]

[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: [1320]

[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 +

 $NAD(P)H + CO_2$

Systematic name: cis-1,2-dihydroxy-4-methylcyclohexa-3,5-diene-1-carboxylate:NAD(P) $^+$ oxidoreductase (decarboxy-

lating)

Comments: Involved in the *p*-xylene degradation pathway in bacteria.

References: [4607]

[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 +

 CO_2

Systematic name: 1,2-dihydroxy-6-methylcyclohexa-3,5-dienecarboxylate:NAD⁺ oxidoreductase (decarboxylating)

Comments: Involved in the *o*-xylene degradation pathway in bacteria.

References: [1647]

[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: [2667]

[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: Δ^{14} -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+ Δ^{14} -oxidoreductase

Comments: This enzyme acts on a range of steroids with a 14(15)-double bond.

References: [404, 3222]

[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 $24(24^1)$ -double bond.

References: [3031, 4945]

[EC 1.3.1.71 created 2001, modified 2002]

EC 1.3.1.72

Accepted name: Δ^{24} -sterol reductase

Reaction: 5α -cholest-7-en-3 β -ol + NADP⁺ = 5α -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 zymos-

terol.

References: [177]

[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: [1271]

[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 re-

ductase

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: [2636, 902]

[EC 1.3.1.74 created 2003, modified 2014]

Accepted name: 3,8-divinyl protochlorophyllide *a* 8-vinyl-reductase (NADPH)

protochlorophyllide $a + \text{NADP}^+ = 3,8$ -divinyl protochlorophyllide $a + \text{NADPH} + \text{H}^+$ **Reaction:**

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 chlorophyl-

lide 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).

[4330, 3237, 3238, 2213, 2962, 648] **References:**

[EC 1.3.1.75 created 2003, modified 2016]

EC 1.3.1.76

Accepted name: precorrin-2 dehydrogenase

 $precorrin-2 + NAD^+ = sirohydrochlorin + NADH + H^+$ **Reaction:**

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 uropor-

> > phyrinogen 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 sep-

arate enzymes carry out each of the steps, with SirC being responsible for the above reaction.

[3748, 4550] **References:**

[EC 1.3.1.76 created 2004]

EC 1.3.1.77

Accepted name: anthocyanidin reductase [(2R,3R)-flavan-3-ol-forming]

Reaction: a (2R,3R)-flavan-3-ol + 2 NAD(P)⁺ = an anthocyanidin with a 3-hydroxy group + 2 NAD(P)H + H⁺ ANR (gene name) (ambiguous); flavan-3-ol:NAD(P)+ oxidoreductase; anthocyanidin reductase (am-Other name(s):

biguous)

Systematic name: (2R,3R)-flavan-3-ol:NAD(P)⁺ 3,4-oxidoreductase

Comments: The enzyme participates in the flavonoid biosynthesis pathway found in plants. It catalyses the dou-

> ble reduction of anthocyanidins, producing (2R,3R)-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 [(2S)-flavan-

3-ol-forming].

[4697, 4696, 3232] **References:**

[EC 1.3.1.77 created 2004, modified 2016]

EC 1.3.1.78

Accepted name: arogenate dehydrogenase (NADP⁺)

> L-arogenate + $NADP^+$ = L-tyrosine + NADPH + CO_2 **Reaction:**

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 [3526, 385].

References: [1255, 3526, 385]

[EC 1.3.1.78 created 2005]

EC 1.3.1.79

Accepted name: arogenate dehydrogenase $[NAD(P)^{+}]$

Reaction: L-arogenate + NAD(P)⁺ = L-tyrosine + NAD(P)H + CO_2

Other name(s): arogenic dehydrogenase (ambiguous); cyclohexadienyl dehydrogenase; pretyrosine dehydrogenase

(ambiguous)

Systematic name: L-arogenate:NAD(P)⁺ 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). Enzymes that can utilize both cofactors have been reported from some Proteobacteria, including *Burkholderia caryophylli*, *Burkholderia cepacia*, *Pseudomonas marginata* and *Delftia aci*-

dovorans.

References: [513]

[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 $^+$

 $\textbf{Systematic name:} \quad \text{(-)-menthone:} NADP^+ \ oxidoreduct as e$

Comments: NADH cannot replace NADPH as reductant. The $\Delta^{8,9}$ -double bond of (+)-cis-isopulegone and the

 $\Delta^{1,2}$ -double bond of (\pm)-piperitone are not substrates. The enzyme from peppermint (*Mentha* \times *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: [3524]

[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 [3524]. 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: [774, 3524]

[EC 1.3.1.82 created 2008]

EC 1.3.1.83

Accepted name: geranylgeranyl diphosphate reductase

Reaction: phytyl diphosphate $+ 3 \text{ NADP}^+ = \text{geranylgeranyl diphosphate} + 3 \text{ NADPH} + 3 \text{ H}^+$

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: [3955, 4197, 2059]

[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 fixa-

tion pathway found in some thermoacidophilic archaea [296]. The enzyme from *Sulfolobus tokodaii* does not act on either NADH or crotonyl-CoA [4249]. Different from EC 1.3.1.8, which acts only on

enoyl-CoA derivatives of carbon chain length 4 to 16. Contains Zn^{2+} .

References: [296, 4249]

[EC 1.3.1.84 created 2009, modified 2014]

EC 1.3.1.85

Accepted name: crotonyl-CoA carboxylase/reductase

Reaction: (2S)-ethylmalonyl-CoA + NADP⁺ = (E)-but-2-enoyl-CoA + CO₂ + NADPH + H⁺

Other name(s): CCR; crotonyl-CoA reductase (carboxylating)

Systematic name: (2S)-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 CO_2 . When CO_2 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 carboxyla-

tion).

References: [1059, 1060]

[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 re-

ductase; 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: [4501]

[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⁺ = <math>3-(2,3-4)

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 de-

hydrogenase

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: [900]

[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: [4700, 4701]

[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: [4700]

[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: [4700]

[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 [3517]. The enzyme specifically modifies uracil²⁰ in tRNA.

References: [4700, 4701, 3517, 2022]

[EC 1.3.1.91 created 2011]

EC 1.3.1.92

Accepted name: artemisinic aldehyde $\Delta^{11(13)}$ -reductase

Reaction: (11R)-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 biosyntheis of artemisinin.

References: [309, 4888]

[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 (3R)-3-hydroxyacyl-CoA dehydratase.

References: [2198, 1246, 2316, 4909]

[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: [3627, 545]

[EC 1.3.1.94 created 2012]

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 [1632]. *cf.* EC 1.3.1.84, acrylyl-CoA reductase

(NADPH).

References: [1632, 1989]

[EC 1.3.1.95 created 2012]

EC 1.3.1.96

Accepted name: Botryococcus squalene synthase

Reaction: squalene + diphosphate + NADP $^+$ = presqualene diphosphate + NADPH + $^+$

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: [3066]

[EC 1.3.1.96 created 2012]

EC 1.3.1.97

Accepted name: botryococcene synthase

Reaction: C_{30} 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: [3066]

[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'-

 $diphospho-\textit{N-}acetyl-2-amino-2-deoxy-3-\textit{O-}lactylglucose:} NADP-oxidoreductase$

Systematic name: UDP-*N*-acetyl- α -D-muramate:NADP⁺ oxidoreductase

Comments: A flavoprotein (FAD). NADH can to a lesser extent replace NADPH.

References: [4187, 4188, 4407]

[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]

[1.3.1.99 Transferred entry. iridoid synthase. Now known to be catalyzed by two different enzymes, EC 1.3.1.122, (S)-8-oxocitronellyl enol synthase, and EC 5.5.1.34, (+)-cis,trans-nepetalactol synthase]

[EC 1.3.1.99 created 2013, deleted 2019]

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 alka-

loid 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: [759, 643, 4506, 4698]

[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 + $8 \text{ NAD(P)H} + 8 \text{ H}^+$

Other name(s): digeranylgeranylglycerophospholipid reductase; Ta0516m (gene name); DGGGPL reductase; 2,3-

digeranylgeranylglycerophospholipid reductase

Systematic name: 2,3-bis-(*O*-phytany)l-*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: [3078, 3079, 4707]

[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 [2639]. 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: [1670, 2710, 2639]

[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 bac-

terium Burkholderia sp. WS.

References: [2298]

[EC 1.3.1.103 created 2013]

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 (ambigu-

ous); 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, Respecific), 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: [1595, 2100, 2098]

[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(2H)-one + NADP⁺ = 4-hydroxy-5-methyl-2-methylenefuran-3(2H)-

one + NADPH + H^+

Other name(s): FaEO; SIEO; enone oxidoreductase; 4-hydroxy-2,5-dimethylfuran-3(2H)-one:NAD(P)⁺ oxidoreduc-

tase

Systematic name: 4-hydroxy-2,5-dimethylfuran-3(2*H*)-one:NADP⁺ oxidoreductase

Comments: The enzyme was dicovered 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 (2E)-2-ethylidene-4-hydroxy-5-methylfuran-3(2H)-one and produces homofuraneol, an important aroma compound in soy

sauce and miso. NADPH is the preferred cofactor.

References: [3418, 2154, 3716, 4369]

[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, which participates in the anaerobic (early cobalt insertion) pathway of adenosylcobal-

amin biosynthesis, catalyses the reduction of the double bond between C-18 and C-19 of cobalt-precorrin-6A. The enzyme from the bacterium *Bacillus megaterium* has no activity with NADPH. See EC 1.3.1.54, precorrin-6A reductase, for the corresponding enzyme that participates in the aerobic

cobalamin biosynthesis pathway.

References: [2110, 2877]

[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 uM) of the dinucleotide. At higher con-

centrations the reaction with NADPH is inhibited but not that with NADH [4578].

References: [4578, 4457]

[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] clus-

ters 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: [319]

[EC 1.3.1.108 created 2015]

EC 1.3.1.109

Accepted name: butanoyl-CoA dehydrogenase complex (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; butanoyl-CoA

dehydrogenase (NAD⁺, ferredoxin)

Systematic name: butanoyl-CoA:NAD⁺, ferredoxin oxidoreductase

Comments: The enzyme is a complex of a flavin-containing dehydrogenase component (Bcd) and an electron-

transfer flavoprotein dimer (EtfAB). The enzyme complex, isolated from the bacteria *Acidaminococcus fermentans* and butanoate-producing *Clostridia* species, couples the exergonic reduction of (*E*)-but-2-enoyl-CoA to butanoyl-CoA by NADH to the endergonic reduction of ferredoxin by NADH,

using electron bifurcation to overcome the steep energy barrier in ferredoxin reduction.

References: [2442, 3328, 683, 682]

[EC 1.3.1.109 created 2015, modified 2021]

[1.3.1.110 Transferred entry. lactate dehydrogenase (NAD $^+$, ferredoxin). Now EC 1.1.1.436, lactate dehydrogenase (NAD $^+$, ferredoxin)

[EC 1.3.1.110 created 2015, deleted 2022]

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, re-

ducing 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: [380, 28, 29, 1525]

[EC 1.3.1.111 created 2016]

EC 1.3.1.112

Accepted name: anthocyanidin reductase [(2S)-flavan-3-ol-forming]

Reaction: (1) a (2S,3R)-flavan-3-ol + 2 NADP⁺ = an anthocyanidin with a 3-hydroxy group + 2 NADPH + H⁺

(2) a (2S,3S)-flavan-3-ol + 2 NADP⁺ = an anthocyanidin with a 3-hydroxy group + 2 NADPH + H⁺

Systematic name: (2S)-flavan-3-ol:NAD(P)⁺ oxidoreductase

Comments: The enzyme, characterized from *Vitis vinifera* (grape), participates in the flavonoid biosynthesis path-

way. It catalyses the double reduction of anthocyanidins, producing a mixture of (2S,3S)- and (2S,3R)-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 [(2R,3R)-flavan-3-ol-forming].

References: [1276, 1275]

[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 [(3S,4R)-4-alkanoyl-5-oxooxolan-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); *scbC* (gene name)

Systematic name: [(3S,4R)-4-alkanoyl-5-oxooxolan-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: [2016, 330]

[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) 12α -hydroxy-3-oxocholan-24-oyl-CoA + NAD⁺ = 12α -hydroxy-3-oxochol-4-en-24-oyl-CoA +

 $NADH + H^{+}$

(4) 12α -hydroxy-3-oxochol-4-en-24-oyl-CoA + NAD⁺ = 12α -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 7α -dehydration.

References: [1539]

[EC 1.3.1.114 created 2018]

Accepted name: 3-oxocholoyl-CoA 4-desaturase

Reaction: (1) 7α , 12α -dihydroxy-3-oxochol-24-oyl-CoA + NAD⁺ = 7α , 12α -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: [1990]

[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: 7 β -hydroxy-3-oxochol-24-oyl-CoA Δ^4 -oxidoreductase

Comments: Contains FAD and FMN. The enzyme, characterized from the bacterium *Clostridium scindens*, par-

ticipates 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: [223, 1168, 1990]

[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: [1784]

[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 C_{20} fatty acids to form C_{60} to C_{90} mycolic acids. The enzyme, which forms a homotetramer, is the target

of the preferred antitubercular drug isoniazid.

References: [3415, 3589, 2658, 4451, 1452, 676]

[EC 1.3.1.118 created 2018]

EC 1.3.1.119

Accepted name: chlorobenzene dihydrodiol dehydrogenase

Reaction: (1R,2R)-3-chlorocyclohexa-3,5-diene-1,2-diol + NAD⁺ = 3-chlorocatechol + NADH + H⁺

Other name(s): tecB (gene name)

Systematic name: (1R,2R)-3-chlorocyclohexa-3,5-diene-1,2-diol:NAD⁺ oxidoreductase

Comments: This bacterial enzyme can transform various dihydrodiols of chlorobenzenes into the respective cate-

chols, 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 spec-

trum EC 1.14.12.26, chlorobenzene dioxygenase.

References: [3985, 3347, 3348]

[EC 1.3.1.119 created 2018]

EC 1.3.1.120

Accepted name: cyclohexane-1-carbonyl-CoA reductase (NADP⁺)

Reaction: cyclohexane-1-carbonyl-CoA + NADP $^+$ = cyclohex-1-ene-1-carbonyl-CoA + NADPH + H $^+$

Other name(s): 1-cyclohexenylcarbonyl-CoA reductase (ambiguous); *chcA* (gene name)

Systematic name: cyclohexane-1-carbonyl-CoA:NADP⁺ 1-oxidoreductase

Comments: The enzyme, characterized from the bacterium Streptomyces collinus, is involved in a pathway that

transforms shikimate to cyclohexane-1-carbonyl-CoA by a series of dehydration and double-bond reduction steps. Most of the steps in this process occur with the carboxylic acid activated as a coenzyme A thioester. The enzyme catalyses three steps in this pathway, also acting on (3R,4R)-3,4-dihydroxycyclohexa-1,5-diene-1-carbonyl-CoA and (5S)-5-hydroxycyclohex-1-ene-1-carbonyl-CoA.

References: [3506, 4523]

[EC 1.3.1.120 created 2019]

EC 1.3.1.121

Accepted name: 4-amino-4-deoxyprephenate dehydrogenase

Reaction: 4-amino-4-deoxyprephenate + NAD^+ = 3-(4-aminophenyl)pyruvate + CO_2 + NADH + H^+

Other name(s): *cmlC* (gene name); *papC* (gene name)

Systematic name: 4-amino-4-deoxyprephenate:NAD⁺ oxidoreductase (decarboxylating)

Comments: The enzyme, characterized from the bacteria Streptomyces venezuelae and Streptomyces pristinaespi-

ralis, participates in the biosynthesis of the antibiotics chloramphenicol and pristinamycin IA, respec-

tively. cf. EC 1.3.1.12, prephenate dehydrogenase.

References: [352, 1590]

[EC 1.3.1.121 created 2019]

EC 1.3.1.122

Accepted name: (S)-8-oxocitronellyl enol synthase

Reaction: (S)-8-oxocitronellyl enol + NAD(P)⁺ = (6E)-8-oxogeranial + NAD(P)H + H⁺

Other name(s): CrISY; 8-oxogeranial:NAD(P)⁺ oxidoreductase (cyclizing, cis-trans-nepetalactol forming); iridoid

synthase (incorrect)

Systematic name: (S)-8-oxocitronellyl enol:NAD(P)⁺ oxidoreductase

Comments: Isolated from the plants Catharanthus roseus, Olea europaea (common olive), and several Nepeta

species. The enzyme reduces 8-oxogeranial, generating an unstable product that is subsequently cyclized into several possible products, either non-enzymically or by dedicated cyclases. The products, known as iridoids, are involved in the biosynthesis of many indole alkaloids. *cf.* EC 1.3.1.123, 7-*epi*-

iridoid synthase.

References: [1312, 1749, 54, 3399, 3846, 2476, 2477]

[EC 1.3.1.122 created 2013 as EC 1.3.1.99, part transferred 2019 to EC 1.3.1.122]

EC 1.3.1.123

Accepted name: 8-oxogeranial reductase

Reaction: (*R*)-8-oxocitronellyl enol + NADP⁺ = (6E)-8-oxogeranial + NADPH + H⁺

Other name(s): AmISY

Systematic name: (R)-8-oxocitronellyl enol:NADP⁺ oxidoreductase

Comments: The enzyme, characterized from the plant *Antirrhinum majus* (snapdragon), is involved in biosyn-

thesis of 7-epi-iridoids such as antirrhinoside. The enzyme catalyses the stereospecific reduction of 8-oxogeranial, forming an unstable product that in the absence of additional cylases undergoes spontaneous cyclization to (-)-cis,trans-nepetalactol. cf. EC 1.3.1.122, (S)-8-oxocitronellyl enol synthase.

References: [2264, 2477]

[EC 1.3.1.123 created 2019]

EC 1.3.1.124

Accepted name: 2,4-dienoyl-CoA reductase [(3*E*)-enoyl-CoA-producing]

Reaction: (1) a (3E)-3-enoyl-CoA + NADP⁺ = a (2E,4E)-2,4-dienoyl-CoA + NADPH + H⁺

(2) a (3E)-3-enoyl-CoA + NADP⁺ = a (2E,4Z)-2,4-dienoyl-CoA + NADPH + H⁺

Other name(s): SPS19 (gene name); DECR1 (gene name); DECR2 (gene name); Δ^2 , Δ^4 -dienoyl-CoA reductase (am-

biguous)

Systematic name: (3E)-3-enoyl-CoA:NADP⁺ 4-oxidoreductase

Comments: This enzyme, characterized from eukaryotic organisms, catalyses the reduction of either (2E,4E)-2,4-

dienoyl-CoA or (2*E*,4*Z*)-2,4-dienoyl-CoA to (3*E*)-3-enoyl-CoA. The best substrates for the enzyme from bovine liver have a chain-length of 8 or 10 carbons. Mammals possess both mitochondrial and peroxisomal variants of this enzyme. *cf.* EC 1.3.1.34, 2,4-dienoyl-CoA reductase [(2*E*)-enoyl-CoA-

producing].

References: [2289, 945, 1453, 1297, 3121, 74]

[EC 1.3.1.124 created 2020]

EC 1.3.1.125

Accepted name: acrylate reductase

Reaction: propanoate + NAD $^+$ = acrylate + NADH + H $^+$ **Other name(s):** *ard* (gene name); NADH:acrylate oxidoreductase

Systematic name: propanoate:NAD⁺ oxidoreductase

Comments: The enzyme, characterized from the marine bacterium *Vibrio harveyi*, enables the organism to utilize

acrylate as the terminal electron acceptor for NADH regeneration under anaerobic conditions.

References: [320]

[EC 1.3.1.125 created 2022]

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 ferrocytochrome $c + 4 H^+$

(overall reaction)

(1a) L-galactono-1,4-lactone + 2 ferricytochrome c = L-ascorbate + 2 ferrocytochrome c + 2 H⁺ (1b) L-ascorbate + 2 ferricytochrome c = L-dehydroascorbate + 2 ferrocytochrome c + 2 H⁺ (sponta-

neous)

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 [3200]. The enzyme is very specific for its substrate L-galactono-1,4-lactone as D-galactono- γ -lactone, D-gulono- γ -lactone, D-gulono- γ -lactone, D-galactonate, D-glucuronate and D-gluconate are not substrates [3200]. FAD, NAD⁺, NADP⁺ and O₂ (cf. EC

1.3.3.12, L-galactonolactone oxidase) cannot act as electron acceptor [3200].

References: [2642, 2643, 1824, 3122, 3200]

[EC 1.3.2.3 created 1961, modified 2006]

EC 1.3.2.4

Accepted name: fumarate reductase (cytochrome)

Reaction: succinate + 2 ferricytochrome c = fumarate + 2 ferrocytochrome c

Other name(s): fccA (gene name); fcc3 (gene name); flavocytochrome c_3

Systematic name: succinate:ferricytochrome-c oxidoreductase

Comments: Contains a non-covalently bound FAD cofactor and four heme c groups. The enzyme, characterized

from the bacterium *Shewanella frigidimarina*, is a soluble periplasmic protein that functions as a terminal electron acceptor during anaerobic growth. The direct electron donor is the membrane-bound tetraheme *c*-type cytochrome CymA (EC 7.1.1.8, quinol—cytochrome-*c* reductase), which receives

the electrons from the membrane quinol pool.

References: [3270, 3271, 1368, 937, 3487, 3764]

[EC 1.3.2.4 created 2022]

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 + O_2 + 2 H⁺ = protoporphyrinogen-IX + 2 CO₂ + 2 H₂O

Other name(s): coproporphyrinogen III oxidase; coproporphyrinogenase Systematic name: coproporphyrinogen:oxygen oxidoreductase (decarboxylating)

References: [239, 2759, 2205]

[EC 1.3.3.3 created 1972, modified 2003]

EC 1.3.3.4

Accepted name: protoporphyrinogen oxidase

Reaction: protoporphyrinogen IX + $3 O_2$ = protoporphyrin IX + $3 H_2 O_2$

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 [622]. Two isoen-

zymes exist in plants: one in plastids and the other in mitochondria. This is the target enzyme of phthalimide-type and diphenylether-type herbicides [622]. The enzyme from oxygen-dependent

species contains FAD [809]. Also slowly oxidizes mesoporphyrinogen IX.

References: [3361, 3362, 805, 4518, 739, 1109, 808, 622, 809]

[EC 1.3.3.4 created 1978, modified 2003]

EC 1.3.3.5

Accepted name: bilirubin oxidase

Reaction: 2 bilirubin + $O_2 = 2$ biliverdin + 2 H_2O

Other name(s): bilirubin oxidase M-1

Systematic name: bilirubin:oxygen oxidoreductase

References: [2942, 4196]

[EC 1.3.3.5 created 1984]

EC 1.3.3.6

Accepted name: acyl-CoA oxidase

Reaction: acyl-CoA + O_2 = trans-2,3-dehydroacyl-CoA + H_2O_2

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: [2041, 3203]

[EC 1.3.3.6 created 1986]

EC 1.3.3.7

Accepted name: dihydrouracil oxidase

Reaction: 5,6-dihydrouracil + O_2 = uracil + H_2O_2 **Systematic name:** 5,6-dihydrouracil:oxygen oxidoreductase

Comments: Also oxidizes dihydrothymine to thymine. A flavoprotein (FMN).

References: [3218]

[EC 1.3.3.7 created 1989]

EC 1.3.3.8

Accepted name: tetrahydroberberine oxidase

Reaction: (S)-tetrahydroberberine + $2 O_2$ = berberine + $2 H_2 O_2$

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: [76, 3154]

[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 + $O_2 = \alpha, \beta$ -didehydrotryptophan + H_2O_2 **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 reac-

tion can hydrolyse spontaneously to form (indol-3-yl)pyruvate.

References: [1299, 1298]

[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 + $3 O_2$ =

4,5-dioxo-4,5-dihydro-1H-pyrrolo[2,3-f]quinoline-2,7,9-tricarboxylate + $2H_2O_2 + 2H_2O_3$

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 oxi-

doreductase (cyclizing)

Comments: So far only a single turnover of the enzyme has been observed, and the pyrroloquinoline quinone re-

mains bound to it. It is not yet known what releases the product in the bacterium.

References: [2610, 2609, 4318, 4320, 3770]

[EC 1.3.3.11 created 2005]

EC 1.3.3.12

Accepted name: L-galactonolactone oxidase

Reaction: L-galactono-1,4-lactone + O_2 = L-ascorbate + H_2O_2

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 galactonolac-

tone dehydrogenase).

References: [358]

[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

 $\textbf{Reaction:} \quad \text{cyclo}(\text{L-leucyl-L-phenylalanyl}) + \textbf{2} \ \text{O}_2 = \text{albonoursin} + \textbf{2} \ \text{H}_2 \text{O}_2 \ (\text{overall reaction})$

 $(1a)\ cyclo(\text{L-leucyl-L-phenylalanyl}) + O_2 = cyclo[(Z) - \alpha, \beta - \text{didehydrophenylalanyl-L-leucyl}] + H_2O_2 + G_2 +$

(1b) $\operatorname{cyclo}[(Z)-\alpha,\beta-\operatorname{didehydrophenylalanyl-L-leucyl}] + O_2 = \operatorname{albonoursin} + H_2O_2$

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) [1358, 2366].

References: [1358, 2366]

[EC 1.3.3.13 created 2013]

EC 1.3.3.14

Accepted name: aclacinomycin-A oxidase

Reaction: aclacinomycin $A + O_2 = aclacinomycin Y + H_2O_2$

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 in-

volved in the modification of the terminal sugar residues in the biosynthesis of aclacinomycins. The enzyme utilizes the same active site to catalyse the oxidation of the rhodinose moiety of aclacinomycin N to the cinerulose A moiety of aclacinomycin A (*cf.* EC 1.1.3.45) and the oxidation of the

latter to the L-aculose moiety of aclacinomycin Y.

References: [4817, 66, 4112]

[EC 1.3.3.14 created 2013]

EC 1.3.3.15

Accepted name: coproporphyrinogen III oxidase (coproporphyrin-forming) Reaction: coproporphyrinogen III + $3 O_2$ = coproporphyrin III + $3 H_2O_2$

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: [1514, 739, 3400, 806]

[EC 1.3.3.15 created 2016]

EC 1.3.3.16

Accepted name: oxazoline dehydrogenase

Reaction: (1) a [protein]-(1S,4R)-2-(C-substituted-aminomethyl)-4-acyl-2-thiazoline + O₂ = a [protein]-(S)-2-

(C-substituted-aminomethyl)-4-acyl-1,3-thiazole + H₂O₂

(2) a [protein]-(S,S)-2-(C-substituted-aminomethyl)-4-acyl-2-oxazoline + O_2 = a [protein]-(S)-2-(C-

substituted-aminomethyl)-4-acyl-1,3-oxazole + H_2O_2

(3) a [protein]-(S,S)-2-(C-substituted-aminomethyl)-4-acyl-5-methyl-2-oxazoline + O_2 = a [protein]-

(S)-2-(C-substituted-aminomethyl)-4-acyl-5-methyl-1,3-oxazole + H_2O_2

Other name(s): azoline oxidase; thiazoline oxidase; cyanobactin oxidase; patG (gene name); mcaG (gene name); artG

(gene name); lynG (gene name); tenG (gene name)

Systematic name: a [protein]-2-oxazoline:oxygen oxidoreductase (2-oxazole-forming)

Comments: Contains FMN. This enzyme oxidizes 2-oxazoline, 5-methyl-2-oxazoline, and 2-thiazoline within

peptides, which were formed by EC 6.2.2.2, oxazoline synthase, and EC 6.2.2.3, thiazoline synthase, to the respective pyrrole-type rings. The enzyme is found as either a stand-alone protein or as a do-

main within a multifunctional protein (the G protein) that also functions as a peptidase.

References: [2468, 3725, 290, 1314]

[EC 1.3.3.16 created 2020]

EC 1.3.3.17

Accepted name: benzylmalonyl-CoA dehydrogenase

Reaction: benzylmalonyl-CoA + $O_2 = (E)$ -cinnamoyl-CoA + $CO_2 + H_2O_2$

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

Systematic name: benzylmalonyl-CoA:oxygen oxidoreductase (decarboxylating)

Comments: The enzyme, characterized from the bacterium *Aromatoleum aromaticum*, is involved in degradation

of (indol-3-yl)acetate, where it is believed to function on (2-aminobenzyl)malonyl-CoA.

References: [3750]

[EC 1.3.3.17 created 2022]

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 oxy-

gen sensitive. It cannot use reduced flavins, reduced coenzyme F_{420} , 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: [2078, 1611]

[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 (ambiguous); succinate:ubiquinone oxidoreductase; fumarate reductase (quinol); FRD; menaquinol-fumarate oxidoreductase; succinate dehydrogenase (menaquinone); succinate:menaquinone oxidoreductase; fumarate reductase

(menaquinone)

Systematic name: succinate:quinone oxidoreductase

Comments: A complex generally comprising an FAD-containing component that also binds the carboxylate sub-

strate (A subunit), a component that contains three different iron-sulfur centers [2Fe-2S], [4Fe-4S], and [3Fe-4S] (B subunit), and a hydrophobic membrane-anchor component (C, or C and D subunits) that is also the site of the interaction with quinones. The enzyme is found in the inner mitochondrial membrane in eukaryotes and the plasma membrane of bacteria and archaea, with the hydrophilic domain extending into the mitochondrial matrix and the cytoplasm, respectively. Under aerobic conditions the enzyme catalyses succinate oxidation, a key step in the citric acid (TCA) cycle, transferring the electrons to quinones in the membrane, thus linking the TCA cycle with the aerobic respiratory chain (where it is known as complex II). Under anaerobic conditions the enzyme functions as a fumarate reductase, transferring electrons from the quinol pool to fumarate, and participating in anaerobic respiration with fumarate as the terminal electron acceptor. The enzyme interacts with the quinone produced by the organism, such as ubiquinone, menaquinone, caldariellaquinone, thermoplasmaquinone, rhodoquinone etc. Some of the enzymes contain two heme subunits in their membrane anchor subunit. These enzymes catalyse an electrogenic reaction and are thus classified as EC 7.1.1.12, succinate dehydrogenase (electrogenic, proton-motive force generating).

References: [2132, 1617, 1855, 583, 1120, 582, 3219, 2303, 1862]

[EC 1.3.5.1 created 1983 (EC 1.3.99.1 created 1961, incorporated 2014, EC 1.3.5.4 created 2010, incorporated 2022), modified 2022]

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 [1078]. 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 [1662, 1078]. 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 [1662]. 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 [1662]. 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 accep-

tor.

References: [1142, 1662, 174, 1078, 341, 3010]

[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 (quinone)

Reaction: protoporphyrinogen IX + 3 quinone = protoporphyrin IX + 3 quinol **Other name(s):** HemG; protoporphyrinogen IX dehydrogenase (menaquinone)

Systematic name: protoporphyrinogen IX:quinone oxidoreductase

Comments: Contains FMN. The enzyme participates in heme b biosynthesis. In the bacterium Escherichia coli it

interacts with either ubiquinone or menaquinone, depending on whether the organism grows aerobi-

cally or anaerobically.

References: [413, 2853]

[EC 1.3.5.3 created 2010, modified 2020]

[1.3.5.4 Transferred entry. fumarate reductase (quinol), now included in EC 1.3.5.1, succinate dehydrogenase.]

[EC 1.3.5.4 created 2010, modified 2013, deleted 2022]

EC 1.3.5.5

Accepted name: 15-cis-phytoene desaturase

Reaction: 15-cis-phytoene + 2 plastoquinone = 9,15,9'-tricis- 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'-tricis- 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⁺ [437].

References: [437, 3734, 1169, 436]

[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'-tricis-neurosporene + a quinol

(1b) 7,9,9'-tricis-neurosporene + a quinone = 7,9,7',9'-tetracis-lycopene + a quinol

Other name(s): ζ-carotene desaturase; ZDS

Systematic name: 9.9'-dicis- ζ -corotene:quinone oxidoreductase

Comments: This enzyme is involved in carotenoid biosynthesis in plants and cyanobacteria.

References: [61, 1954, 434, 436]

[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: [1691]

[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 pro-

posed that this enzyme and EC 1.3.7.3, phycoerythrobilin:ferredoxin oxidoreductase, function as a

dual enzyme complex in the conversion of biliverdin $IX\alpha$ into phycoerythrobilin.

References: [1167]

[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 $IX\alpha$ to phycoerythrobilin.

References: [1167]

[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 IXα. Can use [2Fe-2S] ferredoxins from a num-

ber 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 ferre-

doxin.

References: [1167, 2747, 4247]

[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 IXα (2-electron reduction at both the A and D

rings). Reaction proceeds via an isolatable 2-electron intermediate, 18^1 , 18^2 -dihydrobiliverdin. Flavodoxins can be used instead of ferredoxin. The direct conversion of biliverdin IX α (BV) to (3Z)-phycocyanolbilin (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)-phycocrythrobilin (PEB) as an intermediate [253] and in

the green alga Mesotaenium caldariorum, in which PCB is an isolable intermediate.

References: [1167, 253, 4678]

[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 IXα)

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: [815]

[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 + $2 \text{ ATP} + 2 \text{ H}_2\text{O}$

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 cataly-

ses *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: [1214, 3101, 2940]

[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 + $2 \text{ ATP} + 2 \text{ H}_2\text{O}$

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 es-

ters but will also catalyse the reaction: ammonia + acceptor + 2 ADP + 2 phosphate = hydroxylamine + reduced acceptor + 2 ATP + H_2O . In the presence of reduced acceptor, but in the absence of oxidiz-

able substrate, the enzyme catalyses the hydrolysis of ATP to ADP plus phosphate.

References: [378, 2290]

[EC 1.3.7.8 created 1999 as EC 1.3.99.15, transferred 2011 to EC 1.3.7.8, modified 2011]

[1.3.7.9 Transferred entry. 4-hydroxybenzoyl-CoA reductase. Now classified as EC 1.1.7.1, 4-hydroxybenzoyl-CoA reductase.]

[EC 1.3.7.9 created 2000 as EC 1.3.99.20, transferred 2011 to EC 1.3.7.9, deleted 2020]

[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 [1837].

References: [2939, 3670, 3667, 1837]

[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 chloro-

phyll 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 [3545, 4688]. This reaction takes place while red chlorophyll catabolite is still bound to EC 1.14.15.17, pheophorbide *a* oxygenase [3389]. 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 [3389, 1733]. After modification and export, pFCCs are eventually imported into the vacuole, where the acidic environment causes their non-enzymic conversion into colourless break-

down products called non-fluorescent chlorophyll catabolites (NCCs) [4688].

References: [3545, 4688, 3389, 1733, 3546]

[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 in-

volved 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 protochlorophyl-

lide a 8-vinyl-reductase (NADPH).

References: [648, 3676, 1845]

[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 + $H_2O + 2H^+$

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: [4346, 4345]

[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] clus-

ter + ADP + phosphate = 3-devinyl-3-(1-hydroxyethyl)chlorophyllide a + 2 reduced ferredoxin [iron-sulfur] cluster + ATP + H_2O + 2 H_2^+

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 (7R,8R)-configuration. In addition, the enzyme has a latent activity of EC 1.3.7.13, 3,8-divinyl protochlorophyllide a 8-vinyl-reductase (ferredoxin) [1527]. 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: [3100, 4346, 2345, 1527]

[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 [1396] or pentanoyl-CoA [3834]. The enzyme from rat has only 10% activity with hexanoyl-CoA (compared to butanoyl-CoA) and no activity with octanoyl-CoA [1795]. *cf.* EC 1.3.8.7, medium-chain acyl-CoA dehydrogenase, EC 1.3.8.8, long-chain acyl-CoA de-

hydrogenase, and EC 1.3.8.9, very-long-chain acyl-CoA dehydrogenase.

References: [2613, 1396, 275, 3834, 4277, 1795, 2754]

[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'-diaponeurosporene + FAD = all-trans-4,4'-diapolycopene + 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 oxidoreduc-

tase (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 [4215], it is able to catalyse the last reaction in vitro [4807].

References: [4621, 3432, 3433, 4215, 4807]

[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 + re-

duced 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: [2426, 2427]

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: [172, 1796, 4194]

 $[EC\ 1.3.8.4\ created\ 1978\ as\ EC\ 1.3.99.10,\ modified\ 1986,\ transferred\ 2012\ to\ EC\ 1.3.8.4]$

EC 1.3.8.5

Accepted name: short-chain 2-methylacyl-CoA dehydrogenase

Reaction: 2-methylbutanoyl-CoA + electron-transfer flavoprotein = (E)-2-methylbut-2-enoyl-CoA + reduced

electron-transfer flavoprotein + H⁺

Other name(s): ACADSB (gene name); 2-methylacyl-CoA dehydrogenase; branched-chain acyl-CoA dehydrogenase

(ambiguous); 2-methyl branched chain acyl-CoA dehydrogenase; 2-methylbutanoyl-CoA:(acceptor) oxidoreductase; 2-methyl-branched-chain-acyl-CoA:electron-transfer flavoprotein 2-oxidoreductase;

2-methyl-branched-chain-enoyl-CoA reductase

Systematic name: short-chain 2-methylacyl-CoA:electron-transfer flavoprotein 2-oxidoreductase

Comments: A flavoprotein (FAD). The mammalian enzyme catalyses an oxidative reaction as a step in the mito-

chondrial β -oxidation of short-chain 2-methyl fatty acids and participates in isoleucine degradation. The enzyme from the parasitic helminth *Ascaris suum* catalyses a reductive reaction as part of a fermentation pathway, shuttling reducing power from the electron-transport chain to 2-methyl branched-

chain enoyl CoA.

References: [1794, 2216, 2217, 4456, 102]

[EC 1.3.8.5 created 1992 as EC 1.3.1.52, transferred 2012 to EC 1.3.8.5 (EC 1.3.99.12, created 1986, incorporated 2020), modified 2020]

EC 1.3.8.6

Accepted name: glutaryl-CoA dehydrogenase (ETF)

Reaction: glutaryl-CoA + electron-transfer flavoprotein = crotonyl-CoA + CO_2 + 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 re-

mains bound to the enzyme), and the decarboxylation of the latter to crotonyl-CoA (*cf.* EC 7.2.4.5, 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, glutaryl-CoA dehydrogenase (acceptor)].

References: [321, 1541, 995, 3450]

[EC 1.3.8.6 created 1972 as EC 1.3.99.7, transferred 2012 to EC 1.3.8.6, modified 2013, modified 2019]

EC 1.3.8.7

Accepted name: medium-chain acyl-CoA dehydrogenase

> a medium-chain acyl-CoA + electron-transfer flavoprotein = a medium-chain trans-2,3-dehydroacyl-**Reaction:**

> > 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 [768]. The enzyme from rat does not accept C₁₆ at all and is most active with C₆-C₈ compounds [1795]. 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.

[767, 768, 275, 1795, 4277, 2097, 3303, 4311] **References:**

[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

palmitoyl-CoA dehydrogenase; palmitoyl-coenzyme A dehydrogenase; long-chain acyl-coenzyme A Other name(s):

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 [1563]. 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 [1795]. 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: [767, 1563, 1482, 1795, 930]

[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 C_{14} , C_{16} and C_{18} , 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 [1865]. 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 dehydroge-

nase.

References: [1865, 113, 2738]

[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 aciditroph-

icus, is involved in production of cyclohexane-1-carboxylate, a byproduct produced by that organism

during fermentation of benzoate and crotonate to acetate.

References: [2291]

[EC 1.3.8.10 created 2013]

EC 1.3.8.11

Accepted name: cyclohexane-1-carbonyl-CoA dehydrogenase (electron-transfer flavoprotein)

Reaction: cyclohexane-1-carbonyl-CoA + electron-transfer flavoprotein = cyclohex-1-ene-1-carbonyl-CoA +

reduced electron-transfer flavoprotein

Other name(s): *aliB* (gene name); cyclohexane-1-carbonyl-CoA dehydrogenase (ambiguous) Systematic name: cyclohexane-1-carbonyl-CoA:electron transfer flavoprotein oxidoreductase

Comments: Contains FAD. The enzyme, characterized from the strict anaerobic bacterium Syntrophus aciditroph-

icus, is involved in production of cyclohexane-1-carboxylate, a byproduct produced by that organism

during fermentation of benzoate and crotonate to acetate.

References: [3283, 2291]

[EC 1.3.8.11 created 2013, modified 2020]

EC 1.3.8.12

Accepted name: (2S)-methylsuccinyl-CoA dehydrogenase

Reaction: (2S)-methylsuccinyl-CoA + electron-transfer flavoprotein = 2-methylfumaryl-CoA + reduced

electron-transfer flavoprotein

Other name(s): Mcd

Systematic name: (2S)-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: [1061]

[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 com-

plex 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: [3578, 3376, 1041, 4508]

[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 = 1H-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: [4264, 1533]

[EC 1.3.8.14 created 2017]

EC 1.3.8.15

Accepted name: 3-(aryl)acrylate reductase

Reaction: (1) phloretate + electron-transfer flavoprotein = 4-coumarate + reduced electron-transfer flavoprotein

(2) 3-phenylpropanoate + electron-transfer flavoprotein = *trans*-cinnamate + reduced electron-transfer

flavoprotein

(3) 3-(1*H*-indol-3-yl)propanoate + electron-transfer flavoprotein = 3-(indol-3-yl)acrylate + reduced

electron-transfer flavoprotein

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

Systematic name: 3-(phenyl)propanoate:electron-transfer flavoprotein 2,3-oxidoreductase

Comments: The enzyme, found in some amino acid-fermenting anaerobic bacteria, participates in the fermenta-

tion pathways of L-phenylalanine, L-tyrosine, and L-tryptophan. Unlike EC 1.3.1.31, 2-enoate reduc-

tase, this enzyme has minimal activity with crotonate.

References: [936]

[EC 1.3.8.15 created 2019]

EC 1.3.8.16

Accepted name: 2-amino-4-deoxychorismate dehydrogenase

Reaction: (2S)-2-amino-4-deoxychorismate + FMN = 3-(1-carboxyvinyloxy)anthranilate + FMNH₂

Other name(s): ADIC dehydrogenase; 2-amino-2-deoxyisochorismate dehydrogenase; SgcG

Systematic name: (2S)-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 benzoxazolinate moiety of the enediyne antitumour antibiotic C-1027 [2340,

4837].

References: [2340, 4837]

[EC 1.3.8.16 created 2008 as 1.3.99.24, transferred 2020 to EC 1.3.8.16.]

EC 1.3.8.17

Accepted name: dehydro coenzyme F₄₂₀ reductase

Reaction: oxidized coenzyme F_{420} -0 + FMN = dehydro coenzyme F_{420} -0 + FMNH₂

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

Systematic name: oxidized coenzyme F₄₂₀-0:FMN oxidoreductase

Comments: This enzyme is involved in the biosynthesis of coenzyme F_{420} , a redox-active cofactor found in all

methanogenic archaea, as well as some eubacteria. In some eubacteria the enzyme is multifunctional, also catalysing the activities of EC 6.3.2.31, coenzyme F_{420} -0:L-glutamate ligase, and EC 6.3.2.34,

coenzyme F_{420} -1: γ -L-glutamate ligase.

References: [230]

[EC 1.3.8.17 created 2021]

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); dihydoorotic acid dehydrogenase

nase (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: [342, 3582, 3103, 4858, 1809, 626]

[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 + 25'-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 $^ \rightarrow$ —CH=CH₂ + CO₂ + e $^-$ replaces the electron initially used.

References: [2372, 2371]

[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 $F_{420} = 5a,11a$ -dehydrotetracycline + reduced coenzyme F_{420} **Other name(s):** oxyR (gene name); 12-dehydrotetracycline dehydrogenase; dehydrooxytetracycline dehydrogenase;

12-dehydrotetracycline reductase

 $\textbf{Systematic name:} \quad \text{tetracycline:} coenzyme \ F_{420} \ dehydrogen ase$

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 oxytetracy-

cline.

References: [2743, 2811, 2744, 4522]

[EC 1.3.98.4 created 2016]

EC 1.3.98.5

Accepted name: hydrogen peroxide-dependent heme synthase

Reaction: Fe-coproporphyrin III + $2 H_2O_2$ = protoheme + $2 CO_2$ + $4 H_2O$ (overall reaction)

(1a) Fe-coproporphyrin III + H_2O_2 = harderoheme III + CO_2 + 2 H_2O

(1b) harderoheme III + H_2O_2 = protoheme + CO_2 + **2** H_2O

Other name(s): coproheme III oxidative decarboxylase; *hemQ* (gene name)

Systematic name: Fe-coproporphyrin III:hydrogen peroxide oxidoreductase (decarboxylating)

Comments: The enzyme participates in a heme biosynthesis pathway found in Gram-positive bacteria. The ini-

tial decarboxylation step is fast and yields the three-propanoate harderoheme isomer III. The second

decarboxylation is much slower. cf. EC 1.3.98.6, SAM-dependent heme synthase.

References: [807, 585, 1684, 584]

[EC 1.3.98.5 created 2019]

EC 1.3.98.6

Accepted name: AdoMet-dependent heme synthase

Reaction: Fe-coproporphyrin III + 2 *S*-adenosyl-L-methionine = protoheme + 2 CO₂ + 2 5'-deoxyadenosine + 2

L-methionine

Other name(s): *ahbD* (gene name); SAM-dependent heme synthase

Systematic name: Fe-coproporphyrin III:S-adenosyl-L-methionine oxidoreductase (decarboxylating)

Comments: This radical AdoMet enzyme participates in a heme biosynthesis pathway found in archaea and

sulfur-reducing bacteria. cf. EC 1.3.98.5, hydrogen peroxide-dependent heme synthase.

References: [198, 2278]

[EC 1.3.98.6 created 2019]

EC 1.3.98.7

Accepted name: [mycofactocin precursor peptide]-tyrosine decarboxylase

Reaction: C-terminal [mycofactocin precursor peptide]-glycyl-L-valyl-L-tyrosine + S-adenosyl-L-methionine

= C-terminal [mycofactocin precursor peptide]-glycyl-L-valyl-4-[2-aminoethenyl]phenol + CO₂ +

5'-deoxyadenosine + L-methionine

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

Systematic name: C-terminal [mycofactocin precursor peptide]-glycyl-L-valyl-L-tyrosine L-tyrosine-carboxylyase

Comments: This is a bifunctional radical AdoMet (radical SAM) enzyme that catalyses the first two steps in the

biosynthesis of the enzyme cofactor mycofactocin. Activity requires the presence of the MftB chaperone. The other activity of the enzyme is EC 4.1.99.26, 3-amino-5-[(4-hydroxyphenyl)methyl]-4,4-

dimethylpyrrolidin-2-one synthase.

References: [1470, 466, 2077, 168]

[EC 1.3.98.7 created 2021]

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.] Transferred entry. 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: [2435]

[EC 1.3.99.4 created 1965]

EC 1.3.99.5

Accepted name: 3-oxo-5α-steroid 4-dehydrogenase (acceptor)

Reaction: a 3-oxo-5 α -steroid + acceptor = a 3-oxo- Δ ⁴-steroid + reduced acceptor

Other name(s): steroid 5α -reductase; 3-oxosteroid Δ^4 -dehydrogenase; 3-oxo- 5α -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; testosteroie 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-5α-steroid 4-dehydrogenase (NADP⁺).

References: [2435, 1132, 1723]

[EC 1.3.99.5 created 1965, modified 2012]

EC 1.3.99.6

Accepted name: 3-oxo-5β-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: [838]

[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 + H_2O + 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: [2138]

[EC 1.3.99.8 created 1976]

[1.3.99.9 Transferred entry, \(\beta\)-cyclopiazonate dehydrogenase. Now EC 1.21.99.1, \(\beta\)-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]

[1.3.99.12 Transferred entry. 2-methylacyl-CoA dehydrogenase. Now classified as EC 1.3.8.5, 2-methyl-branched-chain-enoyl-CoA reductase.]

[EC 1.3.99.12 created 1986, deleted 2020]

[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 cyclo-

heptane cannot act as donors.

References: [823]

[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 + H_2O = 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, iodonitrotetrazolium chloride, nitroblue tetrazolium, Mel-

dola blue and phenazine methosulfate.

References: [2405, 2404]

[EC 1.3.99.16 created 1999]

EC 1.3.99.17

Accepted name: quinoline 2-oxidoreductase

Reaction: quinoline + acceptor + H_2O = quinolin-2(1H)-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: [240, 4337, 3296, 3696]

[EC 1.3.99.17 created 1999]

EC 1.3.99.18

Accepted name: quinaldate 4-oxidoreductase

Reaction: quinaldate + acceptor + H_2O = 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: [3678, 1111]

[EC 1.3.99.18 created 1999]

EC 1.3.99.19

Accepted name: quinoline-4-carboxylate 2-oxidoreductase

Reaction: quinoline-4-carboxylate + acceptor + $H_2O = 2$ -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 molyb-

denum 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: [241]

[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 dehydroge-

nase]

[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: [2862]

[EC 1.3.99.23 created 2005]

[1.3.99.24 Transferred entry. 2-amino-4-deoxychorismate dehydrogenase. Now EC 1.3.8.16, 2-amino-4-deoxychorismate dehydrogenase]

[EC 1.3.99.24 created 2008, deleted 2020]

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 un-

known cofactor, which is different from NAD⁺, NADP⁺ or a flavin.

References: [4403]

[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: [1811]

[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 + re-

duced 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 [4015, 62]. The enzyme from the marine bacterium strain P99-3 shows high activity with the monocyclic carotenoid 1'-hydroxy-1',2'-dihydro- γ -carotene [4244]. The enzyme from *Rhodobacter sphaeroides* utilizes molecular oxygen as the electron acceptor *in vitro* [62]. However, oxygen is un-

likely to be the natural electron acceptor under anaerobic conditions.

References: [4244, 4015, 62]

[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 [3431].

References: [3431, 4513]

[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

 $1.3.99.28\ [phytoene\ desaturase\ (neurosporene-forming)],\ EC\ 1.3.99.30\ [phytoene\ desaturase\ (3,4-1)]$

didehydrolycopene-forming)] and EC 1.3.99.31 [phytoene desaturase (lycopene-forming)]).

References: [1811]

[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 reac-

tion)

(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: [1566, 1066]

[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 desatura-

tion 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: [1170]

[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: [4643, 4642]

[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 methyl viologen.

References: [369]

[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 = $C^{3.19}$, S^{21} -cyclocypemycin(1-18)-L-Ala-L-

Leu-N-thioethenyl-L-valinamide + CO_2 + H_2S + 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: [694]

[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 accep-

tor

(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

 C_{50} 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 dihydro-

bisanhydrobacterioruberin.

References: [4768]

[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: [4377]

[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) (ambiguous)

Systematic name: carotenoid β -ring:acceptor oxidoreductase/methyltranferase (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: [2907, 2267, 1188]

[EC 1.3.99.39 created 2018]

EC 1.3.99.40

Accepted name: carotenoid γ-ring synthase

Reaction: carotenoid β -end group + 2 acceptor = carotenoid χ -end group + 2 reduced acceptor

Other name(s): *crtU* (gene name) (ambiguous); *cruE* (gene name)

Systematic name: carotenoid β -ring:acceptor oxidoreductase/methyltranferase (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: [1381, 4458]

[EC 1.3.99.40 created 2018]

EC 1.3.99.41

Accepted name: 3-(methylsulfanyl)propanoyl-CoA 2-dehydrogenase

Reaction: 3-(methylsulfanyl)propanoyl-CoA + acceptor = 3-(methylsulfanyl)acryloyl-CoA + reduced acceptor

Other name(s): dmdC (gene name)

Systematic name: 3-(methylsulfanyl)propanoyl-CoA:acceptor 2-oxidoreductase

Comments: The enzyme, found in marine bacteria, participates in a 3-(methylsulfanyl)propanoate degradation

pathway. Based on similar enzymes, the in vivo electron acceptor is likely electron-transfer flavopro-

tein (ETF).

References: [3493, 491, 3822]

[EC 1.3.99.41 created 2022]

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 NH_3 . 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 + H_2O + NAD^+ = pyruvate + NH_3 + 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 dehydro-

genase

Systematic name: L-alanine:NAD⁺ oxidoreductase (deaminating)

References: [3131, 3317, 4805]

[EC 1.4.1.1 created 1961]

EC 1.4.1.2

Accepted name: glutamate dehydrogenase

Reaction: L-glutamate + H_2O + NAD^+ = 2-oxoglutarate + NH_3 + 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-specific glutamic dehydrogenase; NAD-specific glutamate dehydrogenase; NAD-glutamate oxidoreductase; NAD-linked glutamate dehydrogenase

Systematic name: L-glutamate:NAD⁺ oxidoreductase (deaminating)

References: [1180, 3089, 3220, 3934]

[EC 1.4.1.2 created 1961]

EC 1.4.1.3

Accepted name: glutamate dehydrogenase $[NAD(P)^+]$

Reaction: L-glutamate + $H_2O + NAD(P)^+ = 2$ -oxoglutarate + $NH_3 + NAD(P)H + H^+$

Other name(s): glutamic dehydrogenase; glutamate dehydrogenase [NAD(P)]

Systematic name: L-glutamate:NAD(P)⁺ oxidoreductase (deaminating)

References: [3176, 3934, 4057]

[EC 1.4.1.3 created 1961]

EC 1.4.1.4

Accepted name: glutamate dehydrogenase (NADP⁺)

Reaction: L-glutamate + H_2O + $NADP^+$ = 2-oxoglutarate + NH_3 + 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: [751, 1415, 3859, 3934]

[EC 1.4.1.4 created 1961]

EC 1.4.1.5

Accepted name: L-amino-acid dehydrogenase

Reaction: an L-amino acid + H_2O + NAD^+ = a 2-oxo carboxylate + NH_3 + NADH + H^+

Systematic name: L-amino-acid:NAD⁺ oxidoreductase (deaminating)

Comments: Acts on aliphatic amino acids.

References: [3090]

[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 + $H_2O + NAD^+ = 3$ -hydroxypyruvate + $NH_3 + NADH + H^+$ **Other name(s):** L-serine:NAD oxidoreductase (deaminating); serine dehydrogenase

Systematic name: L-serine:NAD⁺ 2-oxidoreductase (deaminating)

References: [2262]

[EC 1.4.1.7 created 1972, modified 2003]

EC 1.4.1.8

Accepted name: valine dehydrogenase (NADP⁺)

Reaction: L-valine + H_2O + $NADP^+$ = 3-methyl-2-oxobutanoate + NH_3 + NADPH + H^+

Other name(s): valine dehydrogenase (nicotinanide adenine dinucleotide phosphate); valine dehydrogenase (NADP)

Systematic name: L-valine:NADP⁺ oxidoreductase (deaminating)

References: [1973, 1974, 1975]

[EC 1.4.1.8 created 1972]

EC 1.4.1.9

Accepted name: leucine dehydrogenase

Reaction: L-leucine + $H_2O + NAD^+ = 4$ -methyl-2-oxopentanoate + $NH_3 + NADH + H^+$ **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: [3662, 4933]

[EC 1.4.1.9 created 1972]

EC 1.4.1.10

Accepted name: glycine dehydrogenase

Reaction: glycine + H_2O + NAD^+ = glyoxylate + NH_3 + NADH + H^+

Systematic name: glycine:NAD⁺ oxidoreductase (deaminating)

References: [1351]

[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 + H_2O + NAD^+ = (S)-5-amino-3-oxohexanoate + NH_3 + NADH +

 H^+

Other name(s): L-3,5-diaminohexanoate dehydrogenase

Systematic name: L-*erythro*-3,5-diaminohexanoate:NAD⁺ oxidoreductase (deaminating)

References: [194]

[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 cy-

clizes 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: [3956, 3996, 4339]

[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 + NH_3 = L-glutamine + H_2O

(1b) L-glutamate + NADP⁺ + $H_2O = NH_3 + 2$ -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 direc-

tion 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 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 (*cf.* EC 1.4.1.4, glutamate dehydrogenase [NADP⁺]). The β subunit transfers electrons from the cosubstrate. The NH₃ is channeled within the α subunit through a 31 Å channel. The chanelling is very efficient and in the intact α - β complex ammonia is produced only within the complex. In the absence of the β subunit, coupling between the two domains of the α subunit is compromised and some ammonium can leak.

References: [2812, 4239, 4425, 3459]

[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 $^+$

(1a) L-glutamate + NH_3 = L-glutamine + H_2O

(1b) L-glutamate + NAD⁺ + $H_2O = NH_3 + 2$ -oxoglutarate + NADH + H^+

Other name(s): glutamate (reduced nicotinamide adenine dinucleotide) synthase; NADH: GOGAT; L-glutamate syn-

thase (NADH); L-glutamate synthetase; NADH-glutamate synthase; NADH-dependent glutamate syn-

thase

Systematic name: L-glutamate:NAD⁺ oxidoreductase (transaminating)

Comments: A flavoprotein (FMN). The reaction takes place in the direction of L-glutamate production. The pro-

tein 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 sec-

ond molecule of L-glutamate (cf. EC 1.4.1.2, glutamate dehydrogenase).

References: [3569, 375, 2692, 95, 355]

[EC 1.4.1.14 created 1978, modified 2019]

EC 1.4.1.15

Accepted name: lysine dehydrogenase

Reaction: L-lysine + NAD⁺ = 1,2-didehydropiperidine-2-carboxylate + NH₃ + NADH + H⁺

Systematic name: L-lysine:NAD⁺ oxidoreductase (deaminating, cyclizing)

References: [496]

[EC 1.4.1.15 created 1978]

EC 1.4.1.16

Accepted name: diaminopimelate dehydrogenase

Reaction: meso-2,6-diaminoheptanedioate + H₂O + NADP⁺ = L-2-amino-6-oxoheptanedioate + NH₃ +

 $NADPH + H^{+}$

Other name(s): *meso*-α,ε-diaminopimelate dehydrogenase; *meso*-diaminopimelate dehydrogenase

Systematic name: meso-2,6-diaminoheptanedioate:NADP⁺ oxidoreductase (deaminating)

References: [2823, 2824]

[EC 1.4.1.16 created 1981]

EC 1.4.1.17

Accepted name: *N*-methylalanine dehydrogenase

Reaction: N-methyl-L-alanine + H₂O + NADP⁺ = pyruvate + methylamine + NADPH + H⁺ **Systematic name:** N-methyl-L-alanine:NADP⁺ oxidoreductase (demethylating, deaminating)

References: [2492]

[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 reac-

tion)

(1a) L-lysine + NAD⁺ + $H_2O = (S)$ -2-amino-6-oxohexanoate + NADH + H^+ + N H_3

(1b) (S)-2-amino-6-oxohexanoate = (S)-2,3,4,5-tetrahydropyridine-2-carboxylate + H_2O (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 $Agrobacterium\ tume faciens$ can use only NAD⁺, that from the thermophilic bacterium $Geobacillus\ stear other mophilus\ can also use\ NADP^+,$

but more slowly [2822, 1635].

References: [2822, 2825, 2821, 1635]

[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 Ca^{2+} .

References: [4386]

[EC 1.4.1.19 created 1989]

EC 1.4.1.20

Accepted name: phenylalanine dehydrogenase

Reaction: L-phenylalanine + H_2O + NAD^+ = phenylpyruvate + NH_3 + 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: [141, 142]

[EC 1.4.1.20 created 1989]

EC 1.4.1.21

Accepted name: aspartate dehydrogenase

Reaction: L-aspartate + H_2O + $NAD(P)^+$ = oxaloacetate + NH_3 + NAD(P)H + H^+ (overall reaction)

(1a) L-aspartate + NAD(P)⁺ = 2-iminosuccinate + NAD(P)H + H⁺ (1b) 2-iminosuccinate + H₂O = oxaloacetate + NH₃ (spontaneous)

Other name(s): AspDH; NAD-dependent aspartate dehydrogenase; NADH₂-dependent aspartate dehydrogenase;

NADP⁺-dependent aspartate dehydrogenase; nadX (gene name); L-aspartate:NAD(P)⁺ oxidoreduc-

tase (deaminating)

Systematic name: L-aspartate:NAD(P)⁺ oxidoreductase (2-iminosuccinate-forming)

Comments: The enzyme is strictly specific for L-aspartate as substrate. It produces the unstable compound 2-

iminosuccinate, which, in the presence of water, hydrolyses spontaneously to form oxaloacetate. The enzyme from some archaea and thermophilic bacteria is likely to transfer 2-iminosuccinate directly to EC 2.5.1.72, quinolinate synthase, preventing its hydrolysis and enabling the *de novo* biosynthesis of

 NAD^+ .

References: [2263, 3158, 4773, 4798, 4799, 2463, 2462, 2466]

[EC 1.4.1.21 created 2005, modified 2022]

[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 + H_2O + NAD^+ = 3-methyl-2-oxobutanoate + NH_3 + 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 dehydroge-

nase (NADP⁺)].

References: [4418, 3025]

[EC 1.4.1.23 created 2012]

EC 1.4.1.24

Accepted name: 3-dehydroquinate synthase II

Reaction: 2-amino-3,7-dideoxy-D-threo-hept-6-ulosonate $+ H_2O + NAD^+ = 3$ -dehydroquinate $+ NH_3 + NADH$

 $+ H^+$

Other name(s): DHO 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-dehydroquinate (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: [4604]

[EC 1.4.1.24 created 2012]

EC 1.4.1.25

Accepted name: L-arginine dehydrogenase

Reaction: L-arginine + H_2O + $NAD(P)^+$ = 5-guanidino-2-oxopentanoate + NH_3 + 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: [2440]

[EC 1.4.1.25 created 2017]

EC 1.4.1.26

Accepted name: 2,4-diaminopentanoate dehydrogenase (NAD⁺)

Reaction: (2R,4S)-2,4-diaminopentanoate + H₂O + NAD⁺ = (2R)-2-amino-4-oxopentanoate + NH₃ + NADH +

 H^+

Other name(s): DAPDH (ambiguous)

Systematic name: (2R,4S)-2,4-diaminopentanoate:NADP⁺ oxidoreductase (deaminating)

Comments: The enzyme, characterized from an unknown bacterium in an environmental sample, has some ac-

tivity with (2R,4R)-2,4-diaminopentanoate. It has very low activity with NADP⁺ (cf. EC 1.4.1.12,

2,4-diaminopentanoate dehydrogenase).

References: [1135]

[EC 1.4.1.26 created 2017]

EC 1.4.1.27

Accepted name: glycine cleavage system

Reaction: glycine + tetrahydrofolate + NAD^+ = 5,10-methylenetetrahydrofolate + NH_3 + CO_2 + NADH

Other name(s): GCV

Systematic name: glycine:NAD⁺ 2-oxidoreductase (tetrahydrofolate-methylene-adding)

Comments: The glycine cleavage (GCV) system is a large multienzyme complex that

The glycine cleavage (GCV) system is a large multienzyme complex that belongs to the 2-oxoacid dehydrogenase complex family, which also includes EC 1.2.1.25, branched-chain α -keto acid dehydrogenase system, EC 1.2.1.105, 2-oxoglutarate dehydrogenase system, EC 1.2.1.104, pyruvate dehydrogenase system, and EC 2.3.1.190, acetoin dehydrogenase system. The GCV system catalyses the reversible oxidation of glycine, yielding carbon dioxide, ammonia, 5,10-methylenetetrahydrofolate and a reduced pyridine nucleotide. Tetrahydrofolate serves as a recipient for one-carbon units generated during glycine cleavage to form the methylene group. The GCV system consists of four protein components, the P protein (EC 1.4.4.2, glycine dehydrogenase (aminomethyl-transferring)), T protein (EC 2.1.2.10, aminomethyltransferase), L protein (EC 1.8.1.4, dihydrolipoyl dehydrogenase), and the non-enzyme H protein (lipoyl-carrier protein). The P protein catalyses the pyridoxal phosphate-dependent liberation of CO₂ from glycine, leaving a methylamine moiety. The methylamine moiety is transferred to the lipoic acid group of the H protein, which is bound to the P protein prior to decarboxylation of glycine. The T protein catalyses the release of ammonia from the methylamine group and transfers the remaining C₁ unit to tetrahydrofolate, forming 5,10-methylenetetrahydrofolate. The L protein then oxidizes the lipoic acid component of the H protein and transfers the electrons to

NAD⁺, forming NADH.

References: [2910, 1665, 3159, 1216, 3160]

[EC 1.4.1.27 created 2020]

EC 1.4.1.28

Accepted name: secondary-alkyl amine dehydrogenase $[NAD(P)^+]$

Reaction: a secondary-alkyl amine $+ H_2O + NAD(P)^+ = a \text{ ketone} + NH_3 + NAD(P)H + H^+$

Other name(s): AmDH (ambiguous); amine dehydrogenase (ambiguous)

Systematic name: secondary-alkyl amine:NAD(P)⁺ oxidoreductase (deaminating)

Comments: The enzyme has been shown to react preferentially with short-chain ketones such as cyclohexanone,

primary amine groups attached to secondary alkyl groups, or D- and L-amino acids. It also reduces

aldehydes to primary amines. Cosubstrate preference depends on the substrate.

References: [1850, 2733, 2732, 2392]

[EC 1.4.1.28 created 2022]

EC 1.4.2 With a cytochrome as acceptor

EC 1.4.2.1

Accepted name: glycine dehydrogenase (cytochrome)

Reaction: glycine + $H_2O + 2$ ferricytochrome $c = glyoxylate + NH_3 + 2$ ferrocytochrome c + 2 H⁺

Other name(s): glycine—cytochrome *c* reductase

Systematic name: glycine:ferricytochrome-*c* oxidoreductase (deaminating)

References: [3655]

[EC 1.4.2.1 created 1976]

EC 1.4.2.2

Accepted name: nicotine dehydrogenase

Reaction: (S)-nicotine + 2 ferricytochrome c = N-methylmyosmine + 2 ferrocytochrome c + 2 H⁺

Other name(s): *nicA2* (gene name)

Systematic name: (S)-nicotine:cytochrome c oxidoreductase (N-methylmimosine-forming)

Comments: The enzyme, characterized from the bacterium *Pseudomonas putida* S16, contains an FAD cofactor

and belongs to the flavin-containing amine oxidase family. The enzyme from this bacterium is specific for the *c*-type cytochrome CycN. The product undergoes spontaneous hydrolysis to form pseu-

dooxynicotine.

References: [4201, 982]

[EC 1.4.2.2 created 2022]

EC 1.4.2.3

Accepted name: pseudooxynicotine dehydrogenase

Reaction: pseudooxynicotine + $H_2O + 2$ ferricytochrome c = 4-oxo-4-(pyridin-3-yl)butanal + methylamine + 2

ferrocytochrome $c + 2 H^+$

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

Systematic name: 4-(methylamino)-1-(pyridin-3-yl)butan-1-one:c-type cytochrome oxidoreductase (methylamine re-

leasing)

Comments: Contains one non-covalently bound FAD molecule per dimer. This enzyme, characterized from the

soil bacteria Pseudomonas sp. HZN6 and Pseudomonas putida S16, is involved in nicotine degrada-

tion.

References: [3402, 679]

[EC 1.4.2.3 created 2012 as EC 1.4.3.24, transferred 2022 to EC 1.4.2.3]

EC 1.4.3 With oxygen as acceptor

EC 1.4.3.1

Accepted name: D-aspartate oxidase

Reaction: D-aspartate + $H_2O + O_2$ = oxaloacetate + $NH_3 + H_2O_2$

Other name(s): aspartic oxidase; D-aspartic oxidase

Systematic name: D-aspartate:oxygen oxidoreductase (deaminating)

Comments: A flavoprotein (FAD). **References:** [925, 4031, 4032]

[EC 1.4.3.1 created 1961]

EC 1.4.3.2

Accepted name: L-amino-acid oxidase

Reaction: an L-amino acid + $H_2O + O_2 = a$ 2-oxo carboxylate + $NH_3 + H_2O_2$

Other name(s): ophio-amino-acid oxidase (ambiguous)

Systematic name: L-amino-acid:oxygen oxidoreductase (deaminating)

Comments: A flavoprotein (FAD).

References: [2766, 4585]

[EC 1.4.3.2 created 1961]

Accepted name: D-amino-acid oxidase

Reaction: a D-amino acid + $H_2O + O_2 = a$ 2-oxo carboxylate + $NH_3 + H_2O_2$

Other name(s): ophio-amino-acid oxidase (ambiguous); 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: [926, 928, 927, 2687, 2766]

[EC 1.4.3.3 created 1961]

EC 1.4.3.4

Accepted name: monoamine oxidase

Reaction: $RCH_2NHR' + H_2O + O_2 = RCHO + R'NH_2 + H_2O_2$

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-B; monoamine oxidase A; monoamine oxidase B; monoamine:O₂ oxidoreductase (deaminating); polyamine oxidase (ambiguous); serotonin deaminase; spermidine oxidase

dase (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 neu-

rotransmitters and biogenic amines [1019]. 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: [356, 954, 1019, 3858, 4294, 711, 4826, 4825]

[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 + $H_2O + O_2$ = pyridoxal 5'-phosphate + $NH_3 + H_2O_2$

(2) pyridoxine 5'-phosphate + O_2 = pyridoxal 5'-phosphate + H_2O_2

Other name(s): pyridoxamine 5'-phosphate oxidase; pyridoxamine phosphate oxidase; pyridoxam-

ine)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: [672, 4483, 3109, 2322, 2950, 3626, 4890]

[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]

Accepted name: D-glutamate oxidase

Reaction: D-glutamate + $H_2O + O_2 = 2$ -oxoglutarate + $NH_3 + H_2O_2$

Other name(s): D-glutamic oxidase; D-glutamic acid oxidase

Systematic name: D-glutamate:oxygen oxidoreductase (deaminating)

References: [3541, 4379]

[EC 1.4.3.7 created 1972]

EC 1.4.3.8

Accepted name: ethanolamine oxidase

Reaction: ethanolamine + $H_2O + O_2$ = glycolaldehyde + $NH_3 + H_2O_2$

Systematic name: ethanolamine:oxygen oxidoreductase (deaminating)

Comments: A cobamide-protein.

References: [3013]

[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 $+ O_2 + H_2O = 4$ -aminobutanal $+ NH_3 + H_2O_2$

Systematic name: putrescine:oxygen oxidoreductase (deaminating)

Comments: A flavoprotein (FAD). 4-Aminobutanal condenses non-enzymically to 1-pyrroline.

References: [888, 4723]

[EC 1.4.3.10 created 1976]

EC 1.4.3.11

Accepted name: L-glutamate oxidase

Reaction: L-glutamate + O_2 + H_2O = 2-oxoglutarate + NH_3 + H_2O_2

Other name(s): glutamate (acceptor) dehydrogenase; glutamate oxidase; glutamic acid oxidase; glutamic dehydrogenase;

nase (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: [2309]

[EC 1.4.3.11 created 1976, modified 1989]

EC 1.4.3.12

Accepted name: cyclohexylamine oxidase

Reaction: cyclohexylamine + O_2 + H_2O = cyclohexanone + NH_3 + H_2O_2

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: [4301]

[EC 1.4.3.12 created 1978]

Accepted name: protein-lysine 6-oxidase

Reaction: [protein]-L-lysine + O_2 + H_2O = [protein]-(S)-2-amino-6-oxohexanoate + NH_3 + H_2O_2

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 [3223]. 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 [3223, 1972]. Some isoforms can also use [protein]-N(6)-acetyl-L-lysine as substrate deacetamidat-

ing the substrate [3548].

References: [1535, 3468, 4008, 3223, 1972, 3548, 2113, 4705, 2580]

[EC 1.4.3.13 created 1980, modified 1983]

EC 1.4.3.14

Accepted name: L-lysine oxidase

Reaction: L-lysine + O_2 + H_2O = 6-amino-2-oxohexanoate + NH_3 + H_2O_2

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: [2307, 2558]

[EC 1.4.3.14 created 1981]

EC 1.4.3.15

Accepted name: D-glutamate(D-aspartate) oxidase

Reaction: (1) D-glutamate $+ H_2O + O_2 = 2$ -oxoglutarate $+ NH_3 + H_2O_2$

(2) D-aspartate + $H_2O + O_2$ = oxaloacetate + $NH_3 + H_2O_2$

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: [2849]

[EC 1.4.3.15 created 1983, modified 2012]

EC 1.4.3.16

Accepted name: L-aspartate oxidase

Reaction: L-aspartate + O_2 = iminosuccinate + H_2O_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 [402]. 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 [402]. 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 [402].

References: [3021, 2903, 4236, 2722, 402, 2024]

[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: glycine + $H_2O + O_2$ = glyoxylate + $NH_3 + H_2O_2$ (overall reaction)

(1a) glycine + O_2 = 2-iminoacetate + H_2O_2 (1b) 2-iminoacetate + H_2O = glyoxylate + 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: [1921, 3085]

[EC 1.4.3.19 created 2002, modified 2012]

EC 1.4.3.20

Accepted name: L-lysine 6-oxidase

Reaction: L-lysine + O_2 + H_2O = (S)-2-amino-6-oxohexanoate + H_2O_2 + 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 [1352].

References: [2555, 1352]

[EC 1.4.3.20 created 2006, modified 2011]

EC 1.4.3.21

Accepted name: primary-amine oxidase

Reaction: $RCH_2NH_2 + H_2O + O_2 = RCHO + NH_3 + H_2O_2$

Other name(s): amine oxidase (ambiguous); amine oxidase (copper-containing); amine oxidase (pyridoxal contain-

ing) (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); 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: [1584, 4293, 2570, 4625, 2400, 1742, 101, 3690, 3202, 43]

[EC 1.4.3.21 created 2007 (EC 1.4.3.6 created 1961, part-incorporated 2008)]

Accepted name: diamine oxidase

Reaction: histamine + $H_2O + O_2$ = (imidazol-4-yl)acetaldehyde + $NH_3 + H_2O_2$

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: [4868, 763, 612, 1742, 1040]

[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 + O_2 = 2-imino-3-(7-chloroindol-3-yl)propanoate + H_2O_2

Other name(s): RebO

Systematic name: 7-chloro-L-tryptophan:oxygen oxidoreductase

Comments: Contains a noncovalently bound FAD [3086, 1743]. This enzyme catalyses a step in the biosynthesis

of rebeccamycin, an indolocarbazole alkaloid produced by the bacterium *Lechevalieria aerocoloni- genes*. 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 [3086].

References: [3086, 1743]

[EC 1.4.3.23 created 2010]

[1.4.3.24 Transferred entry. pseudooxynicotine oxidase, now classified as EC 1.4.2.3, pseudooxynicotine dehydrogenase]

[EC 1.4.3.24 created 2012, deleted 2022]

EC 1.4.3.25

Accepted name: L-arginine oxidase

Reaction: L-arginine + $H_2O + O_2 = 5$ -guanidino-2-oxopentanoate + $NH_3 + H_2O_2$

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: [2808, 3331, 1284, 2699]

[EC 1.4.3.25 created 2017]

EC 1.4.3.26

Accepted name: pre-mycofactocin synthase

 $\textbf{Reaction:} \quad \text{3-amino-5-[(4-hydroxyphenyl)methyl]-4,4-dimethylpyrrolidin-2-one} + O_2 + H_2O = 5-[(4-hydroxyphenyl)methyl] + O_2 + O_2 + O_3 + O_$

hydroxyphenyl)methyl]-4,4-dimethylpyrrolidine-2,3-dione + NH₃ + H₂O₂ (overall reaction)

(1a) 3-amino-5-[(4-hydroxyphenyl)methyl]-4,4-dimethylpyrrolidin-2-one + O_2 = 5-[(4-hydroxyphenyl)methyl]-4,4-dimethylpyrrolidin-2-one

hydroxyphenyl)methyl]-3-imino-4,4-dimethylpyrrolidin-2-one + H₂O₂

(1b) $5-[(4-hydroxyphenyl)methyl]-3-imino-4,4-dimethylpyrrolidin-2-one + <math>H_2O$ = $5-[(4-hydroxyphenyl)methylpyrrolidin-2-one + <math>H_2O$ = 5-[(4-hydroxyphenyl)methylpyrrolidin-2-one + (hydroxyphenyl)methylpyrrolidin-2-one + (hydroxyphenyl)methylpyrrolidin-2-one + (hydroxyphenyl)methylpyrrolidin-2

hydroxyphenyl)methyl]-4,4-dimethylpyrrolidine-2,3-dione + NH₃ (spontaneous)

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

Systematic name: 3-amino-5-[(4-hydroxyphenyl)methyl]-4,4-dimethylpyrrolidin-2-one:oxygen oxidoreductase

Comments: A flavoprotein (FMN). The enzyme participates in the biosynthesis of the enzyme cofactor mycofac-

tocin. The enzyme uses oxygen as an electron source to oxidize a C-N bond, followed by spontaneous

exchange with water to form an α-keto moiety on the resulting molecule.

References: [169]

[EC 1.4.3.26 created 2020]

EC 1.4.3.27

Accepted name: homospermidine oxidase

Reaction: sym-homospermidine + 2 O_2 + H_2O = 1-formylpyrrolizidine + 2 H_2O_2 + 2 NH_3 (overall reaction)

(1a) sym-homospermidine + $O_2 = N$ -(4-aminobutylpyrrolinium) ion + $H_2O_2 + NH_3$

(1b) N-(4-aminobutylpyrrolinium) ion + O₂ + H₂O = N-(4-oxobutylpyrrolinium) ion + NH₃ + H₂O₂

(1c) *N*-(4-oxobutylpyrrolinium) ion = 1-formylpyrrolizidine (spontaneous)

Other name(s): HSC

Systematic name: homospermidine:oxygen oxidase (deaminating, cyclizing)

Comments: The copper-containing enzyme has been isolated from the plant *Heliotropium indicum*. It is involved

in the biosynthesis of the pyrrolizidine alkaloid (–)-trachelanthamidine which acts as a secondary metabolite for the defense against herbivores. The oxidation of *sym*-homospermidine proceeds in

three steps and results in a cyclization.

References: [4854]

[EC 1.4.3.27 created 2022]

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]- N^6 -lipoyl-L-lysine = [glycine-cleavage complex H

protein]-S-aminomethyl- N^6 -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 (decarboxylat-

ing); 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 [3043]. Previously known as glycine synthase.

References: [1665, 3293, 3043]

[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 $+ H_2O + a$ quinone = a 2-oxo carboxylate $+ NH_3 + a$ 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 spe-

cific 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: [3175, 4207]

[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 + NH_3 = L-glutamine + H_2O

(1b) L-glutamate + 2 oxidized ferredoxin + $H_2O = NH_3 + 2$ -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 hy-

drolysing 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. The NH_3 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 [4399, 4400].

References: [1264, 2373, 3460, 3026, 4399, 4400]

[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 + $H_2O + 2$ amicyanin = formaldehyde + $NH_3 + 2$ reduced amicyanin

Other name(s): amine dehydrogenase; primary-amine dehydrogenase; amine: (acceptor) oxidoreductase (deaminat-

ing); 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 ammo-

nium salts or aromatic amines.

References: [267, 1000, 1002, 577, 2774]

[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: ArCH2NH2 + $H_2O + 2$ azurin = ArCHO + NH₃ + 2 reduced azurin

Other name(s): aromatic amine dehydrogenase; arylamine dehydrogenase; tyramine dehydrogenase; aralky-

lamine:(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: [1860, 1781, 1782, 839, 4110]

[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: taurine + H_2O + acceptor = 2-sulfoacetaldehyde + NH_3 + reduced acceptor

Other name(s): taurine:(acceptor) oxidoreductase (deaminating)

Systematic name: taurine:acceptor oxidoreductase (deaminating)

References: [2218]

[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: glycine + 2 acceptor = hydrogen cyanide + CO_2 + 2 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: [4644, 574, 2367, 363]

[EC 1.4.99.5 created 2002]

EC 1.4.99.6

Accepted name: D-arginine dehydrogenase

Reaction: D-arginine + acceptor + H_2O = 5-guanidino-2-oxopentanoate + NH_3 + reduced acceptor (overall reac-

tion)

(1a) D-arginine + acceptor = iminoarginine + reduced acceptor

(1b) iminoarginine + H_2O = 5-guanidino-2-oxopentanoate + NH_3 (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, ac-

tivity is maximal with D-arginine and D-lysine. Not active on glycine.

References: [4343, 2440, 1199, 4841, 1200, 4842]

[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): Δ^1 -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: [2765, 4560]

[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- Δ^1 -pyrroline car-

boxylic 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: [23, 2765, 3940, 4847]

[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; tase; folic reductase; dihydrofolic acid reductase; dihydrofolate 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: [351, 377, 2033, 4828]

[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): N^5, N^{10} -methylenetetrahydrofolate dehydrogenase; 5,10-methylenetetrahydrofolate:NADP oxidore-

ductase; 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: [1559, 3195, 3446, 4788]

[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

tase; 10-formyl-H₄folate dehydrogenase; N^{10} -formyltetrahydrofolate dehydrogenase; 10-

formyltetrahydrofolate dehydrogenase

Systematic name: 10-formyltetrahydrofolate:NADP⁺ oxidoreductase

References: [2313]

[EC 1.5.1.6 created 1972]

EC 1.5.1.7

Accepted name: saccharopine dehydrogenase (NAD⁺, L-lysine-forming)

Reaction: N^6 -(L-1,3-dicarboxypropyl)-L-lysine + NAD⁺ + H₂O = L-lysine + 2-oxoglutarate + NADH + H⁺ lysine-2-oxoglutarate reductase; dehydrogenase, saccharopine (nicotinamide adenine dinucleotide,

lysine forming); ε -N-(L-glutaryl-2)-L-lysine:NAD oxidoreductase (L-lysine forming); N^6 -(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: N^6 -(L-1,3-dicarboxypropyl)-L-lysine:NAD⁺ oxidoreductase (L-lysine-forming)

References: [1206, 3677]

[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 reduc-

tase; 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: [1778, 2654]

[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: [1778, 2654]

[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) dehydroge-

nase; 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: [1943]

[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: [2062, 4415]

[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 -piperideine-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: [2876]

[EC 1.5.1.15 created 1978]

EC 1.5.1.16

Accepted name: D-lysopine dehydrogenase

Reaction: N^2 -(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: N^2 -(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: [3207]

[EC 1.5.1.16 created 1978]

EC 1.5.1.17

Accepted name: alanopine dehydrogenase

Reaction: 2,2'-iminodipropanoate + 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 (ambiguous);

alanopine:NAD+ oxidoreductase

Systematic name: 2,2'-iminodipropanoate: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: [818, 1118, 1119]

[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: [2148]

[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: [2063]

[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): MTHFR (gene name)

Systematic name: 5-methyltetrahydrofolate: $NAD(P)^+$ oxidoreductase

Comments: A flavoprotein (FAD). The enzyme catalyses the reversible conversion of 5,10-

methylenetetrahydrofolate to 5-methyltetrahydrofolate, playing an important role in folate metabolism by regulating the distribution of one-carbon moieties between cellular methylation reactions and nucleic acid synthesis. This enzyme, characterized from Protozoan parasites of the genus *Leishmania*, is unique among similar characterized eukaryotic enzymes in that it lacks the C-terminal allosteric regulatory domain (allowing it to catalyse a reversible reaction) and uses NADH and NADPH with equal efficiency under physiological conditions. *cf.* EC 1.5.1.53, methylenetetrahydrofolate reductase (NADPH); EC 1.5.1.54, methylenetetrahydrofolate reductase (NADH); and EC 1.5.7.1,

methylenetetrahydrofolate reductase (ferredoxin).

References: [4445]

[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., modified 2021]

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 re-

ductase; DELTA1-piperideine-2-carboxylate/1-pyrroline-2-carboxylate reductase (ambiguous); L-pipecolate:NADP $^+$ 2-oxidoreductase; DELTA1-piperideine-2-carboxylate reductase; Δ^1 -piperideine-2-carboxylate reductase;

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: [3269, 2941, 4560]

[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+ oxi-

doreductase

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: [818]

[EC 1.5.1.22 created 1986]

EC 1.5.1.23

Accepted name: tauropine dehydrogenase

Reaction: tauropine + NAD⁺ + H_2O = 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: [1253]

[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: [4272]

[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: [3011]

[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: [3669]

[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 ex-

tent under physiological conditions.

References: [845]

[EC 1.5.1.27 created 1999, modified 2004]

EC 1.5.1.28

Accepted name: opine dehydrogenase

Reaction: (2S)-2-[1-(R)-carboxyethyl]aminopentanoate + NAD⁺ + H₂O = L-2-aminopentanoic acid + pyruvate

 $+ NADH + H^+$

Other name(s): (2S)-2-[1-(R)-carboxyethyl]aminopentanoate dehydrogenase (NAD⁺, L-aminopentanoate-forming)

Systematic name: (2S)-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 dicarboxy-

lates 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: [143, 812, 2023]

[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 dinu-

cleotide 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 effi-

ciently than NADPH.

References: [4843, 787]

[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 configu-

ration to the precursor of berberine (see EC 1.3.3.8 tetrahydroberberine oxidase). Also acts on 7,8-

dihydroberberine.

References: [244]

[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: [4469]

[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 dif-

fers from EC 1.5.1.3 (dihydrofolate reductase) in being specific for the Si-face of NADPH.

References: [3012, 1378, 1129]

[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; DHPR; NAD(P)H:6,7-dihydropteridine oxidoreductase;

tase; NADH-dihydropteridine reductase; NADPH-dihydropteridine reductase; NADPH-specific dihydropteridine reductase; dihydropteridine (reduced nicotinamide adenine dinucleotide) 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: [1528, 1547, 2036, 2495, 2988]

[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 mag-

nitude lower than activity with NADH.

References: [1256]

[EC 1.5.1.36 created 2011]

EC 1.5.1.37

Accepted name: FAD reductase (NADH)

Reaction: $FADH_2 + NAD^+ = FAD + NADH + H^+$

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: [1330]

[EC 1.5.1.37 created 2011]

EC 1.5.1.38

Accepted name: FMN reductase (NADPH)

Reaction: $FMNH_2 + NADP^+ = FMN + NADPH + H^+$

Other name(s): FRP; flavin reductase P; SsuE Systematic name: FMNH₂:NADP⁺ oxidoreductase

Comments: The enzymes from bioluminescent bacteria contain FMN [2409], while the enzyme from Escherichia

coli does not [1028]. 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 [1305, 1869]. While FMN is the preferred substrate, the enzyme can also use FAD and riboflavin with lower activity

[3,6,8].

References: [1305, 1869, 1870, 2409, 4213, 2520, 2410, 1028]

[EC 1.5.1.38 created 2011]

EC 1.5.1.39

Accepted name: FMN reductase [NAD(P)H]

Reaction: $FMNH_2 + NAD(P)^+ = FMN + NAD(P)H + H^+$

Other name(s): FRG

Systematic name: $FMNH_2:NAD(P)^+$ 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 [4552]. Also reduces riboflavin and

FAD, but more slowly.

References: [4552]

[EC 1.5.1.39 created 2011]

EC 1.5.1.40

Accepted name: 8-hydroxy-5-deazaflavin:NADPH oxidoreductase

Reaction: reduced coenzyme F_{420} + NADP⁺ = oxidized coenzyme F_{420} + 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 [1033].

References: [1033]

[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 ri-

boflavin. 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 ac-

tivity with FMN and no activity with FAD [1136].

References: [1136, 3991, 1810]

[EC 1.5.1.41 created 2011]

EC 1.5.1.42

Accepted name: FMN reductase (NADH)

> Reaction: $FMNH_2 + NAD^+ = FMN + NADH + H^+$

Other name(s): NADH-FMN reductase; NADH-dependent FMN reductase; NADH:FMN oxidoreductase;

NADH:flavin oxidoreductase

FMNH₂:NAD⁺ oxidoreductase **Systematic name:**

> **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 [974, 1305]. While

FMN is the preferred substrate, FAD can also be used with much lower activity [974, 4370].

References: [974, 1305, 4370, 1866]

[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 + H_2O + $NADP^+$ = 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 [2995]. The enzyme from the bacterium Vibrio cholerae is essential for biofilm formation [2384]. The enzyme from Campylobacter jejuni only produces carboxyspermidine in vivo even though it also can produce carboxynorspermidine in

vitro [1504].

References: [2995, 2384, 1504]

[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: [4506]

[EC 1.5.1.44 created 2012]

EC 1.5.1.45

Accepted name: FAD reductase [NAD(P)H]

Reaction: $FADH_2 + NAD(P)^+ = FAD + NAD(P)H + H^+$

Other name(s): GTNG_3158 (gene name)

Systematic name: $FADH_2:NAD(P)^+$ oxidoreductase

Comments: This enzyme, isolated from the bacterium *Geobacillus thermodenitrificans*, participates in the path-

way 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: [2525]

[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-tetradehydroergoline + 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: [2725]

[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; dihy-

dromethanopterin 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 biosyn-

thesis of dephospho-tetrahydromethanopterin. The specific activity with NADH is 15% of that with NADPH at the same concentration [516]. It does not reduce 7,8-dihydrofolate (*cf.* EC 1.5.1.3, dihy-

drofolate reductase).

References: [516]

[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: [2834]

[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-piperideine-2-carboxylate/1-pyrroline-2-carboxylate reductase [NAD(P)H], which shows similar activity with 1-piperideine-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: [4560]

[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: [3378]

[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: [256, 2178]

[EC 1.5.1.51 created 2017]

EC 1.5.1.52

Accepted name: staphylopine dehydrogenase

Reaction: staphylopine + NADP⁺ + $H_2O = (2S)$ -2-amino-4-[(1R)-1-carboxy-2-(1H-imidazol-4-

yl)ethyl]aminobutanoate + pyruvate + NADPH + H⁺

Other name(s): *cntM* (gene name); staphylopine synthase

Systematic name: staphylopine: NADP $^+$ oxidoreductase [(2S)-2-amino-4-[(1R)-1-carboxy-2-(1H-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, cop-

per, and cobalt.

References: [1316, 2748]

[EC 1.5.1.52 created 2018]

EC 1.5.1.53

Accepted name: methylenetetrahydrofolate reductase (NADPH)

Reaction: 5-methyltetrahydrofolate + NADP $^+$ = 5,10-methylenetetrahydrofolate + NADPH + H $^+$

Other name(s): MTHFR (gene name); methylenetetrahydrofolate (reduced nicotinamide adenine dinucleotide phos-

phate) reductase; 5,10-methylenetetrahydrofolate reductase (NADPH); 5,10-methylenetetrahydrofolic

acid reductase (ambiguous); 5,10-CH₂-H₄folate reductase (ambiguous); methylenetetrahydrofolate reductase (NADPH₂); 5,10-methylenetetrahydrofolate reductase (ambiguous); methylenetetrahydrofolate reductase (ambiguous); $N^5,10$ -methylenetetrahydrofolate reductase (ambiguous); $N^5,10$ -methylenetetrahydrofolate reductase (ambiguous); N^5,N^{10} -methylenetetrahydrofolate reductase (ambiguous); methylenetetrahydrofolic acid reductase (ambiguous)

ous); 5-methyltetrahydrofolate:(acceptor) oxidoreductase (incorrect); 5,10-methylenetetrahydrofolate

reductase (FADH₂) (ambiguous)

Systematic name: 5-methyltetrahydrofolate:NADP⁺ oxidoreductase

Comments: A flavoprotein (FAD). The enzyme from yeast and mammals catalyses a physiologically irreversible

reduction of 5,10-methylenetetrahydrofolate to 5-methyltetrahydrofolate using NADPH as the electron donor. It plays an important role in folate metabolism by regulating the distribution of one-carbon moieties between cellular methylation reactions and nucleic acid synthesis. The enzyme contains an N-terminal catalytic domain and a C-terminal allosteric regulatory domain that binds *S*-adenosyl-L-methionine, which acts as an inhibitor. *cf.* EC 1.5.1.54, methylenetetrahydrofolate reductase (NADH); EC 1.5.1.20, methylenetetrahydrofolate reductase [NAD(P)H]; and EC 1.5.7.1, methylenetetrahydro-

folate reductase (ferredoxin).

References: [946, 2314, 834, 4912, 3559, 1193]

[EC 1.5.1.53 created 2021]

EC 1.5.1.54

Accepted name: methylenetetrahydrofolate reductase (NADH)

Reaction: 5-methyltetrahydrofolate + NAD^+ = 5,10-methylenetetrahydrofolate + $NADH + H^+$

Other name(s): metF (gene name); 5,10-methylenetetrahydrofolic acid reductase (ambiguous); 5,10-CH₂-

 H_4 folate reductase (ambiguous); methylenetetrahydrofolate (reduced riboflavin adenine dinucleotide) reductase; 5,10-methylenetetrahydrofolate reductase (ambiguous); methylenetetrahydrofolate reductase (ambiguous); N^5 ,10-methylenetetrahydrofolate reductase (ambiguous); 5,10-methylenetetrahydropteroylglutamate reductase (ambiguous); N^5 , N^{10} -

methylenetetrahydrofolate reductase (ambiguous); methylenetetrahydrofolic acid reductase (ambiguous); 5-methyltetrahydrofolate:(acceptor) oxidoreductase (incorrect); 5,10-methylenetetrahydrofolate

reductase (FADH₂) (ambiguous)

Systematic name: 5-methyltetrahydrofolate:NAD⁺ oxidoreductase

Comments: A flavoprotein (FAD). The enzyme, found in plants and some bacteria, catalyses the reversible con-

version of 5,10-methylenetetrahydrofolate to 5-methyltetrahydrofolate using NADH as the electron donor. It play an important role in folate metabolism by regulating the distribution of one-carbon moieties between cellular methylation reactions and nucleic acid synthesis. These proteins either contain a C-terminal domain that does not mediate allosteric regulation (as in plants) or lack this domain entirely (as in *Escherichia coli*). As a result, the plant enzymes are not inhibited by *S*-adenosyl-L-methionine, unlike other eukaryotic enzymes, and catalyse a reversible reaction. *cf.* EC 1.5.1.53, methylenetetrahydrofolate reductase (NADPH); EC 1.5.1.20, methylenetetrahydrofolate reductase

[NAD(P)H]; and EC 1.5.7.1, methylenetetrahydrofolate reductase (ferredoxin).

References: [4651, 3845, 1438, 3560, 318]

[EC 1.5.1.54 created 2021]

EC 1.5.3 With oxygen as acceptor

EC 1.5.3.1

Accepted name: sarcosine oxidase (formaldehyde-forming)

Reaction: sarcosine + $H_2O + O_2$ = glycine + formaldehyde + H_2O_2

Other name(s): MSOX; monomeric sarcosine oxidase; sarcosine oxidase (ambiguous)

Systematic name: sarcosine:oxygen oxidoreductase (demethylating)

Comments: The enzyme, reported from bacteria and fungi, catalyses the oxidative demethylation of sarcosine.

It contains a FAD cofactor bound to an L-cysteine residue. cf. EC 1.5.3.24, sarcosine oxidase (5,10-

methylenetetrahydrofolate-forming).

References: [2888, 3083, 3084, 4328, 4488, 4898, 1952, 481]

[EC 1.5.3.1 created 1961, modified 2022]

EC 1.5.3.2

Accepted name: *N*-methyl-L-amino-acid oxidase

Reaction: an N-methyl-L-amino acid + $H_2O + O_2 =$ an L-amino acid + formaldehyde + H_2O_2

Other name(s): *N*-methylamino acid oxidase; demethylase

Systematic name: N-methyl-L-amino-acid:oxygen oxidoreductase (demethylating)

Comments: A flavoprotein. **References:** [2894, 2895, 2896]

[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-alkyllysinase; 6-*N*-methyl-L-lysine:oxygen oxidoreductase (demethylating)

Systematic name: N^6 -methyl-L-lysine:oxygen oxidoreductase (demethylating)

References: [2103]

[EC 1.5.3.4 created 1972]

EC 1.5.3.5

Accepted name: (S)-6-hydroxynicotine oxidase

Reaction: (S)-6-hydroxynicotine + $H_2O + O_2 = 1$ -(6-hydroxypyridin-3-yl)-4-(methylamino)butan-1-one + H_2O_2

(overall reaction)

(1a) (S)-6-hydroxynicotine + $O_2 = 5-(N-\text{methyl-4},5-\text{dihydro-1}H-\text{pyrrol-2-yl})$ pyridin-2-ol + H_2O_2

(1b) 5-(N-methyl-4,5-dihydro-1H-pyrrol-2-yl)pyridin-2-ol + H_2O = 1-(6-hydroxypyridin-3-yl)-4-(1-hydroxypyridin-3-yl)

(methylamino)butan-1-one (spontaneous)

Other name(s): L-6-hydroxynicotine oxidase; 6-hydroxy-L-nicotine oxidase; 6-hydroxy-L-nicotine:oxygen oxidore-

ductase; 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: [859, 802, 3708, 3403]

[EC 1.5.3.5 created 1972, modified 2015]

EC 1.5.3.6

Accepted name: (R)-6-hydroxynicotine oxidase

Reaction: (R)-6-hydroxynicotine + $H_2O + O_2 = 1$ -(6-hydroxypyridin-3-yl)-4-(methylamino)butan-1-one + H_2O_2

(overall reaction)

(1a) (R)-6-hydroxynicotine + O_2 = 5-(N-methyl-4,5-dihydro-1H-pyrrol-2-yl)pyridin-2-ol + H_2O_2

(1b) 5-(N-methyl-4,5-dihydro-1H-pyrrol-2-yl)pyridin-2-ol + H_2O = 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) iso-

mer 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: [859, 471, 425, 3708, 2192]

[EC 1.5.3.6 created 1972, modified 2015]

EC 1.5.3.7

Accepted name: L-pipecolate oxidase

Reaction: L-pipecolate + $O_2 = (S)-2,3,4,5$ -tetrahydropyridine-2-carboxylate + H_2O_2

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: [179, 2124]

[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 + 5,6,7,8-tetrahydrofolate + O_2 = sarcosine + 5,10-methylenetetrahydrofolate +

Other name(s): dmg (gene name); N,N-dimethylglycine:oxygen oxidoreductase (demethylating)

Systematic name: N,N-dimethylglycine,5,6,7,8-tetrahydrofolate:oxygen oxidoreductase (demethylating,5,10-

methylenetetrahydrofolate-forming)

Comments: A flavoprotein (FAD). The enzyme, characterized from the bacterium Arthrobacter globiformis, con-

> tains two active sites connected by a large "reaction chamber". An imine intermediate is transferred between the sites, eliminating the production of toxic formaldehyde. In the absence of folate the enzyme does form formaldehyde. Does not oxidize sarcosine. cf. EC 1.5.8.4, dimethylglycine dehydro-

References: [2887, 2775, 232, 2439, 233, 4322, 568]

[EC 1.5.3.10 created 1992, modified 2022]

[1.5.3.11 Deleted entry, polyamine oxidase. Now included with EC 1.5.3.13 (N¹-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 + O_2 = sanguinarine + H_2O_2

(2) dihydrochelirubine + O_2 = chelirubine + H_2O_2 (3) dihydromacarpine + O_2 = macarpine + H_2O_2

dihydrobenzophenanthridine:oxygen oxidoreductase **Systematic name:**

Comments: A Cu^{II} enzyme found in higher plants that produces oxidized forms of the benzophenanthridine alka-

loids

References: [3756, 121]

[EC 1.5.3.12 created 1999]

EC 1.5.3.13

Accepted name: N^1 -acetylpolyamine oxidase

> (1) N^1 -acetylspermidine + O_2 + H_2O = putrescine + 3-acetamidopropanal + H_2O_2 Reaction:

> > (2) N^1 -acetylspermine + O_2 + H_2O = spermidine + 3-acetamidopropanal + H_2O_2

hPAO-1; PAO (ambiguous); mPAO; hPAO; polyamine oxidase (ambiguous) Other name(s):

Systematic name: N^1 -acetylpolyamine:oxygen oxidoreductase (3-acetamidopropanal-forming)

The enzyme also catalyses the reaction: N^1 , N^{12} -diacetylspermine + O_2 + O_2 + O_3 -acetylspermidine **Comments:**

+ 3-acetamamidopropanal + H₂O₂ [4480]. 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 $+ H_2O = \text{spermidine} + 3\text{-aminopropanal} + H_2O_2$, and with weak efficiency 2. spermidine $+ O_2 + H_2O$ = putrescine + 3-aminopropanal + H₂O₂ [1893]. 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-acetamamidopropanal. 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 [N⁸-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: [4480, 1893, 4537, 4679]

[EC 1.5.3.13 created 2009]

EC 1.5.3.14

Accepted name: polyamine oxidase (propane-1,3-diamine-forming)

Reaction: spermidine $+ O_2 + H_2O = \text{propane-1,3-diamine} + 4\text{-aminobutanal} + H_2O_2$

Other name(s): MPAO (ambiguous); 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 [4225]. 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 -acetylspermine 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: [4225, 1096]

[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 -acetylspermine, weak activity with N^1 , N^{12} -diacetylspermine. No activity with

diaminopropane, putrescine, cadaverine, diaminohexane, 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: [3896]

[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 [4224]. 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 -acetylspermine. 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: [2947, 586, 4224, 4538]

[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 -acetylspermine + 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 [2339]. The enzyme from *Ascaris suum* shows high activity with spermine and spermidine, but also oxidizes norspermine [2927]. The enzyme from *Arabidopsis thaliana* shows high activity with spermidine, but also oxidizes other polyamines [2904]. 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: [2904, 2927, 2339]

[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 +

 H_2O_2

Other name(s): FAP2

Systematic name: L-saccharopine:oxygen oxidoreductase (L-glutamate-forming)

Comments: The enzyme is involved in pipecolic acid biosynthesis. A flavoprotein (FAD).

References: [4811, 4617]

[EC 1.5.3.18 created 2011]

EC 1.5.3.19

Accepted name: 4-methylaminobutanoate oxidase (formaldehyde-forming)

Reaction: 4-methylaminobutanoate + O_2 + H_2O = 4-aminobutanoate + formaldehyde + H_2O_2

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 cofac-

tor is covalently bound. Participates in the nicotine degradation pathway of this organism.

References: [657]

[EC 1.5.3.19 created 2012]

EC 1.5.3.20

Accepted name: *N*-alkylglycine oxidase

Reaction: N-alkylglycine + $H_2O + O_2$ = alkylamine + glyoxalate + H_2O_2

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-

[(carboxymethy)amino]hexanoic acid, sarcosine and N-ethylglycine. It has negligible action on

glycine (cf. EC 1.4.3.19 glycine oxidase).

References: [1356]

[EC 1.5.3.20 created 2012]

EC 1.5.3.21

Accepted name: 4-methylaminobutanoate oxidase (methylamine-forming)

Reaction: 4-methylaminobutanoate + O_2 + H_2O = succinate semialdehyde + methylamine + H_2O_2

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

[657].

References: [657, 656]

[EC 1.5.3.21 created 2012]

EC 1.5.3.22

Accepted name: coenzyme F₄₂₀H₂ oxidase

Reaction: 2 reduced coenzyme $F_{420} + O_2 = 2$ oxidized coenzyme $F_{420} + 2$ H_2O

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 Methanother-

mobacter marburgensis is Si-face specific with respect to C-5 of coenzyme F₄₂₀ [3780].

References: [3778, 3780, 3779]

[EC 1.5.3.22 created 2013]

EC 1.5.3.23

Accepted name: glyphosate oxidoreductase

Reaction: 2 glyphosate + O_2 = 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: [1076, 4146]

[EC 1.5.3.23 created 2016]

EC 1.5.3.24

Accepted name: sarcosine oxidase (5,10-methylenetetrahydrofolate-forming)

Reaction: sarcosine + 5,6,7,8-tetrahydrofolate + O_2 = glycine + 5,10-methylenetetrahydrofolate + O_2 + O_3

Other name(s): TSOX; sarcosine oxidase (ambigious); heterotetrameric sarcosine oxidase

Systematic name: sarcosine, 5,6,7,8-tetrahydrofolate:O₂ oxidoreductase (demethylating,5,10-methylenetetrahydrofolate-

orming)

Comments: The enzyme, found in some bacterial species, is composed of four different subunits and two active

sites connected by a large "reaction chamber". An imine intermediate is transferred between the sites, eliminating the production of toxic formaldehyde. The enzyme contains three cofactors: noncovalently bound FAD and NAD⁺, and FMN that is covalently bound to a histidine residue. In the absence of folate the enzyme catalyses the reaction of EC 1.5.3.1, sarcosine oxidase (formaldehyde-forming).

References: [1581, 4140, 663, 662, 1063]

[EC 1.5.3.24 created 2022]

EC 1.5.3.25

Accepted name: fructosyl amine oxidase (glucosone-forming)

Reaction: an N-(1-deoxy-D-fructos-1-yl)amine + O_2 + H_2O = D-glucosone + an amine + H_2O_2 (overall reac-

tion)

(1a) an N-(1-deoxy-D-fructos-1-yl)amine + O_2 = a 2-[(3S,4R,5R)-3,4,5,6-tetrahydroxy-2-

oxohexylidene]amine + H₂O₂

(1b) a 2-[(3S,4R,5R)-3,4,5,6-tetrahydroxy-2-oxohexylidene]amine + H₂O = D-glucosone + an amine

(spontaneous)

Other name(s): amadoriase

Systematic name: N-(1-deoxy-D-fructos-1-yl)amine:oxygen 2-oxidoreductase (glucosone-forming)

Comments: Reducing sugars such as glucose react with amino groups in proteins via the spontaeous Maillard

reaction, forming an unstable product that undergoes spontaneous rearrangement to a keto amine compound. These reactions are known as glycation reactions, and the stable products are known as Amadori products. This enzyme, which contains an FAD cofactor, catalyses a deglycation reaction that regenerates the amine reactant. By-products are glucosone and hydrogen peroxide. The enzymes have been reported from fungi and bacteria, but not from higher eukaryotes. Specific enzymes differ in their substrate specificity. *cf.* EC 1.5.3.26, fructosyl amine oxidase (fructosamine-forming).

References: [1729, 4169, 1672, 4681, 3643]

[EC 1.5.3.25 created 2022]

EC 1.5.3.26

Accepted name: fructosyl amine oxidase (fructosamine-forming)

Reaction: an N-(1-deoxy-D-fructos-1-yl)amine + O_2 + H_2O = (1-deoxy-D-fructos-1-yl)amine + an aldehyde +

 H_2O_2

Systematic name: N-(1-deoxy-D-fructos-1-yl)amine:oxygen oxidoreductase (fructosamine-forming)

Comments: Reducing sugars such as glucose react with amino groups in proteins via the spontaeous Maillard

reaction, forming an unstable product that undergoes spontaneous rearrangement to a keto amine compound. These reactions are known as glycation reactions, and the stable products are known as Amadori products. This enzyme, characterized from a *Pseudomonas* sp. strain, cleaves the Amadori products at the alkylamine bond. All other known fructosyl amine oxidases cleave the ketoamine

bond (cf. EC 1.5.3.25, fructosyl amine oxidase (glucosone-forming)).

References: [1303, 3687, 4681]

[EC 1.5.3.26 created 2022]

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 +

 $H_2O = 6$ -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: [4620, 2096]

[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 O 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: [265, 3610]

[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 [2911]. 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: [3691, 458, 2911]

[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 = (3R,5S)-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: [731, 4116]

[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 ferre-

 $doxin + 2 H^+$

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 1.5.1.53, methylenetetrahydrofolate reductase (NADPH); EC 1.5.1.54, methylenetetrahydrofolate reductase (NADH); or EC 1.5.1.20, methylenetetrahydrofolate reductase (NADH);

trahydrofolate reductase [NAD(P)H], there is no activity with either NADH or NADP⁺.

References: [696]

[EC 1.5.7.1 created 2005, modified 2021]

EC 1.5.7.2

Accepted name: coenzyme F_{420} oxidoreductase (ferredoxin)

Reaction: reduced coenzyme $F_{420} + 2$ oxidized ferredoxin = oxidized coenzyme $F_{420} + 2$ 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: [4586]

[EC 1.5.7.2 created 2013]

EC 1.5.7.3

Accepted name: N,N-dimethylglycine/sarcosine dehydrogenase (ferredoxin)

Reaction: (1) N,N-dimethylglycine + 2 oxidized ferredoxin + H₂O = sarcosine + formaldehyde + 2 reduced

ferredoxin + 2 H+

(2) sarcosine + 2 oxidized ferredoxin + H_2O = glycine + formaldehyde + 2 reduced ferredoxin + 2 H^+

Other name(s): ddhC (gene name); dgcA (gene name)

Systematic name: *N,N*-dimethylglycine/sarcosine:ferredoxin oxidoreductase (demethylating)

Comments: This bacterial enzyme is involved in degradation of glycine betaine. The enzyme contains non-

covalently bound FAD and NAD(P) cofactors, and catalyses the demethylation of both N,N-

dimethylglycine and sarcosine, releasing formaldehyde and forming glycine as the final product. The enzyme can utilize both NAD⁺ and NADP⁺, but the catalytic efficiency with NAD⁺ is 5-fold higher. The native electron acceptor of the enzyme is a membrane-bound clostridial-type ferredoxin, which

transfers the electrons to an electron-transfer flavoprotein (ETF).

References: [4543, 4765]

[EC 1.5.7.3 created 2022]

EC 1.5.8 With a flavin or flavoprotein as acceptor

EC 1.5.8.1

Accepted name: dimethylamine dehydrogenase

Reaction: dimethylamine + H_2O + 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: [4762]

[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 + H_2O + 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: [709, 4012, 1755, 1947, 3776]

[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 + 5,6,7,8-tetrahydrofolate + oxidized [electron-transfer flavoprotein] = glycine + 5,10-

methylenetetrahydrofolate + reduced [electron-transfer flavoprotein]

Other name(s): sarcosine *N*-demethylase; monomethylglycine dehydrogenase; sarcosine:(acceptor) oxidoreductase

(demethylating); sarcosine:electron-transfer flavoprotein oxidoreductase (demethylating)

Systematic name: sarcosine, 5,6,7,8-tetrahydrofolate:electron-transferflavoprotein oxidoreductase (demethylating,5,10-

methylenetetrahydrofolate-forming)

Comments: A flavoprotein (FMN) found in eukaryotes. In the absence of tetrahydrofolate the enzyme produces

formaldehyde. cf. EC 1.5.3.1, sarcosine oxidase (formaldehyde-forming), and EC 1.5.3.24, sarcosine

oxidase (5,10-methylenetetrahydrofolate-forming).

References: [1738, 1190, 4649, 4011]

[EC 1.5.8.3 created 1972 as EC 1.5.99.1, transferred 2012 to EC 1.5.8.3, modified 2022]

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-transferflavoprotein oxidoreductase

(demethylating, 5, 10-methylenetetrahydrofolate-forming)

Comments: A flavoprotein, containing a histidyl(N^{π})-(8 α)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 formalde-

hyde [3356, 155].

References: [1190, 1738, 4650, 4649, 3356, 446, 447, 2557, 155]

[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 $F_{420} = 5,10$ -

methenyltetrahydromethanopterin + reduced coenzyme F₄₂₀

Other name(s): N^5 , N^{10} -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 Methan-

 $other mobacter\ thermautotrophicus.$

References: [1543, 4233]

[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 $F_{420} = 5{,}10$ -

methylenetetrahydromethanopterin + reduced coenzyme F₄₂₀

Other name(s): 5,10-methylenetetrahydromethanopterin cyclohydrolase; N^5,N^{10} -methylenetetrahydromethanopterin

reductase; methylene- H_4MPT reductase; coenzyme F_{420} -dependent N^5, N^{10} -

methenyltetrahydromethanopterin reductase; N^5 , N^{10} -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: [2576, 4233, 2577, 4235, 4234]

[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 F_{420} :methanophenazine dehydrogenase

Reaction: reduced coenzyme F_{420} + methanophenazine = oxidized coenzyme F_{420} + dihydromethanophenazine

Other name(s): $F_{420}H_2$ dehydrogenase; fpoBCDIF (gene names)

Systematic name: reduced coenzyme F_{420} :methanophenazine oxidoreductase

Comments: The enzyme, found in some methanogenic archaea, is responsible for the reoxidation of coenzyme

 F_{420} , 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: [449, 246, 884, 1867]

[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: [179]

[EC 1.5.99.3 created 1972, modified 1986, modified 2011]

EC 1.5.99.4

Accepted name: nicotine dehydrogenase

Reaction: (S)-nicotine + acceptor + $H_2O = (S)$ -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 syn-

thetic (R)-enantiomer of nicotine, with retention of configuration in both cases [1682].

References: [271, 859, 1681, 1682]

[EC 1.5.99.4 created 1972]

EC 1.5.99.5

Accepted name: methylglutamate dehydrogenase

Reaction: N-methyl-L-glutamate + acceptor + $H_2O = L$ -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: [1631]

[EC 1.5.99.5 created 1976]

EC 1.5.99.6

Accepted name: spermidine dehydrogenase

Reaction: spermidine + acceptor + H_2O = propane-1,3-diamine + 4-aminobutanal + reduced acceptor

Other name(s): spermidine:(acceptor) oxidoreductase spermidine:acceptor oxidoreductase

Comments: A flavohemoprotein (FAD). Ferricyanide, 2,6-dichloroindophenol and cytochrome c can act as accep-

tor. 4-Aminobutanal condenses non-enzymically to 1-pyrroline.

References: [4158, 4159]

[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 -prenyladenine + acceptor + H_2O = adenine + 3-methylbut-2-enal + reduced acceptor

Other name(s): N^6 -dimethylallyladenine:(acceptor) oxidoreductase; 6-N-dimethylallyladenine:acceptor oxidoreduc-

tase; OsCKX2; CKX; cytokinin oxidase/dehydrogenase; N⁶-dimethylallyladenine:acceptor oxidore-

ductase

Systematic name: N^6 -prenyladenine: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 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 copper(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 [144].

References: [1263, 144]

[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 effi-

ciency.

References: [4206, 3674]

[EC 1.5.99.13 created 2010, modified 2011]

EC 1.5.99.14

Accepted name: 6-hydroxypseudooxynicotine dehydrogenase

Reaction: 1-(6-hydroxypyridin-3-yl)-4-(methylamino)butan- $1-\text{one} + \text{acceptor} + \text{H}_2\text{O} = 1-(2,6-\text{dihydroxypyridin-}3-\text{yl})$

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 cytidylyl molybdenum cofactor [3621]. The enzyme, which participates in the nicotine

degradation pathway, has been characterized from the soil bacterium Arthrobacter nicotinovorans

[1174, 1407].

References: [1174, 1407, 3621]

[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, dihy-

dromethanopterin reductase $[NAD(P)^+]$.

References: [4531]

[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; 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: [1772, 4820]

[EC 1.6.1.1 created 1961, modified 1986, modified 2013]

EC 1.6.1.2

Accepted name: $NAD(P)^+$ transhydrogenase (*RelSi*-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: [1127, 4820]

[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 dinu-

cleotide (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 (ambiguous); NADPH:NAD+

shydrogenase; 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: [931]

[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 oxi-

dized 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: [4530, 874, 2554]

[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 $b_5 = \text{NAD}^+ + \text{H}^+ + 2$ ferrocytochrome b_5

Other name(s): cytochrome b_5 reductase; dihydronicotinamide adenine dinucleotide-cytochrome b_5 reductase; re-

duced nicotinamide adeninedinucleotide-cytochrome b_5 reductase; NADH-ferricytochrome b_5 oxidoreductase; NADH-cytochrome b_5 reductase; NADH-cytochrome- b_5 reductase;

tase

Systematic name: NADH:ferricytochrome- b_5 oxidoreductase

Comments: A flavoprotein (FAD). **References:** [2616, 4068, 4070]

[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: NADPH + H⁺ + n oxidized hemoprotein = NADP⁺ + n reduced hemoprotein

Other name(s): CPR; FAD-cytochrome *c* reductase; NADP-cytochrome *c* reductase;

NADPH-dependent cytochrome c reductase; NADPH:P-450 reductase; NADPH:ferrihemoprotein oxidoreductase; NADPH—cytochrome e oxidoreductase; NADPH-cytochrome e oxidoreductase; NADPH-cytochrome e oxidoreductase; NADPH—cytochrome e reductase; NADPH-ferrihemoprotein reductase; TPNHe cytochrome e reductase; TPNH-cytochrome e reductase; aldehyde reductase (NADPH-dependent); cytochrome e reductase; cytochrome e reductase (reduced nicotinamide adenine dinucleotide phosphate, NADPH, NADPH-dependent); dihydroxynicotinamide adenine dinucleotide phosphate-cytochrome e reductase; reductase; reduced nicotinamide adenine dinucleotide phosphate-cytochrome e reductase; reductase; reductase; reductase denine dinucleotide phosphate-cytochrome e reductase; reductase; reductase denine 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 co-factors 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 re-

duction.

References: [1462, 1720, 2548, 2691, 4630, 2690, 3810, 4521, 2935, 1456]

[EC 1.6.2.4 created 1972, modified 2003]

EC 1.6.2.5

Accepted name: NADPH—cytochrome- c_2 reductase

Reaction: NADPH + 2 ferricytochrome c_2 = NADP⁺ + H⁺ + 2 ferrocytochrome c_2

Other name(s): cytochrome c_2 reductase (reduced nicotinamide adenine dinucleotide phosphate); cytochrome c_2 re-

ductase (reduced nicotinamide adinine dinucleotide phosphate, NADPH)

Systematic name: NADPH:ferricytochrome- c_2 oxidoreductase

Comments: A flavoprotein (FAD).

References: [3620]

[EC 1.6.2.5 created 1972]

EC 1.6.2.6

Accepted name: leghemoglobin reductase

Reaction: $NAD(P)H + H^+ + 2$ ferrileghemoglobin = $NAD(P)^+ + 2$ ferroleghemoglobin

Other name(s): ferric leghemoglobin reductase

Systematic name: NAD(P)H:ferrileghemoglobin oxidoreductase

References: [3619]

[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 $(H_2O_2$ -forming) **Reaction:** NAD(P)H + H⁺ + O₂ = NAD(P)⁺ + H₂O₂

Other name(s): THOX2; ThOX; dual oxidase; p138tox; thyroid NADPH 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 gen-

erates H_2O_2 by transfering 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 H_2O_2 for the thy-

roid peroxidase-catalysed biosynthesis of thyroid hormones.

References: [2883, 864, 865, 987, 2421, 988]

[EC 1.6.3.1 created 2003, modified 2013]

EC 1.6.3.2

Accepted name: NAD(P)H oxidase (H₂O-forming)

Reaction: 2 NAD(P)H + 2 H⁺ + O₂ = 2 NAD(P)⁺ + 2 H₂O **Systematic name:** NAD(P)H:oxygen oxidoreductase (H₂O-forming) **Comments:** A flavoprotein (FAD). NADPH is a better substrate than NADH [457, 1912]. By removal of oxy-

gen the enzyme is involved in aerobic tolerance in the thermophilic anaerobic archaeon *Thermo-coccus profundus* and in *Giardia intestinalis*, a microaerophilic single-celled parasite of the order

Diplomonadida.

References: [457, 2450, 1912, 1911]

[EC 1.6.3.2 created 2013]

EC 1.6.3.3

Accepted name: NADH oxidase $(H_2O_2\text{-forming})$ Reaction: NADH + H⁺ + O_2 = NAD⁺ + O_2 Other name(s): NOX-1; O_2 -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)) [1648]. The enzymes from the anaerobic archaea *Methanocaldococcus jannaschii* [569] and *Pyrococcus furiosus* [2064] also produce low amounts of H₂O. Unlike EC 1.6.3.1 (NAD(P)H oxidase) it has

no activity towards NADPH.

References: [1648, 4542, 2064, 4767, 1666, 569]

[EC 1.6.3.3 created 2013]

EC 1.6.3.4

Accepted name: NADH oxidase (H₂O-forming)

Reaction: 2 NADH + 2 H⁺ + O₂ = 2 NAD⁺ + 2 H₂O **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))

[3729].

References: [3729, 1648, 2701, 2047, 4889]

[EC 1.6.3.4 created 2013]

EC 1.6.3.5

Accepted name: renalase

Reaction: (1) 1,2-dihydro-β-NAD(P) + H⁺ + O₂ = β-NAD(P)⁺ + H₂O₂ (2) 1,6-dihydro-β-NAD(P) + H⁺ + O₂ = β-NAD(P)⁺ + H₂O₂

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: [4704, 261]

[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. asparagusate reductase (NADH). Now EC 1.8.1.11, asparagusate 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: $NAD(P)H + H^{+} + a$ quinone = $NAD(P)^{+} + a$ hydroquinone

Other name(s): menadione reductase; phylloquinone reductase; quinone reductase; dehydrogenase, reduced nicoti-

namide 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 nicotinamideadenine 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 [3972]. The animal,

but not the plant, form of the enzyme is inhibited by dicoumarol.

References: [899, 1332, 2651, 2820, 4671, 3972, 427, 1878, 2454]

[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: $NADH + H^{+} + 2$ monodehydroascorbate = $NAD^{+} + 2$ ascorbate

Other name(s): NADH:semidehydroascorbic acid oxidoreductase; MDHA; semidehydroascorbate reductase; AFR

> (ambiguous); AFR-reductase; ascorbic free radical reductase; ascorbate free radical reductase; SOR (ambiguous); MDAsA reductase (NADPH); SDA reductase; NADH:ascorbate radical oxidoreductase; NADH-semidehydroascorbate oxidoreductase; ascorbate free-radical reductase; NADH:AFR oxidore-

ductase; monodehydroascorbate reductase (NADH₂)

Systematic name: NADH:monodehydroascorbate oxidoreductase

References: [3755]

[EC 1.6.5.4 created 1961]

EC 1.6.5.5

Accepted name: NADPH:quinone reductase

> $NADPH + H^+ + 2$ quinone = $NADP^+ + 2$ semiquinone Reaction:

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 [3451]. 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 [3451]. In some mammals, the enzyme is abundant in the lens of the eye, where it is identified with the protein ζ -crystallin.

References: [3451, 979, 251, 4199]

[EC 1.6.5.5 created 1999]

EC 1.6.5.6

Accepted name: *p*-benzoquinone reductase (NADPH)

> **Reaction:** $NADPH + H^+ + p$ -benzoquinone = $NADP^+ + hydroquinone$

NADPH:p-benzoquinone oxidoreductase **Systematic name:**

Comments: Involved in the 4-nitrophenol degradation pathway in bacteria.

References: [3971]

[EC 1.6.5.6 created 2000]

EC 1.6.5.7

Accepted name: 2-hydroxy-1,4-benzoquinone reductase

> 2-hydroxy-1,4-benzoquinone + NADH + H⁺ = hydroxyquinol + NAD⁺ Reaction:

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: [4850]

[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:quinone reductase (non-electrogenic) Reaction: NADH + H^+ + a quinone = NAD^+ + a quinol

Other name(s): type II NAD(P)H:quinone oxidoreductase; NDE2 (gene name); ndh (gene name); NDH-II; NDH-

2; NADH dehydrogenase (quinone) (ambiguous); ubiquinone reductase (ambiguous); coenzyme Q reductase (ambiguous); dihydronicotinamide adenine dinucleotide-coenzyme Q reductase (ambiguous); DPNH-coenzyme Q reductase (ambiguous); NADH-ubiquinone reductase (ambiguous); NADH-coenzyme Q oxidoreductase (ambiguous); NADH-coenzyme Q reductase (ambiguous); NADH-CoQ oxidoreductase (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); NADH:ubiquinone oxidoreductase; NADH:ubiquinone

reductase (non-electrogenic)

Systematic name: NADH:quinone oxidoreductase

Comments: A flavoprotein (FAD or FMN). Occurs in mitochondria of yeast and plants, and in aerobic bacteria.

Has low activity with NADPH. Unlike EC 7.1.1.2, NADH:ubiquinone reductase (H⁺-translocating), this enzyme does not pump proteons of sodium ions across the membrane. It is also not sensitive to

rotenone.

References: [300, 2864, 855, 2067, 3454, 2768]

[EC 1.6.5.9 created 2011 (EC 1.6.5.11 created 1972 as EC 1.6.99.5, transferred 2015 to EC 1.6.5.11, incorporated 2019), modified 2019]

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 [1580]. Menaquinone can act as acceptor. The enzyme from hog liver is inhibited by dicoumarol and folic acid derivatives but not by

2,4-dinitrophenol [2212].

References: [2212, 1579, 1580]

[EC 1.6.5.10 created 1972 as EC 1.6.99.6, transferred 2011 to EC 1.6.5.10]

[1.6.5.11 Deleted entry. NADH dehydrogenase (quinone). Identical to EC 1.6.5.9, NADH:quinone reductase (non-electrogenic)]

[EC 1.6.5.11 created 1972 as EC 1.6.99.5, transferred 2015 to EC 1.6.5.11, deleted 2019]

EC 1.6.5.12

Accepted name: demethylphylloquinone reductase

Reaction: demethylphylloquinone + NADPH + H^+ = demethylphylloquinol + NADP⁺

Other name(s): ndbB (gene name); NDC1 (gene name); demethylphylloquinone:NADPH oxidoreductase

Systematic name: NADPH:demethylphylloquinone oxidoreductase

Comments: The enzyme, found in plants and cyanobacteria, is involved in the biosynthesis of phylloquinone (vita-

min K₁), an electron carrier associated with photosystem I. The enzyme is a type II NADPH dehydro-

genase and requires a flavine adenine dinucleotide cofactor.

References: [1095]

[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 reductase]	Transferred entry. 4-(dimethylamino)phenylazoxybenzene reductase. Now EC 1.7.1.11, 4-(dimethylamino)phenylazoxybenzen
	[EC 1.6.6.12 created 1989, deleted 2002]
[1.6.6.13 reductase]	Transferred entry. N-hydroxy-2-acetamidofluorene reductase. Now EC 1.7.1.12, N-hydroxy-2-acetamidofluorene

[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 din-

ucleotide 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: [50, 162, 1876, 4255, 4258]

[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]

 $[EC\ 1.6.99.2\ created\ 1961\ as\ EC\ 1.6.5.2,\ transferred\ 1965\ to\ EC\ 1.6.99.2,\ deleted\ 2005]$

[1.6.99.3 Deleted entry. NADH dehydrogenase. The activity is covered by EC 7.1.1.2, NADH:ubiquinone reductase (H⁺-translocating)]

[EC 1.6.99.3 created 1961 as EC 1.6.2.1, transferred 1965 to EC 1.6.99.3, modified 2018, deleted 2020]

[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 Deleted entry. aquacobalamin reductase. This entry has been deleted since no specific enzyme catalysing this activity has been identified and it has been shown that aquacobalamin is efficiently reduced by free dihydroflavins and by non-specific reduced flavoproteins.]

[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 Deleted entry. aquacobalamin reductase (NADPH). This entry has been deleted since the enzyme the entry was based on was later shown to be EC 1.2.1.51, pyruvate dehydrogenase (NADP $^+$). On the other hand, it has been shown that non-enzymatic reduction of cob(III)alamin to cob(II)alamin occurs efficiently in the presence of free dihydroflavins or non-specific reduced flavoproteins.]

[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⁺ + H_2O = nitrate + NADH + H^+

Other name(s): assimilatory nitrate reductase (ambiguous); NADH-nitrate reductase; NADH-dependent nitrate reduc-

tase; assimilatory NADH: nitrate reductase; nitrate reductase (NADH2); NADH2:nitrate oxidoreduc-

tase

Systematic name: nitrite:NAD⁺ oxidoreductase

Comments: An iron-sulfur molybdenum flavoprotein.

References: [1114, 3019, 3063, 3977, 301]

[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 (ambiguous); 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: [3019, 3230, 541, 301]

[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+ + H_2O = nitrate + NADPH + H^+

Other name(s): assimilatory nitrate reductase (ambiguous); assimilatory reduced nicotinamide adenine dinu-

cleotide 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: [3019, 3020, 3062, 4209, 301]

[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: $NH_3 + 3 NAD(P)^+ + 2 H_2O = nitrite + 3 NAD(P)H + 5 H^+$

Other name(s): nitrite reductase (reduced nicotinamide adenine dinucleotide (phosphate)); assimilatory nitrite reduc-

tase (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 [3061], Emericella nidulans [3260] and Candida nitratophila [2326] can use either NADPH

or NADH as electron donor. cf. EC 1.7.1.15, nitrite reductase (NADH).

References: [3061, 3260, 3529, 2326, 4427, 1398, 3386, 1074, 708]

[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: [2758]

[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 ox-

idoreductase

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 [4145].

References: [2914, 4145]

[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: $IMP + NH_3 + NADP^+ = GMP + NADPH + H^+$

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: [2593, 2608]

[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 oxidore-

ductase

Systematic name: 4-(hydroxyamino)quinoline *N*-oxide:NADP⁺ oxidoreductase

References: [4313, 4003]

[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: $NH_3 + NAD^+ + H_2O = hydroxylamine + NADH + H^+$

Other name(s): hydroxylamine reductase; ammonium dehydrogenase; NADH-hydroxylamine reductase; N-hydroxy

amine reductase; hydroxylamine reductase (NADH2); NADH2:hydroxylamine oxidoreductase

Systematic name: ammonium:NAD⁺ oxidoreductase

Comments: Also acts on some hydroxamates.

References: [306, 307, 4528]

[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)phenylazosenzene + 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 oxi-

doreductase

Systematic name: 4-(dimethylamino)phenylazobenzene:NADP⁺ oxidoreductase

References: [1936]

[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: [1458, 2134]

[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: $preQ_1$ 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 syn-

thesis 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 [4797] 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: [2341, 4797, 2273, 3153, 3097, 4147]

[EC 1.7.1.13 created 2006]

EC 1.7.1.14

Accepted name: nitric oxide reductase $[NAD(P)^+$, nitrous oxide-forming]

Reaction: $N_2O + NAD(P)^+ + H_2O = 2 NO + NAD(P)H + H^+$

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: [3892, 3889, 4879, 3196]

[EC 1.7.1.14 created 2011]

EC 1.7.1.15

Accepted name: nitrite reductase (NADH)

Reaction: $NH_3 + 3 NAD^+ + 2 H_2O = nitrite + 3 NADH + 5 H^+$

Other name(s): nitrite reductase (reduced nicotinamide adenine dinucleotide); NADH-nitrite oxidoreductase; assimi-

latory 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: [4428, 1873, 538, 1530]

[EC 1.7.1.15 created 2013]

EC 1.7.1.16

Accepted name: nitrobenzene nitroreductase

Reaction: N-phenylhydroxylamine + 2 NADP⁺ + H_2O = nitrobenzene + 2 NADPH + 2 H⁺ (overall reaction)

(1a) *N*-phenylhydroxylamine + NADP⁺ = nitrosobenzene + NADPH + H⁺ (1b) nitrosobenzene + NADP⁺ + H_2O = nitrobenzene + NADPH + H⁺

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

Systematic name: N-phenylhydroxylamine:NADP⁺ oxidoreductase

Comments: Contains FMN. The enzyme, characterized from *Pseudomonas* species, catalyses two succes-

sive reductions of nitrobenzene, via a nitrosobenzene intermediate. It is also active on 1-chloro-4-

nitrobenzene.

References: [3958, 4674]

[EC 1.7.1.16 created 2017]

EC 1.7.1.17

Accepted name: FMN-dependent NADH-azoreductase

Reaction: anthranilate + N,N-dimethyl-1,4-phenylenediamine + 2 NAD⁺ = 2-(4-

dimethylaminophenyl)diazenylbenzoate + 2 NADH + 2 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 com-

pounds to form the corresponding amines. Does not accept NADPH. cf. EC 1.7.1.6, azobenzene re-

ductase.

References: [2987, 1846, 1847, 2773]

[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 + H_2O + ferricytochrome c = nitrite + ferrocytochrome c + $\mathbf{2}$ H⁺

Other name(s): cd-cytochrome nitrite reductase; [nitrite reductase (cytochrome)] [misleading, see comments.]; cy-

tochrome c-551:O₂, NO₂+ oxidoreductase; cytochrome cd; cytochrome cd; hydroxylamine (acceptate)

tor) 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 perimplasm of denitrifying bacte-

ria. 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: [2839, 691, 4499, 3909, 2791, 1349, 4635, 1695, 4941, 1103, 4450]

[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 ferrocytochrome 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: [1030]

[EC 1.7.2.2 created 2001]

EC 1.7.2.3

Accepted name: trimethylamine-*N*-oxide reductase

Reaction: trimethylamine + 2 (ferricytochrome c)-subunit + H_2O = trimethylamine N-oxide + 2 (ferrocy-

tochrome 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: [125, 2161, 794, 1357, 4881, 4793]

[EC 1.7.2.3 created 2002, modified 2018]

EC 1.7.2.4

Accepted name: nitrous-oxide reductase

Reaction: nitrogen + $H_2O + 2$ ferricytochrome c = nitrous oxide + 2 ferrocytochrome 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: [758, 4942, 873]

[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 $c + H_2O = 2$ nitric oxide + 2 ferrocytochrome 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: [1626, 1625, 1614, 624, 2286, 1663]

[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: hydroxylamine + H_2O + 4 ferricytochrome c = nitrite + 4 ferrocytochrome c + 5 H^+

Other name(s): HAO (ambiguous); hydroxylamine oxidoreductase (ambiguous); hydroxylamine oxidase (misleading)

Systematic name: hydroxylamine:ferricytochrome-*c* oxidoreductase (nitrite-forming)

Comments: The enzymes from the nitrifying bacterium *Nitrosomonas europaea* [3480, 2505] and the methy-

lotrophic bacterium *Methylococcus capsulatus* [3354] 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 [1710]. While nitrite is the main product, the enzyme from *Nitrosomonas europaea* can also produce nitric oxide by catalysing the activity of EC 1.7.2.9, hydroxy-

lamine oxidase [1711].

References: [3480, 1711, 1710, 2505, 3354]

[EC 1.7.2.6 created 1972 as EC 1.7.3.4, part transferred 2012 to EC 1.7.2.6, modified 2021, modified 2021]

EC 1.7.2.7

Accepted name: hydrazine synthase

Reaction: hydrazine + $H_2O + 3$ ferricytochrome c = nitric oxide + ammonium + 3 ferrocytochrome 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 a

few enzymes that are known to form an N-N bond (other examples include EC 1.7.1.14, nitric oxide reductase $[NAD(P)^+$, nitrous oxide-forming] and EC 4.8.1.1, L-piperazate synthase). The enzyme from the bacterium *Candidatus Kuenenia stuttgartiensis* is a dimer of heterotrimers and contains mul-

tiple *c*-type cytochromes.

References: [2002, 910]

[EC 1.7.2.7 created 2016, modified 2021]

EC 1.7.2.8

Accepted name: hydrazine dehydrogenase

Reaction: hydrazine + **4** ferricytochrome $c = N_2 + 4$ ferrocytochrome 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 bacte-

ria, has been purified from the bacterium Candidatus Kuenenia stuttgartiensis. The electrons derived

from hydrazine are eventually transferred to the quinone pool.

References: [3701, 1909, 2002, 2001]

[EC 1.7.2.8 created 2003 as EC 1.7.99.8, modified 2010, transferred 2016 to EC 1.7.2.8]

EC 1.7.2.9

Accepted name: hydroxylamine oxidase

Reaction: hydroxylamine + 3 ferricytochrome c = nitric oxide + 3 ferrocytochrome $c + 3 \text{ H}^+$

Other name(s): HOX

Systematic name: hydroxylamine:ferricytochrome-c oxidoreductase (nitric acid-forming)

Comments: The enzyme, characterized from the anaerobic ammonium-oxidizing (anammox) bacterium Kuene-

nia stuttgartiensis, is very similar to EC 1.7.2.6, hydroxylamine dehydrogenase. Both enzymes are homotrimeric enzymes in which each subunit contains seven *c*-type hemes and one specialized *P*460-type heme that is bound to a tyrosine residue in an adjacent subunit. However, this enzyme catalyses only the 3 electron oxidation of hydroxylamine, forming nitric oxide, and is not capable of performing

further oxidation to form nitrite.

References: [2581]

[EC 1.7.2.9 created 2021]

EC 1.7.3 With oxygen as acceptor

EC 1.7.3.1

Accepted name: nitroalkane oxidase

Reaction: a nitroalkane $+ H_2O + O_2 =$ an aldehyde or ketone + nitrite $+ H_2O_2$ **Other name(s):** nitroethane oxidase; NAO; nitroethane:oxygen oxidoreductase

Systematic name: nitroalkane:oxygen oxidoreductase

Comments: Has an absolute requirement for FAD [1130]. While nitroethane may be the physiological substrate

[2086], the enzyme also acts on several other nitroalkanes, including 1-nitropropane, 2-nitropropane, 1-nitrobutane, 1-nitropentane, 1-nitrohexane, nitrocyclohexane and some nitroalkanols [1130]. Differs from EC 1.13.12.16, nitronate monooxygenase, in that the preferred substrates are neutral nitroalka-

nes rather than anionic nitronates [1130].

References: [2509, 2086, 833, 1130, 4392]

[EC 1.7.3.1 created 1961, modified 2006, modified 2009]

EC 1.7.3.2

Accepted name: acetylindoxyl oxidase

Reaction: N-acetylindoxyl + $O_2 = N$ -acetylisatin + (?) **Systematic name:** N-acetylindoxyl:oxygen oxidoreductase

References: [269]

[EC 1.7.3.2 created 1961]

EC 1.7.3.3

Accepted name: factor-independent urate hydroxylase

Reaction: urate $+ O_2 + H_2O = 5$ -hydroxyisourate $+ H_2O_2$ **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 CO_2 , 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: [2537, 2614, 3535, 1977, 714, 1806]

[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 + O_2 + O_2 + O_3 + O_4 + O_4 - O_4 - O_5 -

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 nitro-

propanoate free radical and superoxide. Also acts, more slowly, on 4-aci-nitrobutanoate.

References: [3357]

[EC 1.7.3.5 created 1990]

EC 1.7.3.6

Other name(s):

Accepted name: hydroxylamine oxidase (cytochrome)

Reaction: hydroxylamine + O_2 = nitrite + H_2O + H^+ (overall reaction)

(1a) hydroxylamine + 2 ferricytochrome c = nitroxyl + 2 ferrocytochrome c + 2 H⁺

(1b) nitroxyl + 2 ferrocytochrome $c + O_2 + H^+ = nitrite + 2$ ferricytochrome $c + H_2O$ (spontaneous) 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 [4573, 2861]. Under anaerobic conditions *in vitro* only nitrous oxide is formed [2861]. Presumably nitroxyl is released and combines with a second nitroxyl to give nitrous oxide and water. When oxy-

gen is present, nitrite is formed.

References: [2302, 4573, 2861, 4572]

[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 con-

ditions 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: [1051, 313, 2337, 312, 384, 1440, 1822]

[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 + H_2O

Comments: Contains copper. **References:** [764, 4109, 4108]

[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

> 3 nitrite + 2 H⁺ = 2 nitric oxide + nitrate + H_2O Reaction:

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. Ni-

trophorins 2 and 4 can also catalyse this reaction.

References: [1585, 1586]

[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

> $NH_3 + 2 H_2O + 6$ oxidized ferredoxin = nitrite + 6 reduced ferredoxin + 7 H⁺ **Reaction:**

Systematic name: ammonia:ferredoxin oxidoreductase

> **Comments:** An iron protein. Contains siroheme and [4Fe-4S] clusters.

References: [1956, 3447, 4944]

[EC 1.7.7.1 created 1972, modified 1999]

EC 1.7.7.2

Accepted name: ferredoxin—nitrate reductase

> Reaction: nitrite + H_2O + 2 oxidized ferredoxin = nitrate + 2 reduced ferredoxin + 2 H^+

assimilatory nitrate reductase (ambiguous); nitrate (ferredoxin) reductase; assimilatory ferredoxin-Other name(s):

nitrate reductase

Systematic name: nitrite:ferredoxin oxidoreductase

Comments: A molybdenum-iron-sulfur protein.

References: [2803]

[EC 1.7.7.2 created 1986]

EC 1.7.99 With unknown physiological acceptors

EC 1.7.99.1

Accepted name: hydroxylamine reductase

> $NH_3 + H_2O + acceptor = hydroxylamine + reduced acceptor$ Reaction:

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).

[4209, 4498, 3516] **References:**

[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 nitrousoxide 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 H_2O = sulfite + 3 NADPH + 3 H_2

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); *cysI* (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: [1660, 4818, 3901, 2175, 3902, 756, 766]

[EC 1.8.1.2 created 1961, modified 2015]

[1.8.1.3 Deleted entry. hypotaurine dehydrogenase. The reaction is now known to be catalyzed by EC 1.14.13.8, flavin-containing monooxygenase.]

EC 1.8.1.4

Accepted name: dihydrolipoyl dehydrogenase

Reaction: protein N^6 -(dihydrolipoyl)lysine + NAD⁺ = protein N^6 -(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; lipoic acid dehydrogenase; lipoyl dehydrogenase; lipoyl

nase; protein-6-N-(dihydrolipoyl)lysine:NAD+ oxidoreductase

Systematic name: protein- N^6 -(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 [3043].

References: [2685, 2686, 3679, 4055, 3293, 3043]

[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: CoM + acetoacetate + NADP⁺ = 2-oxopropyl-CoM + CO_2 + NADPH

 $\textbf{Other name}(s) : \quad \text{NADPH:2-} (2\text{-ketopropylthio}) ethane sulfonate \ oxidoreductase/carboxylase; \ NADPH:2\text{-ketopropyl-name}(s) : \quad \text{NADPH:2-ketopropyl-name}(s) : \quad \text{$

coenzyme M oxidoreductase/carboxylase; 2-mercaptoethanesulfonate, acetoacetate: NADP+ oxidore-

ductase (decarboxylating)

Systematic name: 2-sulfanylethane-1-sulfonate,acetoacetate:NADP⁺ oxidoreductase (decarboxylating)

Comments: Also acts on thioethers longer in chain length on the oxo side, e.g. 2-oxobutyl-CoM, but this por-

tion must be attached to CoM (2-sulfanylethane-1-sulfonate); no CoM analogs will substitute. This enzyme forms component II 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: [68, 695]

[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: [3562, 564, 2649]

[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 re-

ductase; 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: [3221, 3324, 3421, 4408, 4670, 373, 2475]

[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: [1557]

[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:** [2874, 3978, 133]

[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 reduc-

tase; 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: [3182, 3183, 557]

[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-sulfanyl-2-(sulfanylmethyl)propanoate + NAD^+ = asparagusate + $NADH + H^+$

Other name(s): asparagusate dehydrogenase; asparagusic dehydrogenase; asparagusate reductase (NADH₂);

NADH₂:asparagusate oxidoreductase; 3-mercapto-2-mercaptomethylpropanoate:NAD⁺ oxidoreduc-

tase

Systematic name: 3-sulfanyl-2-(sulfanylmethyl)propanoate:NAD⁺ oxidoreductase

Comments: Also acts on lipoate. **References:** [4759, 4760]

[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 $^+$ 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: [3816, 2660, 786]

[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 -glutamylcysteine + NADP⁺ = bis- γ -glutamylcystine + NADPH + H⁺

Other name(s): NADPH₂:bis-γ-glutamylcysteine oxidoreductase; GSR

Systematic name: γ -glutamylcysteine:NADP⁺ oxidoreductase

Comments: Contains FAD. The enzyme, which is found only in halobacteria, maintains the concentration of γ -

glutamylcysteine, 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: [4127, 4128, 2093]

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

Other name(s): CoA-disulfide reductase (NADH₂); NADH₂:CoA-disulfide oxidoreductase; CoA:NAD⁺ oxidoreduc-

tase (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 [2553], while the bacterium *Bacillus megaterium*

contains both NADH and NADPH-dependent enzymes [3802].

References: [3802, 872, 2553]

[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: [3254, 3255]

[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 [4436].

References: [4436, 4437]

[EC 1.8.1.16 created 2010]

EC 1.8.1.17

Accepted name: dimethylsulfone reductase

Reaction: dimethyl sulfoxide + H_2O + NAD^+ = dimethyl sulfone + NADH + H^+

Comments: A molybdoprotein.

References: [394, 395]

[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: [3762, 439, 1534]

[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 oxida-

tion of NADPH which is produced in peptide degradation. The enzyme also catalyses the reduction of

sulfur with lower activity.

References: [2573, 1473]

[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

cofator.

References: [2075, 2076]

[EC 1.8.1.20 created 2017]

EC 1.8.1.21

Accepted name: dissimilatory dimethyldisulfide reductase

Reaction: 2 methanethiol + NAD⁺ = dimethyl disulfide + NADH + H⁺ **Systematic name:** methanethiol:NAD⁺ oxidoreductase (dimethyl disulfide-forming)

Comments: The enzyme's activity has been demonstrated in the bacterium *Thiobacillus thioparus* E6. The

methanethiol formed is eventually oxidized to sulfate and carbon dioxide, and the latter assimilated

for autotrophic growth.

References: [3942, 3943]

[EC 1.8.1.21 created 2019]

EC 1.8.2 With a cytochrome as acceptor

EC 1.8.2.1

Accepted name: sulfite dehydrogenase (cytochrome)

Reaction: sulfite + 2 ferricytochrome $c + H_2O = \text{sulfate} + 2$ ferrocytochrome 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: [607, 2572, 4747, 2551, 1992]

[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 ferrocytochrome 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 Allochromatium vinosum, lack TsdB. The electron ac-

ceptor in these organisms may be the high-potential iron-sulfur protein (HiPIP).

References: [2552, 1224, 2526, 444, 2305]

[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 ferrocytochrome c + 2 H⁺

Systematic name: hydrogen-sulfide:flavocytochrome c oxidoreductase

Comments: The enzyme from Allochromatium vinosum contains covalently bound FAD and covalently-bound

c-type hemes.

References: [2306, 1225, 1390, 640, 3970, 2242]

[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 + H_2O = dimethyl sulfoxide + 2 ferrocytochrome c_2 + H_2O = dimethyl sulfoxide + 2 ferrocytochrome c_2 + H_2O = dimethyl sulfoxide + 2 ferrocytochrome C_2 + H_2O = dimethyl sulfoxide + 2 ferrocytochrome C_2 + H_2O = dimethyl sulfoxide + 2 ferrocytochrome C_2 + H_2O = dimethyl sulfoxide + 2 ferrocytochrome C_2 + H_2O = dimethyl sulfoxide + 2 ferrocytochrome C_2 + H_2O = dimethyl sulfoxide + 2 ferrocytochrome C_2 + H_2O = H_2O =

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 dinu-

cleotide, heme b and [4Fe-4S] clusters.

References: [1506, 2746]

[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** ferrocytochrome c_3 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: [1834, 1833, 2998, 1546, 1558, 51]

[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** ferrocytochrome 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 trans-

ferred to the electron chain via cytochrome c.

References: [1187, 219, 1379]

[EC 1.8.2.6 created 2018]

EC 1.8.2.7

Accepted name: thiocyanate desulfurase

Reaction: thiocyanate + 2 ferricytochrome $c + H_2O = \text{cyanate} + \text{sulfur} + 2 \text{ ferrocytochrome } c + 2 \text{ H}^+$

Other name(s): TcDH; thiocyanate dehydrogenase

Systematic name: thiocyanate:cytochrome c oxidoreductase (cyanate and sulfur-forming)

Comments: The enzyme, characterized from the haloalkaliphilic sulfur-oxidizing bacterium *Thioalkalivibrio*

paradoxus, contains three copper ions in its active site. It catalyses the direct conversion of thio-

cyanate into cyanate and elemental sulfur without involvement of molecular oxygen.

References: [4290]

[EC 1.8.2.7 created 2020]

EC 1.8.3 With oxygen as acceptor

EC 1.8.3.1

Accepted name: sulfite oxidase

Reaction: sulfite $+ O_2 + H_2O = \text{sulfate} + H_2O_2$ **Systematic name:** sulfite:oxygen oxidoreductase

Comments: A molybdohemoprotein. **References:** [2073, 2595, 4163]

[EC 1.8.3.1 created 1961]

EC 1.8.3.2

Accepted name: thiol oxidase

Reaction: 2 R'C(R)SH + O_2 = R'C(R)S-S(R)CR' + H_2O_2

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: [156, 3044, 3201, 1709, 1879, 3807, 797, 1093, 1422, 850, 3519]

[EC 1.8.3.2 created 1961, modified 2010, modified 2011]

EC 1.8.3.3

Accepted name: glutathione oxidase

Reaction: 2 glutathione $+ O_2 =$ glutathione disulfide $+ H_2O_2$

Systematic name: glutathione:oxygen oxidoreductase

Comments: A flavoprotein (FAD). Also acts, more slowly, on L-cysteine and several other thiols.

References: [2308]

[EC 1.8.3.3 created 1989]

EC 1.8.3.4

Accepted name: methanethiol oxidase

Reaction: methanethiol + O_2 + H_2O = formaldehyde + hydrogen sulfide + H_2O_2

Other name(s): methylmercaptan oxidase; methyl mercaptan oxidase; (MM)-oxidase; MT-oxidase

Systematic name: methanethiol:oxygen oxidoreductase

References: [4134]

[EC 1.8.3.4 created 1990]

EC 1.8.3.5

Accepted name: prenylcysteine oxidase

Reaction: an S-prenyl-L-cysteine + O_2 + H_2O = a prenal + L-cysteine + H_2O_2

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-geranylgeranylcysteine. N-Acetyl-prenylcysteine and prenylcysteinyl 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: [4882, 4336]

[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-(2E,6E)-farnesyl-L-cysteine + O_2 + O_2 + O_3 + O_4 + O_4 + O_5 + O_5 + O_5 + O_6 + O_7 + O_8 + O_8 + O_9 + $O_$

Other name(s): FC lyase; FCLY

Systematic name: S-(2E,6E)-farnesyl-L-cysteine oxidase

Comments: A flavoprotein (FAD). In contrast to mammalian EC 1.8.3.5 (prenylcysteine oxidase) the farnesyl-

cysteine lyase from Arabidopsis is specific for S-farnesyl-L-cysteine and shows no activity with S-

geranylgeranyl-L-cysteine.

References: [1769, 775]

[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 disul-

fide $+ H_2O$

Other name(s): sulfatase-modifying factor 1; Cα-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 eukary-

otes, 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 alo acts in vitro, but it is not known whether it is used in vivo.

References: [909, 908, 3377, 3554, 559, 1693, 2171, 2170, 2784]

[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 homocysteine

Systematic name: glutathione:homocystine oxidoreductase

Comments: The reactions catalysed by this enzyme and by others in this subclass may be similar to those catal-

ysed by EC 2.5.1.18 glutathione transferase.

References: [3420]

[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 disulphide

oxidoreductase

Systematic name: glutathione:protein-disulfide oxidoreductase

Comments: Reduces insulin and some other proteins.

References: [2031, 2204]

[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 glu-

tathione disulfide transhydrogenase; glutathione coenzyme A-glutathione transhydrogenase; glutathione:coenzyme A-glutathione transhydrogenase; coenzyme A:oxidized-glutathione oxidoreduc-

tase; coenzyme A:glutathione-disulfide oxidoreductase

Systematic name: CoA:glutathione-disulfide oxidoreductase

References: [597]

[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: [2956]

[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;

ductase

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: [238]

[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 + thiore-

doxin

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: [293]

[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,sulfate:oxidized-glutathione oxidore-

ductase (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 reduc-

tant. Glutathione can be replaced by γ -glutamylcysteine or dithiothreitol, but not by thioredoxin, glutaredoxin or 2-sulfanylethan-1-ol (2-mercaptoethanol). The enzyme from the mouseear 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, Ulva intestinalis.

References: [1457, 3803, 331]

[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: [332, 5, 4636, 3051]

[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 + H_2O = peptide-L-methionine (S)-S-oxide + thioredoxin

doxin

(2) L-methionine + thioredoxin disulfide + H_2O = 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 sulfox-

ide 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 [3174]. On the free amino acid, it can also reduce D-methionine (*S*)-*S*-oxide but more slowly [3174]. 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 [2908, 399]. The reaction proceeds via a

sulfenic-acid intermediate [1075, 452].

References: [2908, 4226, 3913, 399, 1075, 4579, 2032, 4475, 3174, 452]

EC 1.8.4.12

Accepted name: peptide-methionine (R)-S-oxide reductase

Reaction: peptide-L-methionine + thioredoxin disulfide + H_2O = peptide-L-methionine (R)-S-oxide + thioredoxin

doxin

Other name(s): MsrB; methionine sulfoxide reductase (ambiguous); pMSR; methionine S-oxide reductase (ambiguous)

ous); selenoprotein R; methionine S-oxide reductase (R-form oxidizing); methionine sulfoxide reduc-

tase 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 speci-

ficity 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 [3174]. While both free and protein-bound methionine (*R*)-*S*-oxide act as substrates, the activity with the peptide-bound form is far greater [3628]. 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 [3913, 1075]. The reaction proceeds via a sulfenic-acid intermediate [1075, 3628]. For MsrB2 and MsrB3, thioredoxin is a poor reducing agent but thionein works

well []. The enzyme from some species contains selenocysteine and Zn^{2+} .

References: [2908, 4226, 3913, 399, 1075, 4579, 2032, 4475, 3174, 3628]

[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 + H_2O = L-methionine (S)-S-oxide + thioredoxin

Other name(s): fSMsr; methyl sulfoxide reductase I and II; acetylmethionine sulfoxide reductase; methionine sulfox-

ide 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 [1031]. The reaction occurs in the opposite direction to that given above. Dithio-

threitol 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: [344, 1031, 1032, 4579]

[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 + H_2O = 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 can-

not use peptide-bound methionine (R)-S-oxide as a substrate [1068]. Differs from EC 1.8.4.13, L-

methionine (S)-S-oxide in that L-methionine (S)-S-oxide is not a substrate.

References: [1068]

[EC 1.8.4.14 created 1984 as EC 1.8.4.5, part transferred 2006 to EC 1.8.4.14]

EC 1.8.4.15

Accepted name: protein dithiol oxidoreductase (disulfide-forming)

Reaction: a [DsbA protein] carrying a disulfide bond + a [protein] with reduced L-cysteine residues = a [DsbA

protein] with reduced L-cysteine residues + a [protein] carrying a disulfide bond

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

Systematic name: protein dithiol:[DsbA protein] oxidoreductase (protein disulfide-forming)

Comments: DsbA is a periplasmic thiol:disulfide oxidoreductase found in Gram-negative bacteria that promotes

protein disulfide bond formation. DsbA contains a redox active disulfide bond that is catalytically transferred via disulfide exchange to a diverse range of newly translocated protein substrates. The protein is restored to the oxidized state by EC 1.8.5.9, protein dithiol:quinone oxidoreductase DsbB.

References: [220, 52, 4861, 175, 1436, 1968]

[EC 1.8.4.15 created 2019]

EC 1.8.4.16

Accepted name: thioredoxin:protein disulfide reductase

Reaction: a [protein] with reduced L-cysteine residues + thioredoxin disulfide = a [protein] carrying a disulfide

bond + thioredoxin (overall reaction)

(1a) a [DsbD protein] with reduced L-cysteine residues + thioredoxin disulfide = a [DsbD protein]

carrying a disulfide bond + thioredoxin

(1b) a [DsbD protein] carrying a disulfide bond + a [protein] with reduced L-cysteine residues = a

[DsbD protein] with reduced L-cysteine residues + a [protein] carrying a disulfide bond

Other name(s): dsbD (gene name); dipZ (gene name)

Systematic name: thioredoxin:protein disulfide oxidoreductase (dithiol-forming)

Comments: DsbD is an inner membrane protein found in Gram-negative bacteria that transfers electrons from

cytoplasmic thioredoxin to the periplasmic substrate proteins DsbC, DsbG and CcmG, reducing disulfide bonds in the target proteins to dithiols. DsbD consists of three domains: a periplasmic N-terminal

domain, a central transmembrane domain and a periplasmic C-terminal domain.

References: [2827, 1367, 2029, 1376, 2030, 3587]

[EC 1.8.4.16 created 2019]

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 oxidoreduc-

tase

Systematic name: glutathione:dehydroascorbate oxidoreductase

References: [771]

[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; thiosulfate: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: [2922]

EC 1.8.5.3

Accepted name: respiratory dimethylsulfoxide reductase

Reaction: dimethylsulfide + menaquinone + H_2O = dimethylsulfoxide + menaquinol

Other name(s): dmsABC (gene names); DMSO reductase (ambiguous); dimethylsulfoxide reductase (ambiguous)

Systematic name: dimethyl sulfide:menaquinone oxidoreductase

Comments: The enzyme participates in bacterial electron transfer pathways in which dimethylsulfoxide (DMSO)

is the terminal electron acceptor. It is composed of three subunits - DmsA contains a bis(guanylyl molybdopterin) cofactor and a [4Fe-4S] cluster, DmsB is an iron-sulfur protein, and DmsC is a transmembrane protein that anchors the enzyme and accepts electrons from the quinol pool. The electrons are passed through DmsB to DmsA and on to DMSO. The enzyme can also reduce pyridine-*N*-oxide

and trimethylamine N-oxide to the corresponding amines with lower activity.

References: [830, 2798, 3903, 3579]

[EC 1.8.5.3 created 2011, modified 2019]

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); sulfide:quinone oxidoreductase

Systematic name: sulfide:quinone oxidoreductase (polysulfide-producing)

Comments: Contains FAD. Ubiquinone, plastoquinone or menaquinone can act as acceptor in different species.

In some organisms the 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, sulfide quinone oxidoreductase.

References: [132, 3489, 3115, 445, 647, 2645, 4699]

[EC 1.8.5.4 created 2011, modified 2017, modified 2019]

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 mem-

brane.

References: [2318, 697, 56, 1613, 4042]

[EC 1.8.5.5 created 2016, modified 2017]

EC 1.8.5.6

Accepted name: sulfite dehydrogenase (quinone)

Reaction: sulfite + a quinone + H_2O = 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 cy-

toplasm. 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: [799]

[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 chlorophenolicum* 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 en-

zymes are often formed spontaneously by interaction of benzoquinones with glutathione.

References: [1756, 4711, 2329, 1395]

[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: [4570, 1651, 1872, 2474]

[EC 1.8.5.8 created 2017]

EC 1.8.5.9

Accepted name: protein dithiol:quinone oxidoreductase DsbB

Reaction: a [DsbA protein] with reduced L-cysteine residues + a quinone = a [DsbA protein] carrying a disulfide

bond + a quinol (overall reaction)

(1a) a [DsbA protein] with reduced L-cysteine residues + a [DsbB protein] carrying a disulfide bond = a [DsbA protein] carrying a disulfide bond + a [DsbB protein] with reduced L-cysteine residues
(1b) a [DsbB protein] with reduced L-cysteine residues + a quinone = a [DsbB protein] carrying a

disulfide bond + a quinol

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

Systematic name: protein dithiol:quinone oxidoreductase (disulfide-forming)

Comments: DsbB is a protein found in Gram-negative bacteria that functions within a pathway for protein disul-

fide bond formation. The enzyme catalyses the oxidation of the DsbA protein by generating disulfide bonds *de novo* via the reduction of membrane quinones. *cf.* EC 1.8.4.15, protein dithiol oxidoreduc-

tase (disulfide-forming).

References: [1441, 2130, 2129, 712, 993, 1807]

[EC 1.8.5.9 created 2019]

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 ferre-

doxin [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 [3051]. 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: [3724, 1331, 393, 3051]

[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 thiore-

doxin 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 (phospho-

ribulokinase) as well as other chloroplast enzymes by disulfide reduction.

References: [484, 680, 4004]

[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, and

EC 1.8.98.1, dihydromethanophenazine:CoB-CoM heterodisulfide reductase.

References: [480, 4758]

[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 re-

ductase and EC 1.8.98.4, coenzyme F₄₂₀:CoB-CoM heterodisulfide, ferredoxin reductase.

References: [1598, 4, 3904, 2936]

[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 ox-

idized 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: [338, 599, 4663]

[EC 1.8.98.2 created 2005]

EC 1.8.98.3

Accepted name: sulfite reductase (coenzyme F_{420})

Reaction: hydrogen sulfide + 3 oxidized coenzyme F_{420} + 3 H_2O = sulfite + 3 reduced coenzyme F_{420}

Other name(s): coenzyme F_{420} -dependent sulfite reductase; Fsr Systematic name: hydrogen sulfide:coenzyme F_{420} oxidoreductase

Comments: The enzyme, isolated from the archaeon Methanocaldococcus jannaschii, is involved in sulfite detoxi-

fication and assimilation.

References: [1928, 1929]

[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 $F_{420} + 2$ reduced ferredoxin [iron-sulfur] cluster + CoB + CoM + 2 H⁺ = 2 re-

duced 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: [4758]

[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 H_2 + 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 *Methan-*

othermobacter 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 CoBCoM 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:CoBCoM 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: [3482, 1599, 3805, 4044, 2007, 745]

[EC 1.8.98.5 created 2017]

EC 1.8.98.6

Accepted name: formate:CoB-CoM heterodisulfide,ferredoxin reductase

Reaction: $2 \text{ CO}_2 + 2 \text{ reduced ferredoxin [iron-sulfur] cluster} + \text{CoB} + \text{CoM} + 2 \text{ H}^+ = 2 \text{ formate} + 2 \text{ oxidized}$

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 *Methanococ*-

cus 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: [746, 745]

[EC 1.8.98.6 created 2017]

EC 1.8.98.7

Accepted name: cysteine-type anaerobic sulfatase-maturating enzyme

Reaction: S-adenosyl-L-methionine + a [sulfatase]-L-cysteine + H_2O = a [sulfatase]-3-oxo-L-alanine + 5'-

deoxyadenosine + L-methionine + hydrogen sulfide

Other name(s): anSME; Cys-type anaerobic sulfatase-maturating enzyme; anaerobic sulfatase maturase **Systematic name:** [sulfatase]-L-cysteine: S-adenosyl-L-methionine oxidoreductase (3-oxo-L-alanine-forming)

Comments: A radical S-adenosylmethionine (AdoMet) enzyme that contains three [4Fe-4S] clusters. The enzyme,

found in some bacteria, activates a type I sulfatase enzyme (EC 3.1.6.1) by converting a conserved L-cysteine residue in the active site to a unique 3-oxo-L-alanine residue that is essential for the sulfatase activity. Some enzymes can also act on L-serine, see EC 1.1.98.7, serine-type anaerobic sulfatase-

maturating enzyme and EC 1.8.3.7, formylglycine-generating enzyme.

References: [311, 287, 286, 288, 1430]

[EC 1.8.98.7 created 2020]

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). Methyl viologen can act as acceptor.

References: [2786]

[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 H_2O = sulfite + a [DsrC protein]-dithiol + 2 reduced acceptor + 2 H_2O = sulfite + a [DsrC protein]-dithiol +

(2) a [DsrC protein]-S-sulfanyl-L-cysteine + 3 acceptor + 3 H_2O = sulfite + a [DsrC protein]-disulfide + 3 reduced acceptor + 2 H^+ (overall reaction)

(2a) a [DsrC protein]-S-sulfanyl-L-cysteine + 3 acceptor + 3 H_2O = 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) [3706]. 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 [4432]. 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.

[3706, 3792, 3358, 3169, 4432] **References:**

[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

[1.9.3.1 Transferred entry. cytochrome-c oxidase. Now EC 7.1.1.9, cytochrome-c oxidase]

[EC 1.9.3.1 created 1961, modified 2000, deleted 2019]

[1.9.3.2 Transferred entry. Pseudomonas cytochrome oxidase. Now included with EC 1.7.2.1, nitrite reductase (NOforming)]

[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)

2 ferrocytochrome + 2 H⁺ + nitrate = 2 ferricytochrome + nitrite Reaction: Other name(s): respiratory nitrate reductase; benzyl viologen-nitrate reductase

Systematic name: ferrocytochrome:nitrate oxidoreductase

References: [3622]

[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: ferrocytochrome $c + \text{Fe}^{3+} = \text{ferricytochrome } c + \text{Fe}^{2+}$

iron-cytochrome c reductase Other name(s):

ferrocytochrome-c:Fe³⁺ oxidoreductase **Systematic name:**

Comments: An iron protein.

References: [4782]

[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: (\pm)-trans-acenaphthene-1,2-diol + 2 NADP⁺ = acenaphthenequinone + 2 NADPH + 2 H⁺

Other name(s): *trans*-1,2-acenaphthenediol dehydrogenase

Systematic name: (\pm) -trans-acenaphthene-1,2-diol:NADP⁺ oxidoreductase

Comments: Some preparations also utilize NAD⁺.

References: [1713]

[EC 1.10.1.1 created 1976]

EC 1.10.2 With a cytochrome as acceptor

[1.10.2.1 Deleted entry. L-ascorbate—cytochrome- b_5 reductase. The activity is covered by EC 7.2.1.3, ascorbate ferrireductase (transmembrane)]

[EC 1.10.2.1 created 1972, modified 2000, deleted 2021]

[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 + O_2 = 2 1,2-benzoquinone + 2 H_2O

Other name(s): diphenol oxidase; o-diphenolase; polyphenol oxidase; pyrocatechol oxidase; dopa oxidase; cate-

cholase; 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: [459, 842, 1405, 2682, 2729, 3261, 3350, 3533, 1302]

[EC 1.10.3.1 created 1961, deleted 1972, reinstated 1978]

EC 1.10.3.2

Accepted name: laccase

Reaction: 4 benzenediol + O_2 = 4 benzosemiquinone + 2 H_2O **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: [842, 2057, 2633, 2729, 2981, 2982, 3282, 3492]

[EC 1.10.3.2 created 1961, deleted 1972, reinstated 1978]

EC 1.10.3.3

Accepted name: L-ascorbate oxidase

Reaction: 4 L-ascorbate + O_2 = 4 monodehydroascorbate + 2 H_2O

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:** [4753, 4006, 2779]

[EC 1.10.3.3 created 1961, modified 2011]

EC 1.10.3.4

Accepted name: o-aminophenol oxidase

Reaction: 4 2-aminophenol + 3 O_2 = 2 2-aminophenoxazin-3-one + 6 H_2O

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* re-

quires Mn^{2+} and FAD [2969] whereas the fungus *Pycnoporus coccineus* requires Mn^{2+} and riboflavin 5'-phosphate [2971], the bacteria *Streptomyces antibioticus* requires Cu^{2+} [227] and the plant *Bauhe*-

nia monandra does not require any co-factors [3452].

References: [2969, 2971, 3452, 227]

[EC 1.10.3.4 created 1972, modified 2006]

EC 1.10.3.5

Accepted name: 3-hydroxyanthranilate oxidase

Reaction: 3-hydroxyanthranilate $+ O_2 = 6$ -imino-5-oxocyclohexa-1,3-dienecarboxylate $+ H_2O_2$

Other name(s): 3-hydroxyanthranilic acid oxidase

Systematic name: 3-hydroxyanthranilate:oxygen oxidoreductase

References: [2884]

[EC 1.10.3.5 created 1972]

EC 1.10.3.6

Accepted name: rifamycin-B oxidase

Reaction: rifamycin B + O_2 = rifamycin O + H_2O_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: [1501]

[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 $H_2O + 2$ plastoquinone + 4 $hv = O_2 + 2$ plastoquinol **Systematic name:** H_2O :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: [2163, 1454]

[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 ubiquinol + O₂ = 2 ubiquinone + 2 H₂O

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* alterna-

tive 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 photo-

synthesis in response to changing conditions.

References: [285, 3900, 314, 4629, 1269]

[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 O_2 = grixazone B + 4 H_2O + CO_2

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, cataly-

ses 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: [4135, 3553]

[EC 1.10.3.15 created 2014]

EC 1.10.3.16

Accepted name: dihydrophenazinedicarboxylate synthase

Reaction: (1) (1R,6R)-1,4,5,5a,6,9-hexahydrophenazine-1,6-dicarboxylate + O₂ = (1R,10aS)-1,4,10,10a-

tetrahydrophenazine-1,6-dicarboxylate + H_2O_2

(2) (1R,10aS)-1,4,10,10a-tetrahydrophenazine-1,6-dicarboxylate + $O_2 = (5aS)$ -5,5a-dihydrophenazine-

1,6-dicarboxylate + H_2O_2

(3) (1R,10aS)-1,4,10,10a-tetrahydrophenazine-1-carboxylate + $O_2 = (10aS)-10,10a$ -dihydrophenazine-

1-carboxylate + H_2O_2

(4) (1R)-1,4,5,10-tetrahydrophenazine-1-carboxylate + O_2 = (10aS)-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: [4706]

[EC 1.10.3.16 created 2016]

EC 1.10.3.17

Accepted name: superoxide oxidase

Reaction: 2 O_2 + ubiquinol = 2 superoxide + ubiquinone + 2 H^+

Other name(s): SOO; CybB; cytochrome b_{561} ; superoxide:ubiquinone oxidoreductase

Systematic name: ubiquinol:oxygen oxidoreductase (superoxide-forming)

Comments: This membrane-bound, di-heme containing enzyme, identified in the bacterium Escherichia coli, is

responsible for the detoxification of superoxide in the periplasm. *In vivo* the reaction proceeds in the opposite direction of that shown and produces oxygen. Superoxide production was only observed

when the enzyme was incubated *in vitro* with an excess of ubiquinol.

References: [2937, 2938, 2567]

[EC 1.10.3.17 created 2019]

EC 1.10.5 With a quinone or related compound as acceptor

EC 1.10.5.1

Accepted name: ribosyldihydronicotinamide dehydrogenase (quinone)

Reaction: $1-(\beta-D-ribofuranosyl)-1,4-dihydronicotinamide + a quinone = <math>1-(\beta-D-ribofuranosyl)$ 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-ribosyl- and N-alkyldihydronicotinamides. Polycyclic aromatic hydrocarbons, such as benz[a]anthracene, and the estrogens 17 β -estradiol and diethylstilbestrol are potent inhibitors, but dicoumarol is only a very weak inhibitor [4902]. This enzyme can catalyse both 2-electron and 4-electron reductions, but one-electron acceptors, such as potassium ferricyanide,

cannot be reduced [4676].

References: [2473, 4902, 4676, 1877]

[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. ribosyldihydronicotinamide dehydrogenase (quinone). Now classified as EC 1.10.5.1, ribosyldihydronicotinamide 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: NADH + H⁺ + $H_2O_2 = NAD^+ + 2 H_2O$

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: [940, 2850, 4497]

[EC 1.11.1.1 created 1961]

EC 1.11.1.2

Accepted name: NADPH peroxidase

Reaction: NADPH + H⁺ + $H_2O_2 = NADP^+ + 2 H_2O$

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: [720]

[EC 1.11.1.2 created 1961]

EC 1.11.1.3

Accepted name: fatty-acid peroxidase

Reaction: palmitate + $2 H_2 O_2$ = pentadecanal + CO_2 + $3 H_2 O$

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: [2668]

[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 ferrocytochrome $c + H_2O_2 = 2$ ferricytochrome $c + 2 H_2O$

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: ferrocytochrome-*c*:hydrogen-peroxide oxidoreductase

Comments: A hemoprotein. **References:** [75, 4746, 4800]

[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: [1628, 1629, 2054, 2224, 3064, ?]

[EC 1.11.1.6 created 1961, modified 1986, modified 1999, modified 2013]

EC 1.11.1.7

Accepted name: peroxidase

Reaction: 2 phenolic donor + $H_2O_2 = 2$ phenoxyl radical of the donor + $2 H_2O$

Other name(s): lactoperoxidase; guaiacol peroxidase; plant peroxidase; Japanese radish peroxidase; horseradish per-

oxidase (HRP); soybean peroxidase (SBP); extensin peroxidase; heme peroxidase; oxyperoxidase; protoheme peroxidase; pyrocatechol peroxidase; scopoletin peroxidase; *Coprinus cinereus* peroxi-

dase; 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: [2065, 2900, 3264, 4162, 4256, 1089, 44, 984, 4314]

[EC 1.11.1.7 created 1961, modified 2011]

EC 1.11.1.8

Accepted name: iodide peroxidase

Reaction: (1) 2 iodide + $H_2O_2 + 2H^+$ = diiodine + 2 H_2O

(2) [thyroglobulin]-L-tyrosine + iodide + H_2O_2 = [thyroglobulin]-3-iodo-L-tyrosine + $\mathbf{2}$ H_2O_1

(3) [thyroglobulin]-3-iodo-L-tyrosine + iodide + H_2O_2 = [thyroglobulin]-3,5-diiodo-L-tyrosine + $2 H_2O_2$ = [thyroglobulin]-L-thyroxine + [thyroglobulin]-

aminoacrylate + 2 H₂O

(5) [thyroglobulin]-3-iodo-L-tyrosine + [thyroglobulin]-3,5-diiodo-L-tyrosine + H_2O_2 =

[thyroglobulin]-3,5,3'-triiodo-L-thyronine + [thyroglobulin]-aminoacrylate + 2 H₂O

Other name(s): thyroid peroxidase; iodoperoxidase (heme type); iodide peroxidase-tyrosine iodinase; thyroperoxi-

dase; tyrosine iodinase; TPO; iodinase

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: [784, 1740, 755, 1289, 3149, 2611, 4453, 3464, 4119, 4222, 3599]

[EC 1.11.1.8 created 1961, modified 2012]

EC 1.11.1.9

Accepted name: glutathione peroxidase

Reaction: 2 glutathione + H_2O_2 = glutathione disulfide + 2 H_2O

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

H₂O₂ (cf. EC 1.11.1.12 phospholipid-hydroperoxide glutathione peroxidase).

References: [618, 1429, 2985]

[EC 1.11.1.9 created 1965, modified 1989]

EC 1.11.1.10

Accepted name: chloride peroxidase

Reaction: RH + chloride + H_2O_2 = RCl + **2** H_2O

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: [2899, 1474, 4252, 4123, 4241, 4240, 2637, 2277, 2638]

[EC 1.11.1.10 created 1972, modified 2011]

EC 1.11.1.11

Accepted name: L-ascorbate peroxidase

Reaction: 2 L-ascorbate + H₂O₂ + 2 H⁺ = L-ascorbate + L-dehydroascorbate + 2 H₂O (overall reaction)

(1a) 2 L-ascorbate + H_2O_2 + 2 H^+ = 2 monodehydroascorbate + 2 H_2O

(1b) **2** monodehydroascorbate = L-ascorbate + 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 monodehy-

droascorbate radical produced is either directly reduced back to ascorbate by EC 1.6.5.4 [monode-hydroascorbate reductase (NADH)] or undergoes non-enzymic disproportionation to ascorbate and

dehydroascorbate.

References: [3857, 3856, 2993, 3263, 3830, 2587]

[EC 1.11.1.11 created 1983, modified 2010, modified 2011]

EC 1.11.1.12

Accepted name: phospholipid-hydroperoxide glutathione peroxidase

Reaction: 2 glutathione + a hydroperoxy-fatty-acyl-[lipid] = glutathione disulfide + a hydroxy-fatty-acyl-[lipid]

+ H₂O

Other name(s): peroxidation-inhibiting protein; PHGPX; peroxidation-inhibiting protein:peroxidase, glutathione

(phospholipid hydroperoxide-reducing); phospholipid hydroperoxide glutathione peroxidase; hy-

droperoxide 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; H₂O₂ can also act, but much more slowly (cf. EC 1.11.1.9 glu-

tathione peroxidase).

References: [4381, 3738]

[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+} [2269]. The complexed Mn^{3+} ion can diffuse into the lignified cell wall, where it oxidizes phenolic components of lignin and other organic substrates [1343]. It is inactive with veratryl alcohol or nonphenolic sub-

strates.

References: [1343, 3252, 4544, 2269]

[EC 1.11.1.13 created 1992]

EC 1.11.1.14

Accepted name: lignin peroxidase

Reaction: (1) 1-(3,4-dimethoxyphenyl)-2-(2-methoxyphenoxy)propane-1,3-diol + $H_2O_2 = 3,4$ -

 $dimethoxybenzaldehyde + 2\text{-methoxyphenol} + glycolaldehyde + H_2O$

(2) 2 (3,4-dimethoxyphenyl)methanol + H_2O_2 = 2 (3,4-dimethoxyphenyl)methanol radical + 2 H_2O

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:

Comments:

1-(3,4-dimethoxyphenyl)-2-(2-methoxyphenoxy)propane-1,3-diol:hydrogen-peroxide oxidoreductase 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: [2070, 3252, 1544, 4545, 526, 2083, 2084, 2082, 960, 3346]

[EC 1.11.1.14 created 1992, modified 2006, modified 2011, modified 2016]

[1.11.1.15] Transferred entry. peroxiredoxin. Now described by EC 1.11.1.24, thioredoxin-dependent peroxiredoxin; EC 1.11.1.25, glutaredoxin-dependent peroxiredoxin; EC 1.11.1.26, NADH-dependent peroxiredoxin; EC 1.11.1.27, glutathione-dependent peroxiredoxin; EC 1.11.1.28, lipoyl-dependent peroxiredoxin; and EC 1.11.1.29, mycoredoxin-dependent peroxiredoxin.]

[EC 1.11.1.15 created 2004, deleted 2020]

EC 1.11.1.16

Accepted name: versatile peroxidase

Reaction: (1) 1-(4-hydroxy-3-methoxyphenyl)-2-(2-methoxyphenoxy)propane-1,3-diol + H_2O_2 = 4-hydroxy-3-

 $methoxybenzaldehyde + 2\text{-}methoxyphenol} + glycolaldehyde + H_2O$

(2) 2 manganese(II) + 2 H⁺ + H_2O_2 = 2 manganese(III) + 2 H_2O_2

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 oxidore-

ductase

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 lowand high-redox-potential dyes, due to a hybrid molecular architecture that involves multiple binding

sites for substrates [1612, 534].

References: [2671, 1612, 3018, 534, 3017, 533, 3016, 209, 3290, 552]

[EC 1.11.1.16 created 2006, modified 2016]

EC 1.11.1.17

Accepted name: glutathione amide-dependent peroxidase

Reaction: 2 glutathione amide $+ H_2O_2 =$ glutathione amide disulfide $+ 2 H_2O$

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 [4436]. The glutathione amide disulfide produced by this enzyme can be restored to glutathione amide by EC 1.8.1.16 (glu-

tathione amide reductase).

References: [4436]

[EC 1.11.1.17 created 2010]

EC 1.11.1.18

Accepted name: bromide peroxidase

Reaction: $RH + HBr + H_2O_2 = RBr + 2 H_2O$

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: [367, 4333, 1840, 566, 3147]

[EC 1.11.1.18 created 2010]

EC 1.11.1.19

Accepted name: dye decolorizing peroxidase

Reaction: Reactive Blue $5 + 2 H_2 O_2 = \text{phthalate} + 2.2' - \text{disulfonyl azobenzene} + 3 - [(4-amino-6-chloro-1,3,5-$

triazin-2-yl)amino]benzenesulfonate + $\mathbf{2}$ 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: [2105, 4094, 4938, 4095, 4093, 3135, 4398, 2483, 1687]

[EC 1.11.1.19 created 2011, modified 2015]

EC 1.11.1.20

Accepted name: prostamide/prostaglandin $F_{2\alpha}$ synthase

Reaction: thioredoxin + $(5Z,9\alpha,11\alpha,13E,15S)$ -9,11-epidioxy-15-hydroxy-prosta-5,13-dienoate = thioredoxin

disulfide + $(5Z,9\alpha,11\alpha,13E,15S)$ -9,11,15-trihydroxyprosta-5,13-dienoate

Other name(s): prostamide/PGF synthase; prostamide F synthase; prostamide/prostaglandin F synthase; tPGF synthase;

thase

Systematic name: thioredoxin: $(5Z,9\alpha,11\alpha,13E,15S)-9,11$ -epidioxy-15-hydroxy-prosta-5,13-dienoate oxidoreductase

Comments: The enzyme contains a thioredoxin-type disulfide as a catalytic group. Prostamide H₂ and

prostaglandin H_2 are the best substrates; the latter is converted to prostaglandin $F_{2\alpha}$. The enzyme also reduces *tert*-butyl hydroperoxide, cumene hydroperoxide and H_2O_2 , but not prostaglandin D_2

or prostaglandin E₂.

References: [2897, 4816]

[EC 1.11.1.20 created 2011]

EC 1.11.1.21

Accepted name: catalase-peroxidase

Reaction: (1) donor + H_2O_2 = oxidized donor + **2** H_2O

(2) $\mathbf{2} \, H_2 O_2 = O_2 + \mathbf{2} \, H_2 O$

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 tuber-

culosis it is responsible for activation of the commonly used antitubercular drug, isoniazid.

References: [2532, 1680, 1157, 317, 4455]

[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+ + H_2O

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: [1244, 1245]

[EC 1.11.1.22 created 2013]

EC 1.11.1.23

Accepted name: (S)-2-hydroxypropylphosphonic acid epoxidase

Reaction: (S)-2-hydroxypropylphosphonate + $H_2O_2 = (1R,2S)-1,2$ -epoxypropylphosphonate + $H_2O_2 = (1R,2S)-1,2$ -epoxyprop

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 fosfomycin, a broad-spectrum antibiotic pro-

duced 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 [4512].

References: [2933, 4756, 1641, 2521, 1645, 535, 4512]

[EC 1.11.1.23 created 2011 as EC 1.14.19.7, transferred 2014 to EC 1.11.1.23]

EC 1.11.1.24

Accepted name: thioredoxin-dependent peroxiredoxin

Reaction: thioredoxin + ROOH = thioredoxin disulfide + H_2O + ROH **Other name(s):** thioredoxin peroxidase; bcp (gene name); tpx (gene name); PrxQ

Systematic name: thioredoxin: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 [4667]. The peroxidase reaction comprises two steps centred around a redox-active cysteine called the peroxidatic cysteine. All three peroxides 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 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. The 1-Cys Prxs conserve only the peroxidatic cysteine, so its regeneration involves direct interaction with a reductant molecule. Thioredoxin-dependent peroxiredoxins are the most common. They have been reported from archaea, bacteria, fungi, plants, and animals.

References: [1991, 2221, 1905, 4667, 1903, 3292]

[EC 1.11.1.24 created 1983 as EC 1.11.1.15, part transferred 2020 to EC 1.11.1.24]

EC 1.11.1.25

Accepted name: glutaredoxin-dependent peroxiredoxin

Reaction: glutaredoxin + ROOH = glutaredoxin disulfide + H_2O + ROH

Other name(s): PRXIIB (gene name)

Systematic name: glutaredoxin: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 [4667]. The peroxidase reaction comprises two steps centred around a redox-active cysteine called the peroxidatic cysteine. All three peroxideoxin 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 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. To recycle the disulfide, known atypical 2-Cys Prxs appear to use thioredoxin as an electron donor. The 1-Cys Prxs conserve only the peroxidatic cysteine, so its regeneration involves direct interaction with a reductant molecule. Glutaredoxin-dependent peroxiredoxins have been reported from bacteria, fungi, plants, and animals. These enzymes are often able to use an alternative reductant such as thioredoxin or glutathione.

References: [3581, 4667, 3278, 1509, 2485, 754]

[EC 1.11.1.25 created 1983 as EC 1.11.1.15, part transferred 2020 to EC 1.11.1.25]

EC 1.11.1.26

Accepted name: NADH-dependent peroxiredoxin

Reaction: NADH + ROOH + H^+ = NAD⁺ + H_2O + ROH

Other name(s): ahpC (gene name); ahpF (gene name); alkyl hydroperoxide reductase

Systematic name: NADH: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 [4667]. 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 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. The 1-Cys Prxs conserve only the peroxidatic cysteine, so its regeneration involves direct interaction with a reductant molecule. This bacterial peroxiredoxin differs from most other forms by comprising two types of subunits. One subunit (AhpC) is a typical 2-Cys peroxiredoxin. Following the reduction of the substrate, one AhpC subunit forms a disulfide bond with an identical unit. The disulfide bond is reduced by the second type of subunit (AhpF). This second subunit is a flavin-containing protein that uses electrons from NADH to reduce the cysteine residues on the AhpC subunits back to their active state.

References: [4667, 921, 3014]

[EC 1.11.1.26 created 1983 as EC 1.11.1.15, part transferred 2020 to EC 1.11.1.26]

EC 1.11.1.27

Comments:

Accepted name: glutathione-dependent peroxiredoxin

Reaction: 2 glutathione + ROOH = glutathione disulfide + H_2O + ROH

Other name(s): PRDX6 (gene name); *prx3* (gene name)

Systematic name: glutathione:hydroperoxide oxidoreductase

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 [4667]. The peroxidase reaction comprises two steps centred around a redox-active cysteine called the peroxidatic cysteine. All

tion 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 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. The 1-Cys Prxs conserve only the peroxidatic cysteine, so its regeneration involves direct interaction with a reductant molecule. Glutathione-dependent peroxiredoxins have been reported from bacteria and animals, and appear to be 1-Cys enzymes. The mechanism for the mammalian PRDX6 enzyme involves heterodimerization of the enzyme with π -glutathione S-transferase, followed by glutathionylation of the oxidized cysteine residue. Subsequent dissociation of the heterodimer yields glutathionylated peroxiredoxin, which is restored to the active form via spontaneous reduction by a second glutathione molecule.

References: [4667, 3267, 2635, 1402, 2485]

[EC 1.11.1.27 created 1983 as EC 1.11.1.15, part transferred 2020 to EC 1.11.1.27]

EC 1.11.1.28

Accepted name: lipoyl-dependent peroxiredoxin

Reaction: a [lipoyl-carrier protein]- N^6 -[(R)-dihydrolipoyl]-L-lysine + ROOH = a [lipoyl-carrier protein]- N^6 -

[(R)-lipoyl]-L-lysine + H₂O + ROH

Other name(s): Ohr; *ahpC* (gene name); *ahpD* (gene name)

Systematic name: Comments:

[lipoyl-carrier protein]- N^6 -[(R)-dihydrolipoyl]-L-lysine:hydroperoxide oxidoreductase

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 [4667]. 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 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. The 1-Cys Prxs conserve only the peroxidatic cysteine, so its regeneration involves direct interaction with a reductant molecule. Two types of lipoyl-dependent peroxiredoxins have been reported from bacteria. One type is the AhpC/AhpD system, originally described from Mycobacterium tuberculosis. In that system, AhpC catalyses reduction of the substrate, resulting in an intramolecular disulfide. AhpD then forms an intermolecular disulfide crosslink with AhpC, reducing it back to active state. AhpD is reduced in turn by lipoylated proteins. The second

type, which has been characterized in Xylella fastidiosa, consists of only one type of subunit, which

interacts directly with lipoylated proteins.

[1653, 4667, 2240, 2239, 3850, 791]

[EC 1.11.1.28 created 1983 as EC 1.11.1.15, part transferred 2020 to EC 1.11.1.28]

EC 1.11.1.29

References:

Accepted name: mycoredoxin-dependent peroxiredoxin

Reaction: mycoredoxin + ROOH = mycoredoxin disulfide + H_2O + ROH

Other name(s): ahpE (gene name)

Systematic name: mycoredoxin: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 [4667]. 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 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. The 1-Cys Prxs conserve only the peroxidatic cysteine, so its regeneration involves direct interaction with a reductant molecule. Mycoredoxin-dependent enzymes are found in Mycobacteria. Following the reduction of the substrate, the sulfenic acid derivative of the peroxidatic cysteine forms a protein mixed disulfide with the N-terminal cysteine of mycoredoxin, which is then reduced by the C-terminal cysteine of mycoredoxin, restoring the peroxiredoxin to active state and resulting in an intra-protein disulfide in mycoredoxin. The disulfide is eventually re-

duced by mycothiol.

References: [4667, 1766, 1765, 2282, 3279]

[EC 1.11.1.29 created 1983 as EC 1.11.1.15, part transferred 2020 to EC 1.11.1.29]

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: $RH + H_2O_2 = ROH + H_2O$

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, sulfooxidation, 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: [4375, 4374, 105, 4373, 123, 2122, 2160, 2123, 3276]

[EC 1.11.2.1 created 2011]

EC 1.11.2.2

Accepted name: myeloperoxidase

Reaction: $Cl^- + H_2O_2 + H^+ = HClO + H_2O$

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 moder-

ate peroxygenase activity toward styrene.

References: [36, 1540, 1235, 4356, 2149, 1116, 1286]

[EC 1.11.2.2 created 2011]

EC 1.11.2.3

Accepted name: plant seed peroxygenase

Reaction: $R^1H + R^2OOH = R^1OH + R^2OH$

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

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, respec-

tively. Plant seed peroxygenase is involved in the synthesis of cutin.

References: [1832, 357, 1488, 2419, 1503]

[EC 1.11.2.3 created 2011]

EC 1.11.2.4

Accepted name: fatty-acid peroxygenase

Reaction: fatty acid + H_2O_2 = 3- or 2-hydroxy fatty acid + H_2O

Other name(s): fatty acid hydroxylase (ambiguous); P450 peroxygenase; CYP152A1; P450BS; P450SPα

Systematic name: fatty acid:hydroperoxide oxidoreductase (RH-hydroxylating)

Comments: A cytosolic heme-thiolate protein with sequence homology to *P*-450 monooxygenases. Unlike the lat-

ter, 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: [2708, 2707, 2705, 1804, 2706, 2382, 2704, 3890]

[EC 1.11.2.4 created 2011]

EC 1.11.2.5

Accepted name: 3-methyl-L-tyrosine peroxygenase

Reaction: 3-methyl-L-tyrosine + H_2O_2 = 3-hydroxy-5-methyl-L-tyrosine + H_2O **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: [4204]

[EC 1.11.2.5 created 2014]

EC 1.11.2.6

Accepted name: L-tyrosine peroxygenase

Reaction: L-tyrosine + H_2O_2 = L-dopa + H_2O

Systematic name: L-tyrosine:hydrogen-peroxide oxidoreductase (L-dopa-forming)

Comments: The enzyme from the bacterium *Streptomyces lincolnensis* participates in the biosynthesis of the an-

tibiotic lincomycin A, while that from *Streptomyces refuineus* is involved in anthramycin biosynthesis. The enzyme, which contains a heme *b* cofactor, is rapidly inactivated in the presence of hydrogen peroxide, but the presence of L-tyrosine protects it. *cf.* EC 1.11.2.5, 3-methyl-L-tyrosine peroxyge-

nase.

References: [3052, 722]

[EC 1.11.2.6 created 2020]

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 H_2 . 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:** $H_2 + NAD^+ = H^+ + NADH$

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: [382, 3735]

[EC 1.12.1.2 created 1972, modified 2002]

EC 1.12.1.3

Accepted name: hydrogen dehydrogenase (NADP⁺) **Reaction:** $H_2 + NADP^+ = H^+ + NADPH$

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 [852], 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: [852, 478, 2575, 2579, 4406]

[EC 1.12.1.3 created 2002, modified 2013]

EC 1.12.1.4

Accepted name: hydrogenase (NAD⁺, ferredoxin)

Reaction: $2 \text{ H}_2 + \text{NAD}^+ + 2 \text{ oxidized ferredoxin} = 5 \text{ H}^+ + \text{NADH} + 2 \text{ reduced ferredoxin}$

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: [4438, 3761]

[EC 1.12.1.4 created 2011]

EC 1.12.1.5

Accepted name: hydrogen dehydrogenase $[NAD(P)^+]$ **Reaction:** $H_2 + NAD(P)^+ = H^+ + NAD(P)H$ **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: [2578]

[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: $H_2 + 2$ ferricytochrome $c_3 = 2$ H⁺ + 2 ferrocytochrome c_3

Other name(s): H_2 : ferricytochrome c_3 oxidoreductase; cytochrome c_3 reductase; cytochrome hydrogenase; hydrogenase;

nase [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: [887, 1649, 3523, 3623, 4460, 1272]

[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 + menaquinone = menaquinol

Other name(s): hydrogen-ubiquinone oxidoreductase; hydrogen:menaquinone oxidoreductase; membrane-bound hy-

drogenase; 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 (benzyl viologen or methyl viologen).

References: [968, 969, 1427, 304, 1102, 1830]

[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: $H_2 + 2$ oxidized ferredoxin = 2 reduced ferredoxin + 2 H^+

Other name(s): H₂ oxidizing hydrogenase; H₂ producing hydrogenase [ambiguous]; bidirectional hydrogenase;

hydrogen-lyase [ambiguous]; hydrogenase (ferredoxin); hydrogenase I; hydrogenase II; hydro-

genlyase [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: [3895, 4161, 4391, 4943, 26, 3299]

[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 + oxidized coenzyme F_{420} = reduced coenzyme F_{420}

Other name(s): 8-hydroxy-5-deazaflavin-reducing hydrogenase; F₄₂₀-reducing hydrogenase; coenzyme F₄₂₀-

dependent hydrogenase

Systematic name: hydrogen:coenzyme F₄₂₀ oxidoreductase

Comments: An iron-sulfur flavoprotein (FAD) containing nickel. The enzyme from some sources contains seleno-

cysteine. The enzyme also reduces the riboflavin analogue of F₄₂₀, flavins and methyl viologen, but to

a lesser extent. The hydrogen acceptor coenzyme F_{420} is a deazaflavin derivative.

References: [27, 4754, 1156, 2952, 222]

[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: $H_2 + 5,10$ -methenyltetrahydromethanopterin = $H^+ + 5,10$ -methylenetetrahydromethanopterin

Other name(s): H_2 -forming N^5 , $N^{\hat{1}0}$ -methylenetetrahydromethanopterin dehydrogenase; nonmetal hy-

drogenase; N⁵,N¹⁰-methenyltetrahydromethanopterin hydrogenase; hydrogen:N⁵,N¹⁰-

methenyltetrahydromethanopterin oxidoreductase

Systematic name: hydrogen:5,10-methenyltetrahydromethanopterin oxidoreductase

Comments: Does not catalyse the reduction of artificial dyes. Does not by itself catalyse a H_2/H^+ exchange reac-

tion. Does not contain nickel or iron-sulfur clusters.

References: [4934, 2153]

[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: $H_2 + 2$ -(2,3-dihydropentaprenyloxy)phenazine = 2-dihydropentaprenyloxyphenazine

Other name(s): methanophenazine hydrogenase; methylviologen-reducing hydrogenase hydrogen:2-(2,3-dihydropentaprenyloxy)phenazine oxidoreductase

Comments: Contains nickel, iron-sulfur clusters and cytochrome b. The enzyme from some sources contains se-

lenocysteine.

References: [4, 885, 272]

[EC 1.12.98.3 created 2002]

EC 1.12.98.4

Accepted name: sulfhydrogenase

Reaction: $H_2 + (\text{sulfide})_n = \text{hydrogen sulfide} + (\text{sulfide})_{n-1}$

Other name(s): sulfur reductase

Systematic name: H₂: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 [2575].

References: [4937, 2575, 2579, 2578]

[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} -methenyltetrahydromethanopterin hydrogenase. Now EC 1.12.98.2, 5,10-methenyltetrahydrometh 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: H_2 + 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: [3895, 27, 4449]

[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] Transferred entry. Now EC 1.13.11.8, protocatechuate 4,5-dioxygenase] [1.13.1.8 [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] Transferred entry. Now EC 1.13.99.1, inositol oxygenase] [1.13.1.11 [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 + $O_2 = cis, cis$ -muconate

Other name(s): catechol-oxygen 1,2-oxidoreductase; 1,2-pyrocatechase; catechol 1,2-oxygenase; catechol

dioxygenase; pyrocatechase; pyrocatechol 1,2-dioxygenase; CD I; CD II

Systematic name: catechol:oxygen 1,2-oxidoreductase

Comments: Requires Fe^{3+} . Involved in the metabolism of nitro-aromatic compounds by a strain of *Pseudomonas*

putida.

References: [1570, 1571, 3918, 4872]

 $[EC\ 1.13.11.1\ created\ 1961\ as\ EC\ 1.99.2.2,\ transferred\ 1965\ to\ EC\ 1.13.1.1,\ transferred\ 1972\ to\ EC\ 1.13.11.1]$

EC 1.13.11.2

Accepted name: catechol 2,3-dioxygenase

Reaction: catechol + O_2 = 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: [1570, 2208, 3114, 2976, 1962, 1964]

[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 + O_2 = 3-carboxy-*cis*,*cis*-muconate

Other name(s): protocatechuate oxygenase; protocatechuic acid oxidase; protocatechuic 3,4-dioxygenase; protocatechuic

chuic 3,4-oxygenase; protocatechuate:oxygen 3,4-oxidoreductase (decyclizing)

Systematic name: protocatechuate:oxygen 3,4-oxidoreductase (ring-opening)

Comments: Requires Fe^{3+} . 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: [1208, 1428, 4001]

[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 + O_2 = maleylpyruvate

Other name(s): gentisate oxygenase; 2,5-dihydroxybenzoate dioxygenase; gentisate dioxygenase; gentisic acid oxi-

dase; gentisate:oxygen 1,2-oxidoreductase (decyclizing)

Systematic name: gentisate:oxygen 1,2-oxidoreductase (ring-opening)

Comments: Requires Fe^{2+} . **References:** [1570, 4104, 4103]

[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 $+ O_2 = 4$ -maleylacetoacetate

Other name(s): homogentisicase; homogentisate oxygenase; homogentisate dioxygenase; homogentisate oxidase;

homogentisic acid oxidase; homogentisic acid oxygenase; homogentisic oxygenase; homogenti-

sate:oxygen 1,2-oxidoreductase (decyclizing)

Systematic name: homogentisate:oxygen 1,2-oxidoreductase (ring-opening)

Comments: Requires Fe^{2+} .

References: [11, 765, 1570, 2131, 2174, 3461]

[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 + O_2 = 2-amino-3-carboxymuconate semialdehyde

Other name(s): 3-hydroxyanthranilate oxygenase; 3-hydroxyanthranilic acid oxygenase; 3-hydroxyanthranilic oxy-

genase; 3-hydroxyanthranilic acid oxidase; 3HAO; 3-hydroxyanthranilate:oxygen 3,4-oxidoreductase

(decyclizing)

Systematic name: 3-hydroxyanthranilate:oxygen 3,4-oxidoreductase (ring-opening)

Comments: Requires Fe^{2+} .

References: [860, 1570]

[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 + O_2 = 4-carboxy-2-hydroxymuconate semialdehyde

Other name(s): protocatechuate 4,5-oxygenase; protocatechuic 4,5-dioxygenase; protocatechuic 4,5-oxygenase; pro-

tocatechuate: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 Fe^{2+} .

References: [4332]

[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 + $O_2 = N$ -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 Fe^{2+} .

References: [271, 1287, 1288, 1915]

[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 + $O_2 = 5$ -(3-carboxy-3-oxopropenyl)-4,6-dihydroxykynurenate + $O_2 = 5$ -(3-carboxy-3-oxopropenyl)-4,6-dihydroxykynurenate + $O_2 = 5$ -(3-carboxy-3-oxopropenyl)

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 Fe^{2+} .

References: [2292]

[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 + $O_2 = N$ -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 [2510]. The enzyme is specific for tryptophan as substrate, but is far more active with L-tryptophan than with D-tryptophan [3497].

References: [4360, 3497, 2402, 822, 2510]

[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 + $O_2 = (9Z, 11E, 13S)-13$ -hydroperoxyoctadeca-9,11-dienoate

(2) α -linolenate + O₂ = (9Z,11E,13S,15Z)-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: [685, 4259, 4932, 3586, 173]

[EC 1.13.11.12 created 1961 as EC 1.99.2.1, transferred 1965 to EC 1.13.11.13, 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 + O_2 = 3-carboxy-2-hydroxymuconate semialdehyde

Other name(s): *o*-pyrocatechuate oxygenase; 2,3-dihydroxybenzoate 1,2-dioxygenase; 2,3-dihydroxybenzoic oxygenase;

nase; 2,3-dihydroxybenzoate oxygenase; 2,3-dihydroxybenzoate:oxygen 3,4-oxidoreductase (decy-

clizing)

Systematic name: 2,3-dihydroxybenzoate:oxygen 3,4-oxidoreductase (ring-opening)

References: [3511]

[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 + O_2 = 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, 218, 2312]

[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 + $O_2 = (2Z,4E)-2$ -hydroxy-6-oxonona-2,4-diene-1,9-dioate

(2) (2E)-3-(2,3-dihydroxyphenyl)prop-2-enoate + O₂ = (2Z,4E,7E)-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-dihydroxy-β-phenylpropionate oxygenase)

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 degra-

dation.

References: [798, 2331, 900]

[EC 1.13.11.16 created 1972, modified 2011, modified 2012]

EC 1.13.11.17

Accepted name: indole 2,3-dioxygenase

Reaction: indole + O_2 = 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-benzoisoxazole) (*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: [2968, 620, 924, 2288]

[EC 1.13.11.17 created 1972, modified 1986]

EC 1.13.11.18

Accepted name: persulfide dioxygenase

Reaction: S-sulfanylglutathione + O_2 + H_2O = glutathione + sulfite + $\mathbf{2}$ H⁺ (overall reaction)

(1a) S-sulfanylglutathione + O_2 = S-sulfinatoglutathione + H^+

(1b) S-sulfinatoglutathione + H_2O = glutathione + sulfite + H^+ (spontaneous)

Other name(s): sulfur oxygenase (incorrect); sulfur:oxygen oxidoreductase (incorrect); sulfur dioxygenase (incorrect)

Systematic name: S-sulfanylglutathione: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

35571.

References: [4136, 3557, 2514, 1694, 3308]

[EC 1.13.11.18 created 1972, modified 2015]

EC 1.13.11.19

Accepted name: cysteamine dioxygenase

Reaction: cysteamine + O_2 = hypotaurine

Other name(s): ADO (gene name); 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. 3-Aminopropanethiol (homo-

cysteamine) and 2-sulfanylethan-1-ol (2-mercaptoethanol) can also act as substrates, but glutathione,

cysteine, and cysteine ethyl- and methyl esters are not good substrates [578, 579].

References: [578, 4664, 579, 3513, 943]

[EC 1.13.11.19 created 1972, modified 2006]

EC 1.13.11.20

Accepted name: cysteine dioxygenase

Reaction: L-cysteine + O_2 = 3-sulfinoalanine

Other name(s): cysteine oxidase

Systematic name: L-cysteine:oxygen oxidoreductase **Comments:** Requires Fe²⁺ and NAD(P)H.

References: [2536]

[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 + O_2 = 3-(2-carboxyethenyl)-cis,cis-muconateOther 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: [3787]

[EC 1.13.11.22 created 1972]

EC 1.13.11.23

Accepted name: 2,3-dihydroxyindole 2,3-dioxygenase

Reaction: 2,3-dihydroxyindole + O_2 = anthranilate + CO_2

Other name(s): 2,3-dihydroxyindole:oxygen 2,3-oxidoreductase (decyclizing)

Systematic name: 2,3-dihydroxyindole:oxygen 2,3-oxidoreductase (ring-opening)

References: [1207]

[EC 1.13.11.23 created 1972]

EC 1.13.11.24

Accepted name: quercetin 2,3-dioxygenase

Reaction: quercetin + O_2 = 2-(3,4-dihydroxybenzoyloxy)-4,6-dihydroxybenzoate + $CO + H^+$ quercetinase; flavonol 2,4-oxygenase; quercetin:oxygen 2,3-oxidoreductase (decyclizing)

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: [3151, 4018, 409]

[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 + O_2 = 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 (decyclizing)

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: [1322]

[EC 1.13.11.25 created 1972]

EC 1.13.11.26

Accepted name: peptide-tryptophan 2,3-dioxygenase

Reaction: [protein]-L-tryptophan + O_2 = [protein]-N-formyl-L-kynurenine

Other name(s): pyrrolooxygenase; peptidyltryptophan 2,3-dioxygenase; tryptophan pyrrolooxygenase; [protein]-L-

tryptophan:oxygen 2,3-oxidoreductase (decyclizing)

Systematic name: [protein]-L-tryptophan:oxygen 2,3-oxidoreductase (ring-opening)

Comments: Also acts on tryptophan.

References: [1198, 539]

[EC 1.13.11.26 created 1972, modified 2011]

EC 1.13.11.27

Accepted name: 4-hydroxyphenylpyruvate dioxygenase

Reaction: 4-hydroxyphenylpyruvate + O_2 = homogentisate + CO_2

Other name(s): p-hydroxyphenylpyruvic hydroxylase; p-hydroxyphenylpyruvate hydroxylase; p-

hydroxyphenylpyruvate oxidase; *p*-hydroxyphenylpyruvic oxidase; *p*-hydroxyphenylpyruvic acid dioxygenase; *p*-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: [2502, 3543]

[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 + O_2 = 2-carboxy-*cis*,*cis*-muconate

Other name(s): 2,3-dihydroxybenzoate 2,3-oxygenase; 2,3-dihydroxybenzoate:oxygen 2,3-oxidoreductase (decycliz-

ing)

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-

is opropyl benzo ate.

References: [971, 3825]

[EC 1.13.11.28 created 1978]

EC 1.13.11.29

Accepted name: stizolobate synthase

Reaction: L-dopa + O_2 = 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 stizolo-

bic acid. The enzyme requires Zn^{2+} .

References: [3631, 3632]

[EC 1.13.11.29 created 1978]

EC 1.13.11.30

Accepted name: stizolobinate synthase

Reaction: L-dopa + $O_2 = 5$ -(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 sti-

zolobinic acid. The enzyme requires Zn²⁺.

References: [3631, 3632]

[EC 1.13.11.30 created 1978]

EC 1.13.11.31

Accepted name: arachidonate 12-lipoxygenase

Reaction: arachidonate + $O_2 = (5Z,8Z,10E,14Z)-(12S)-12$ -hydroperoxyicosa-5,8,10,14-tetraenoate **Other name(s):** Δ^{12} -lipoxygenase; 12-lipoxygenase; 12 Δ -lipoxygenase; 12 Δ -li

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: [1489, 3118, 4502]

[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 + $O_2 = (5Z, 8Z, 11Z, 13E) - (15S) - 15$ -hydroperoxyicosa-5,8,11,13-tetraenoate

Other name(s): 15-lipoxygenase; linoleic acid ω^6 -lipoxygenase; ω^6 lipoxygenase

Systematic name: arachidonate:oxygen 15-oxidoreductase

Comments: The product is rapidly reduced to the corresponding 15S-hydroxy compound.

References: [479, 3015, 3170, 3853]

[EC 1.13.11.33 created 1984]

EC 1.13.11.34

Accepted name: arachidonate 5-lipoxygenase

Reaction: arachidonate + O_2 = leukotriene A_4 + H_2O (overall reaction)

(1a) arachidonate + O_2 = (6*E*,8*Z*,11*Z*,14*Z*)-(5*S*)-5-hydroperoxyicosa-6,8,11,14-tetraenoate (1b) (6*E*,8*Z*,11*Z*,14*Z*)-(5*S*)-5-hydroperoxyicosa-6,8,11,14-tetraenoate = leukotriene $A_4 + H_2O$

Other name(s): leukotriene- A_4 synthase; Δ^5 -lipoxygenase; Δ^5 -lipoxygenase; arachidonic 5-lipoxygenase; arachidonic

acid 5-lipoxygenase; C-5-lipoxygenase; LTA synthase; leukotriene A₄ synthase

Systematic name: arachidonate:oxygen 5-oxidoreductase

References: [2703, 3138, 3871, 3872]

[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 + $O_2 = (2Z,4E)$ -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: [1421]

[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 + O_2 = 5-amino-4-chloro-2-(2-

hydroxymuconoyl)-3(2H)-pyridazinone

Other name(s): 5-amino-4-chloro-2-(2,3-dihydroxyphenyl)-3(2*H*)-pyridazinone 1,2-oxidoreductase (decyclizing) 5-amino-4-chloro-2-(2,3-dihydroxyphenyl)-3(2*H*)-pyridazinone 1,2-oxidoreductase (ring-opening)

Comments: An iron protein, requiring additional Fe^{2+} . 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: [2925, 2926]

[EC 1.13.11.36 created 1984]

EC 1.13.11.37

Accepted name: hydroxyquinol 1,2-dioxygenase **Reaction:** hydroxyquinol $+ O_2 =$ 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: [4156, 1108, 1562]

[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 + $O_2 = (3Z)$ -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 (decyclizing)

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: [221]

[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 + O_2 = 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 (decyclizing)

Systematic name: biphenyl-2,3-diol:oxygen 1,2-oxidoreductase (ring-opening)

Comments: Contains Fe^{2+} or Mn^{2+} [1561]. 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 [1042]. The enzyme from the carbazole-degrader *Pseudomonas resinovorans* strain CA10 also accepts 2'-aminobiphenyl-2,3-diol [1863]. The enzyme from *Ralstonia* sp. SBUG 290 can also accept 1,2-dihydroxydibenzofuran and 1,2-dihydroxynaphthalene [4592]. The enzyme is strongly inhibited by the substrate [1042]. Not iden-

tical with EC 1.13.11.2 catechol 2,3-dioxygenase.

References: [1042, 4378, 1561, 4592, 1863]

[EC 1.13.11.39 created 1989]

EC 1.13.11.40

Accepted name: arachidonate 8-lipoxygenase

Reaction: arachidonate + $O_2 = (5Z,9E,11Z,14Z)-(8R)-8$ -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: [493]

[EC 1.13.11.40 created 1989]

EC 1.13.11.41

Accepted name: 2,4'-dihydroxyacetophenone dioxygenase

Reaction: 2,4'-dihydroxyacetophenone + $O_2 = 4$ -hydroxybenzoate + formate

Other name(s): (4-hydroxybenzoyl)methanol oxygenase

Systematic name: 2,4'-dihydroxyacetophenone oxidoreductase (C-C-bond-cleaving)

References: [1715]

[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 αβ-dioxygenase

Reaction: 1,2-bis(4-hydroxy-3-methoxyphenyl)ethylene + $O_2 = 2$ 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 syn-

thetic substrate and lignin-derived stilbenes. It is responsible for the degradation of a diarylpropane-

type structure in lignin.

References: [1987]

[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 + $O_2 = (9Z,12Z)-(11S)-11$ -hydroperoxyoctadeca-9,12-dienoate

Other name(s): linoleate dioxygenase; manganese lipoxygenase

Systematic name: linoleate:oxygen 11*S*-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 *Gaeumanno-myces graminis* requires Mn^{2+} . It also acts on α-linolenate, whereas γ-linolenate is a poor substrate.

Oleate and arachidonate are not substrates.

References: [1491, 3171, 4084]

[EC 1.13.11.45 created 2000]

Accepted name: 4-hydroxymandelate synthase

Reaction: 4-hydroxyphenylpyruvate + $O_2 = (S)$ -4-hydroxymandelate + CO_2

Other name(s): 4-hydroxyphenylpyruvate dioxygenase II

Systematic name: (S)-4-hydroxyphenylpyruvate:oxygen oxidoreductase (decarboxylating)

Comments: Requires Fe^{2+} . Involved in the biosynthesis of the vancomycin group of glycopeptide antibiotics.

References: [1758, 678]

[EC 1.13.11.46 created 2001]

EC 1.13.11.47

Accepted name: 3-hydroxy-4-oxoquinoline 2,4-dioxygenase

Reaction: 3-hydroxy-1*H*-quinolin-4-one + $O_2 = N$ -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-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 Pseudomonas putida is

highly specific for this substrate.

References: [242, 243, 1126]

[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 + $O_2 = N$ -acetylanthranilate + CO

Other name(s): (1*H*)-3-hydroxy-4-oxoquinaldine 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: [242, 243, 1126]

[EC 1.13.11.48 created 2001]

EC 1.13.11.49

Accepted name: chlorite O_2 -lyase **Reaction:** chloride + O_2 = 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: [4405, 4021]

[EC 1.13.11.49 created 2001]

EC 1.13.11.50

Accepted name: acetylacetone-cleaving enzyme

Reaction: pentane-2,4-dione + O_2 = acetate + 2-oxopropanal

Other name(s): Dke1; acetylacetone dioxygenase; diketone cleaving dioxygenase; diketone cleaving enzyme

Systematic name: acetylacetone:oxygen oxidoreductase

Comments: An iron(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: [4053]

[EC 1.13.11.50 created 2003]

EC 1.13.11.51

Accepted name: 9-cis-epoxycarotenoid dioxygenase

Reaction: (1) a 9-cis-epoxycarotenoid + $O_2 = 2$ -cis,4-trans-xanthoxin + a 12'-apo-carotenal

(2) 9-cis-violaxanthin + $O_2 = 2$ -cis, 4-trans-xanthoxin + (3S, 5R, 6S)-5, 6-epoxy-3-hydroxy-5, 6-dihydro-

12'-apo-β-caroten-12'-al

(3) 9'-cis-neoxanthin + $O_2 = 2$ -cis,4-trans-xanthoxin + (3S,5R,6R)-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

[4192, 3401]. 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: [3768, 4192, 3401, 4269, 1852, 1853]

[EC 1.13.11.51 created 2005]

EC 1.13.11.52

Accepted name: indoleamine 2,3-dioxygenase

Reaction: (1) D-tryptophan + $O_2 = N$ -formyl-D-kynurenine

(2) L-tryptophan + $O_2 = N$ -formyl-L-kynurenine

Other name(s): IDO (ambiguous); tryptophan pyrrolase (ambiguous); D-tryptophan:oxygen 2,3-oxidoreductase (decy-

clizing)

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 [4742]. It is induced in response to pathological conditions and host-defense mechanisms and its distribution in mammals is not confined to the liver [4779]. 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 [4779, 2510]. Super-

oxide radicals can replace O₂ as oxygen donor [1668, 4267].

References: [4742, 4779, 4186, 1668, 822, 2510, 4267, 3964]

[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 + O_2 = 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)

Requires Ni²⁺. If iron(II) is bound instead of Ni²⁺, the reaction catalysed by EC 1.13.11.54, acire-**Comments:**

ductone dioxygenase [iron(II)-requiring], occurs instead [4672]. The enzyme from the bacterium Klebsiella oxytoca (formerly Klebsiella pneumoniae) ATCC strain 8724 is involved in the methion-

ine salvage pathway.

[4672, 4673, 1233, 804, 2852, 803, 53, 3338] **References:**

[EC 1.13.11.53 created 2006]

EC 1.13.11.54

Accepted name: acireductone dioxygenase [iron(II)-requiring]

1,2-dihydroxy-5-(methylsulfanyl)pent-1-en-3-one + $O_2 = 4$ -(methylsulfanyl)-2-oxobutanoate + for-**Reaction:**

mate

Other name(s): ARD'; 2-hydroxy-3-keto-5-thiomethylpent-1-ene dioxygenase (ambiguous); acireductone dioxyge-

nase (ambiguous); E-2'; E-3 dioxygenase; 1,2-dihydroxy-5-(methylthio)pent-1-en-3-one:oxygen oxi-

doreductase (formate-forming)

Systematic name: 1,2-dihydroxy-5-(methylsulfanyl)pent-1-en-3-one:oxygen oxidoreductase (formate-forming)

Requires iron(II). If Ni²⁺ is bound instead of iron(II), the reaction catalysed by EC 1.13.11.53, acire-**Comments:**

ductone 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: [4672, 4673, 1233, 804, 2852, 803, 53, 3338]

[EC 1.13.11.54 created 2006]

EC 1.13.11.55

Accepted name: sulfur oxygenase/reductase

 $4 \text{ sulfur} + 4 \text{ H}_2\text{O} + \text{O}_2 = 2 \text{ hydrogen sulfide} + 2 \text{ sulfite}$ **Reaction:** 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 none-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 nonenzymically by a reaction between sulfite and sulfur [2155]. 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: [2155, 2156, 4117, 4380]

[EC 1.13.11.55 created 2006]

EC 1.13.11.56

Accepted name: 1,2-dihydroxynaphthalene dioxygenase

naphthalene-1,2-diol + O_2 = 2-hydroxy-2*H*-chromene-2-carboxylate Reaction:

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 Fe^{2+} .

References: [2275, 2051, 3258]

[EC 1.13.11.56 created 2010, modified 2010]

EC 1.13.11.57

Accepted name: gallate dioxygenase

> 3,4,5-trihydroxybenzoate + $O_2 = (1E)$ -4-oxobut-1-ene-1,2,4-tricarboxylate **Reaction:**

Other name(s): GalA; gallate:oxygen oxidoreductase

Systematic name: 3,4,5-trihydroxybenzoate:oxygen oxidoreductase

Comments: Contains non-heme Fe^{2+} . The enzyme is a ring-cleavage dioxygenase that acts specifically on 3,4,5-

trihydroxybenzoate to produce the keto-tautomer of 4-oxalomesaconate [3094, 3093].

References: [3094, 3093]

[EC 1.13.11.57 created 2011]

EC 1.13.11.58

Accepted name: linoleate 9S-lipoxygenase

Reaction: linoleate + $O_2 = (9S, 10E, 12Z)$ -9-hydroperoxy-10,12-octadecadienoate

Other name(s): 9-lipoxygenase; 9S-lipoxygenase; linoleate 9-lipoxygenase; LOX1 (gene name); 9S-LOX

Systematic name: linoleate:oxygen 9S-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 [213]. EC 1.13.11.12 (linoleate 13*S*-lipoxygenase) catalyses a similar reaction at another

position of these fatty acids.

References: [4430, 366, 99, 213]

[EC 1.13.11.58 created 2011]

EC 1.13.11.59

Accepted name: torulene dioxygenase

Reaction: torulene + $O_2 = 4'$ -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 neccessary for this reaction.

References: [3368, 3624, 1066]

[EC 1.13.11.59 created 2011]

EC 1.13.11.60

Accepted name: linoleate 8*R*-lipoxygenase

Reaction: linoleate + $O_2 = (8R, 9Z, 12Z)$ -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 [450, 4083]. 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 (8R,9Z,12Z)-8-hydroperoxyoctadeca-9,12-dienoate, which is subsequently isomerized by the C-terminal *P*-450 heme thiolate domain to (5S,8R,9Z,12Z)-5,8-dihydroxyoctadeca-9,12-dienoate (*cf.* EC 5.4.4.5, 9,12-octadecadienoate 8-hydroperoxide 8*R*-isomerase) [450]. The bifunctional enzyme from *Gaeumannomyces graminis* also catalyses the oxidation of linoleic acid to (8R,9Z,12Z)-8-hydroperoxyoctadeca-9,12-dienoate, but its second domain isomerizes it to (7S,8S,9Z,12Z)-5,8-dihydroxyoctadeca-9,12-dienoate (*cf.* EC 5.4.4.6, 9,12-

octadecadienoate 8-hydroperoxide 8S-isomerase) [4083].

References: [450, 1492, 1278, 4083]

[EC 1.13.11.60 created 2011]

Accepted name: linolenate 9*R*-lipoxygenase

Reaction: α -linolenate + O₂ = (9R, 10E, 12Z, 15Z)-9-hydroperoxyoctadeca-10,12,15-trienoate

Other name(s): NspLOX; (9R)-LOX; linoleate 9R-dioxygenase Systematic name: α -linolenate:oxygen (9R)-oxidoreductase

Comments: In cyanobacteria the enzyme is involved in oxylipin biosynthesis. The enzyme also converts linoleate

to (9R,10E,12Z)-9-hydroperoxyoctadeca-10,12-dienoate.

References: [1908, 100, 2342]

[EC 1.13.11.61 created 2011]

EC 1.13.11.62

Accepted name: linoleate 10*R*-lipoxygenase

Reaction: linoleate + $O_2 = (8E, 10R, 12Z)-10$ -hydroperoxy-8,12-octadecadienoate

Other name(s): 10R-DOX; (10R)-dioxygenase; 10R-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: [1279, 1907]

[EC 1.13.11.62 created 2011]

EC 1.13.11.63

Accepted name: β-carotene 15,15'-dioxygenase **Reaction:** β-carotene + $O_2 = 2$ *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 [870]. 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 C_{30} is mandatory [2116]. 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

[2115, 2117].

References: [1364, 1363, 4757, 2424, 2116, 2115, 2117, 870]

[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 + O_2 = 2-oxo-3-(5-oxofuran-2-ylidene)propanoate + nitrite (overall reaction)

(1a) 5-nitrosalicylate + O_2 = 4-nitro-6-oxohepta-2,4-dienedioate

(1b) 4-nitro-6-oxohepta-2,4-dienedioate = 2-oxo-3-(5-oxofuran-2-ylidene)propanoate + nitrite (spon-

taneous)

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 path-

way 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 lactoniza-

tion, with concurrent elimination of the nitro group.

References: [3408, 3409]

[EC 1.13.11.64 created 2012]

EC 1.13.11.65

Accepted name: carotenoid isomerooxygenase

Reaction: zeaxanthin + $O_2 = (3R)-11$ -cis-3-hydroxyretinal + (3R)-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 caroteoids 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: [3124]

[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 + $O_2 = (2Z,4E)$ -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 pro-

duce the corresponding 4-hydroxymuconic semialdehydes.

References: [2841, 2871, 3841]

[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 + $O_2 = 14'$ -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 (3E,5E)-7-hydroxy-6-methylhepta-3,5-dien-2-one.

References: [932]

[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 + O_2 = 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 Fe^{2+} . The enzyme participates in a pathway leading to biosynthesis of strigolactones, plant

hormones involved in promotion of symbiotic associations known as arbuscular mycorrhiza.

References: [388, 63]

[EC 1.13.11.68 created 2012]

Accepted name: carlactone synthase

Reaction: 9-cis-10'-apo- β -carotenal + 2 O₂ = carlactone + (2E,4E,6E)-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: [3969, 3767, 63]

[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 + O_2 = 13-apo-β-carotenone + (2E,4E,6E)-4-methylocta-2,4,6-trienedial **Other name(s):** CCD8 (gene name); MAX4 (gene name); NCED8 (gene name); all-trans-10'-apo-β-carotenal: O_2 oxi-

doreductase (13,14-cleaving)

Systematic name: *all-trans*-10′-apo-β-carotenal:oxygen oxidoreductase (13,14-cleaving)

Comments: Requires Fe^{2+} . The enzyme from the plant *Arabidopsis thaliana* also catalyses EC 1.13.11.69, carlac-

tone synthase, 10-fold faster.

References: [3767]

[EC 1.13.11.70 created 2012]

EC 1.13.11.71

Accepted name: carotenoid-9',10'-cleaving dioxygenase

Reaction: all-trans-β-carotene + $O_2 = all$ -trans-10'-apo-β-carotenal + β-ionone

Other name(s): BCO₂ (gene name); β-carotene 9',10'-monooxygenase (misleading); all-trans-β-carotene:O₂ oxidore-

ductase (9',10'-cleaving)

Systematic name: *all-trans*-β-carotene:oxygen oxidoreductase (9',10'-cleaving)

Comments: Requires Fe^{2+} . The enzyme catalyses the asymmetric oxidative cleavage of carotenoids. The mam-

malian enzyme can also cleave all-trans-lycopene.

References: [2087, 2500]

[EC 1.13.11.71 created 2012]

EC 1.13.11.72

Accepted name: 2-hydroxyethylphosphonate dioxygenase

Reaction: 2-hydroxyethylphosphonate + O_2 = hydroxymethylphosphonate + formate

Other name(s): HEPD; *phpD* (gene name); 2-hydroxyethylphosphonate:O₂ 1,2-oxidoreductase (hydroxymethylphosphonate)

phonate forming)

Systematic name: 2-hydroxyethylphosphonate:oxygen 1,2-oxidoreductase (hydroxymethylphosphonate-forming)

Comments: Requires non-heme-iron(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: [693, 4612, 3274]

[EC 1.13.11.72 created 2012]

EC 1.13.11.73

Accepted name: methylphosphonate synthase

Reaction: 2-hydroxyethylphosphonate + O_2 = methylphosphonate + HCO_3

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: [2781]

[EC 1.13.11.73 created 2012]

EC 1.13.11.74

Accepted name: 2-aminophenol 1,6-dioxygenase

Reaction: 2-aminophenol + O_2 = 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 [4182]. 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 [4675].

References: [4182, 4675, 2441]

[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 + (2E,4E,6E)-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 Fe^{2+} -4His arrangement. The enzyme is involved in retinal biosynthesis in bacteria

[2157].

References: [3591, 2157]

[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 + O_2 = 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: [4675]

[EC 1.13.11.76 created 2013]

EC 1.13.11.77

Accepted name: oleate 10*S*-lipoxygenase

Reaction: (1) oleate + O_2 = (8*E*,10*S*)-10-hydroperoxyoctadeca-8-enoate

(2) linoleate + O_2 = (8*E*,10*S*,12*Z*)-10-hydroperoxyoctadeca-8,12-dienoate

(3) α -linolenate + O₂ = (8E,10S,12Z,15Z)-10-hydroperoxyoctadeca-8,12,15-trienoate

Other name(s): 10S-DOX; (10S)-dioxygenase; 10S-dioxygenase

Systematic name: oleate:oxygen (10*S*)-oxidoreductase

Comments: Binds Fe^{2+} . The enzyme isolated from the bacterium *Pseudomonas* sp. 42A2 has similar activity with

all the three Δ^9 fatty acids. cf. EC 1.13.11.62, linoleate 10R-lipoxygenase.

References: [511]

[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: [2757, 4669]

[EC 1.13.11.78 created 2014]

EC 1.13.11.79

Accepted name: aerobic 5,6-dimethylbenzimidazole synthase

Reaction: FMNH₂ + O_2 = 5,6-dimethylbenzimidazole + D-erythrose 4-phosphate + other product(s)

Other name(s): BluB; flavin destructase

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 B_{12} . 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 [4536]. 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: [1392, 1005, 4160, 4536, 713]

[EC 1.13.11.79 created 2010 as EC 1.14.99.40, transferred 2014 to EC 1.13.11.79, modified 2019]

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 antibi-

otic vancomycin.

References: [630, 4618, 1117]

[EC 1.13.11.80 created 2015]

EC 1.13.11.81

Accepted name: 7,8-dihydroneopterin oxygenase

Reaction: 7.8-dihydroneopterin + $O_2 = 7.8$ -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: [793]

[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 + $O_2 = 13$ -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: [2118]

[EC 1.13.11.82 created 2015]

EC 1.13.11.83

Accepted name: 4-hydroxy-3-prenylphenylpyruvate oxygenase

Reaction: 3-(4-hydroxy-3-prenylphenyl)pyruvate + $O_2 = 4-hydroxy-3-prenylmandelate + <math>CO_2$

Other name(s): CloF

Systematic name: 3-(4-hydroxy-3-prenylphenyl)pyruvate:oxygen 1,2-oxidoreductase (4-hydroxy-3-prenylmandelate-

forming)

Comments: Requires non-heme-iron(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, 4-hydroxy-3-prenylbenzoate synthase.

References: [3342]

[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 + $O_2 = 3\beta$ -hydroxy-8'-apo- β -carotenal + 3β -hydroxy- β -cyclocitral

(1b) 3β -hydroxy-8'-apo- β -carotenal + O_2 = 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: [1197, 41, 40]

 $[EC\ 1.13.11.84\ created\ 2011\ as\ EC\ 1.14.99.42,\ modified\ 2014,\ transferred\ 2017\ to\ EC\ 1.13.11.84]$

EC 1.13.11.85

Accepted name: exo-cleaving rubber dioxygenase

Reaction: cis-1,4-polyisoprene + n O₂ = n (4Z,8Z)-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 [(4Z,8Z)-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

The enzyme, studied mainly from the bacterium X anthomonas 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 X anthomonas sp. 35Y contains two c-type

cytochromes. It attacks the substrate from its end, producing a single product of 15 carbons.

References: [4338, 1898, 416, 415, 3786, 336]

[EC 1.13.11.85 created 2018]

EC 1.13.11.86

Accepted name: 5-aminosalicylate 1,2-dioxygenase

Reaction: 5-aminosalicylate + $O_2 = (2Z,4E)$ -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 iron(II). The enzyme, characterized from different bacteria, is a nonheme iron dioxygenase

in the bicupin family.

References: [4047, 4834]

[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

 $((4Z,8Z,12Z,16Z,20Z,24Z)-4,8,12,16,20,24-hexamethyl-28-oxononacosa-4,8,12,16,20,24-hexaenal), a C_{25}\ compound\ ((4Z,8Z,12Z,16Z,20Z)-4,8,12,16,20-pentamethyl-24-oxopentacosa-4,8,12,16,20-pentaenal), a C_{30}\ compound\ ((4Z,8Z,12Z,16Z)-4,8,12,16-tetramethyl-20-oxohenicosa-4,8,12,16-pentaenal), a C_{30}\ compound\ ((4Z,8Z,12Z,16Z)-4,8,12,16-pentaenal), a C_{30}\ compound\ ((4Z,8Z,12Z,16Z)-4,8,12,16-pentaenal), a C_{30}\ compound\ ((4Z,8Z,12Z,16Z)-4,8,12,16-pentaenal), a C_{30}\ compound\ ((4Z,8Z,12Z)-4,8,12,16-pentaenal), a C_{30}\ compound\ ((4Z,8Z,12Z)-4,8,12,16-pentaenal), a C_{30}\ compound\ ((4Z,8Z,12Z)-4,8,12Z)$

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 C_{20} , C_{25} , C_{30} , 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 C_{35} or smaller products into shorter fragments.

References: [4338, 1898, 416, 415, 3786, 336, 337]

[EC 1.13.11.87 created 2018]

EC 1.13.11.88

Accepted name: isoeugenol monooxygenase

Reaction: isoeugenol + O_2 = vanillin + acetaldehyde

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

Systematic name: isoeugenol:oxygen 7,8-oxidoreductase (bond-cleaving)

Comments: Contains iron(II). The enzyme, charcterised from the bacteria Pseudomonas putida and Pseudomonas

nitroreducens, catalyses the epoxidation of the double bond in the side chain of isoeugenol, followed

by a second oxygenation and cleavage of the side chain in the form of acetaldehyde.

References: [3879, 4724, 4725, 3614, 3613]

[EC 1.13.11.88 created 2019]

EC 1.13.11.89

Accepted name: (hydroxymethyl)phosphonate dioxygenase

Reaction: (hydroxymethyl)phosphonate + O_2 = formate + phosphate

Other name(s): phnZ1 (gene name)

Systematic name: (hydroxymethyl)phosphonate:oxygen 1-oxidoreductase (formate-forming)

Comments: Requires iron(II). The enzyme, characterized from the marine bacterium *Gimesia maris*, participates

in a methylphosphonate degradation pathway. It also has the activity of EC 1.13.11.78, (2-amino-1-

hydroxyethyl)phosphonate dioxygenase (glycine-forming).

References: [1265]

[EC 1.13.11.89 created 2019]

EC 1.13.11.90

Accepted name: [1-hydroxy-2-(trimethylamino)ethyl]phosphonate dioxygenase (glycine-betaine-forming) Reaction: [1-hydroxy-2-(trimethylamino)ethyl]phosphonate $+ O_2 =$ glycine betaine +phosphate

Other name(s): tmpB (gene name)

Systematic name: [(1R)-1-hydroxy-2-(trimethylamino)ethyl]phosphonate:oxygen 1R-oxidoreductase (glycine-betaine-

forming)

Comments: Requires Fe^{2+} . This bacterial enzyme is involved in a degradation pathway for [2-

(trimethylamino)ethyl]phosphonate.

References: [3437]

[EC 1.13.11.90 created 2020]

EC 1.13.11.91

Accepted name: 3-mercaptopropionate dioxygenase

Reaction: 3-sulfanylpropanoate $+ O_2 = 3$ -sulfinopropanoate

Other name(s): mdo (gene name); 3-mercaptopropionic acid dioxygenase; 3-sulfanylpropanoate dioxygenase

Systematic name: 3-sulfanylpropanoate:oxygen oxidoreductase

Comments: This bacterial enzyme contains an iron(2+) atom coordinated by three protein-derived histidines and a

Ser-His-Tyr motif. It is similar to EC 1.13.11.20, cysteine dioxygenase, and can act on L-cysteine, but

has a much higher activity with its native substrate, 3-sulfanylpropanoate.

References: [473, 966, 3318, 4231, 1097, 776, 72, 3663]

[EC 1.13.11.91 created 2020]

EC 1.13.11.92

Accepted name: fatty acid α-dioxygenase

Reaction: a fatty acid + O_2 = a (2R)-2-hydroperoxyfatty acid

Other name(s): DOX1 (gene name)

Systematic name: fatty acid:oxygen 2-oxidoreductase [(2R)-2-hydroperoxyfatty acid-forming]

Comments: Contains heme. This plant enzyme catalyses the (2R)-hydroperoxidation of fatty acids. It differs from

lipoxygenases and cyclooxygenases in that the oxygen addition does not target an unsaturated region in the fatty acid. *In vitro* the product undergoes spontaneous decarboxylation, resulting in formation of a chain-shortened aldehyde. *In vivo* the product may be reduced to a (2*R*)-2-hydroxyfatty acid. The enzyme, which is involved in responses to different abiotic and biotic stresses, has a wide substrate

range that includes both saturated and unsaturated fatty acids.

References: [45, 1490, 3625, 2187, 2524, 2764]

[EC 1.13.11.92 created 2021]

EC 1.13.11.93

Accepted name: 2-oxoadipate dioxygenase/decarboxylase

Reaction: 2-oxoadipate + $O_2 = (R)$ -2-hydroxyglutarate + CO_2

Other name(s): ydcJ (gene name)

Systematic name: 2-oxoadipate dioxygenase/carboxy lyase

Comments: The enzyme, characterized from the bacterium *Pseudomonas putida*, is involved in an L-lysine

catabolic pathway. Contains Fe(II).

References: [4274]

[EC 1.13.11.93 created 2022]

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 + O_2 = 4-guanidinobutanamide + CO_2 + H_2O

Other name(s): arginine monooxygenase; arginine decarboxylase (incorrect); arginine oxygenase (decarboxylating);

arginine decarboxy-oxidase

Systematic name: L-arginine:oxygen 2-oxidoreductase (decarboxylating)

Comments: A flavoprotein. Also acts on canavanine and homoarginine.

References: [3173, 4260, 4261]

[EC 1.13.12.1 created 1972]

EC 1.13.12.2

Accepted name: lysine 2-monooxygenase

Reaction: L-lysine + O_2 = 5-aminopentanamide + CO_2 + H_2O

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: [3002, 4177, 4178]

[EC 1.13.12.2 created 1972]

EC 1.13.12.3

Accepted name: tryptophan 2-monooxygenase

Reaction: L-tryptophan + O_2 = (indol-3-yl)acetamide + CO_2 + H_2O

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: [2243, 2295, 1776, 3181, 1043]

[EC 1.13.12.3 created 1972]

EC 1.13.12.4

Accepted name: lactate 2-monooxygenase

Reaction: (S)-lactate + O_2 = acetate + CO_2 + H_2O

Other name(s): lactate oxidative decarboxylase; lactate oxidase; lactic oxygenase; lactate oxygenase; lactate oxidase;

L-lactate monooxygenase; lactate monooxygenase; L-lactate-2-monooxygenase

Systematic name: (S)-lactate:oxygen 2-oxidoreductase (decarboxylating)

Comments: A flavoprotein (FMN).

References: [1575, 4132]

[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 $h + O_2 =$ excited coelenteramide h monoanion + CO_2 (over-all reaction)

(1a) coelenterazine $h + O_2 = coelenterazine h dioxetanone$

(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: [738, 1721, 94, 3876, 606, 2541, 2531]

[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 + O_2 = oxidized Cypridina luciferin + CO_2 + hv

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: [737, 1997, 2128, 4341]

[EC 1.13.12.6 created 1976, modified 1982]

EC 1.13.12.7

Accepted name: firefly luciferase

Reaction: D-firefly luciferin + O_2 + ATP = firefly oxyluciferin + CO_2 + AMP + diphosphate + hv

Other name(s): Photinus-luciferin 4-monooxygenase (ATP-hydrolysing); luciferase (firefly luciferin); Photinus lu-

ciferin 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 biolouminescence. 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: [1394, 4601, 1714, 4602, 2227, 856, 2980, 4126]

[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 + O_2 = oxidized Watasenia luciferin + CO_2 + hv

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: [1816]

[EC 1.13.12.8 created 1982]

EC 1.13.12.9

Accepted name: phenylalanine 2-monooxygenase

Reaction: L-phenylalanine + O_2 = 2-phenylacetamide + CO_2 + H_2O

Other name(s): L-phenylalanine oxidase (deaminating and decarboxylating); phenylalanine (deaminating, decarboxy-

lating)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:ipi L-

phenylalanine + O_2 + H_2O = 3-phenylpyruvic acid + ammonia + H_2O_2 ; p_i , a reaction similar to that

of EC 1.4.3.2, L-amino-acid oxidase.

References: [2250, 2252, 2251, 2253]

[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 + O_2 = oxidized Oplophorus luciferin + CO_2 + hv

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 bisdeoxycoe-

lenterazine being good substrates.

References: [3878, 1818]

[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 L-dopa + O_2 = 2 3,4-dihydroxyphenylpyruvate + 2 NH₃

Other name(s): 3,4-dihydroxy-L-phenylalanine: oxidative deaminase; oxidative deaminase; DOPA oxidative deami-

nase; 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 [3449]), 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: [3449]

[EC 1.13.12.15 created 2008]

EC 1.13.12.16

Accepted name: nitronate monooxygenase

> Reaction: ethylnitronate + O_2 = acetaldehyde + nitrite + other products

Other name(s): NMO; 2-nitropropane dioxygenase (incorrect) Systematic name: nitronate:oxygen 2-oxidoreductase (nitrite-forming)

Previously classified as 2-nitropropane dioxygenase (EC 1.13.11.32), but it is now recognized that this **Comments:**

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 en-

zyme from N. crassa can also utilize neutral nitroalkanes, but with lower activity.

References: [1164, 1459, 1250, 1163]

[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 O₂ + 4 NADH + 4 H⁺ = dichloroarcyriaflavin A + 2 CO₂ + 6 H₂O + 4

> > NAD^{+}

Systematic name: dichlorochromopyrrolate, NADH: oxygen 2,5-oxidoreductase (dichloroarcyriaflavin A-forming)

The conversion of dichlorochromopyrrolate to dichloroarcyriaflavin A is a complex process that in-**Comments:**

volves 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 [2627]. 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 [1744]. The enzymes are similar, but not identical, to StaP and StaC, which

are involved in the synthesis of staurosporine [3652].

References: [2627, 1744, 3652]

[EC 1.13.12.17 created 2010]

EC 1.13.12.18

Accepted name: dinoflagellate luciferase

> dinoflagellate luciferin + O_2 = oxidized dinoflagellate luciferin + $H_2O + hv$ **Reaction:**

(dinoflagellate luciferin) luciferase; Gonyaulax luciferase Other name(s): **Systematic name:** dinoflagellate-luciferin:oxygen 13²-oxidoreductase

Comments: A luciferase from dinoflagellates 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: [985, 2902, 178, 2448, 2901, 3753]

[EC 1.13.12.18 created 2011]

EC 1.13.12.19

Accepted name: 2-oxoglutarate dioxygenase (ethene-forming) **Reaction:** 2-oxoglutarate $+ O_2 =$ ethene $+ 3 CO_2 + H_2O$

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

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: [2954, 1222, 1221]

[EC 1.13.12.19 created 2011]

EC 1.13.12.20

Accepted name: noranthrone monooxygenase

Reaction: norsolorinic acid anthrone + O_2 = norsolorinic acid + H_2O

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: [1026]

[EC 1.13.12.20 created 2013]

EC 1.13.12.21

Accepted name: tetracenomycin-F1 monooxygenase

Reaction: tetracenomycin F1 + O_2 = tetracenomycin D3 + H_2O

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 bac-

terium Streptomyces glaucescens.

References: [3838]

[EC 1.13.12.21 created 2013]

EC 1.13.12.22

Accepted name: deoxynogalonate monooxygenase

Reaction: deoxynogalonate + O_2 = nogalonate + H_2O

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; deoxynogalonate oxidoreductase

Systematic name: deoxynogalonate:oxygen oxidoreductase

Comments: The enzyme, characterized from the bacterium *Streptomyces nogalater*, is involved in the biosynthesis

of the aromatic polyketide nogalamycin.

References: [2241, 1416]

[EC 1.13.12.22 created 2015]

EC 1.13.12.23

Accepted name: 4-hydroxy-3-prenylbenzoate synthase

Reaction: 4-hydroxy-3-prenylmandelate + O_2 = 4-hydroxy-3-prenylbenzoate + CO_2 + H_2O

Other name(s): CloR; *novR* (gene name)

Systematic name: 4-hydroxy-3-prenylmandelate:oxygen oxidoreductase (4-hydroxy-3-prenylbenzoate forming)

Comments: Isolated from the bacterium *Streptomyces roseochromogenes* DS 12976. A bifunctional enzyme in-

volved in clorobiocin biosynthesis that also catalyses the activity of EC 1.13.11.83, 4-hydroxy-3-

prenylphenylpyruvate oxygenase.

References: [3342]

[EC 1.13.12.23 created 2017]

EC 1.13.12.24

Accepted name: calcium-regulated photoprotein

Reaction: [apoaequorin] + coelenterazine + O_2 + 3 Ca^{2+} = [excited state blue fluorescent protein] + CO_2 (over-

all reaction)

(1a) [apoaequorin] + coelenterazine = [apoaequorin containing coelenterazine]

(1b) [apoaequorin containing coelenterazine] + O_2 = [aequorin] (1c) [aequorin] + 3 Ca^{2+} = [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; mitro-

comin; 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 jelly-fish *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: [3874, 2892, 1817, 1594, 878]

[EC 1.13.12.24 created 2018]

EC 1.13.99 Miscellaneous

EC 1.13.99.1

Accepted name: inositol oxygenase

Reaction: myo-inositol + O_2 = D-glucuronate + H_2O

Other name(s): *meso*-inositol oxygenase; *myo*-inositol oxygenase; MOO

Systematic name: *myo*-inositol:oxygen oxidoreductase

Comments: An iron protein. **References:** [604, 3472, 134]

[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 + O_2 = (indol-3-yl)glycolaldehyde + CO_2 + NH_3

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: [3536, 4173]

[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. Subsubclasses 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 1.14.99 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 11β-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 17α-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 6β-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 + $O_2 = 3$ -hydroxy-4-trimethylammoniobutanoate +

succinate $+ CO_2$

Other name(s): α-butyrobetaine hydroxylase; γ-butyrobetaine hydroxylase; butyrobetaine hydroxylase Systematic name: 4-trimethylammoniobutanoate,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)

Comments: Requires Fe^{2+} and ascorbate.

References: [2501]

[EC 1.14.11.1 created 1972]

Accepted name: procollagen-proline 4-dioxygenase

Reaction: procollagen L-proline + 2-oxoglutarate + O₂ = procollagen *trans*-4-hydroxy-L-proline + succinate +

 CO_2

Other name(s): P4HA (gene name); P4HB (gene name); protocollagen hydroxylase; proline hydroxylase; proline,2-

oxoglutarate 4-dioxygenase; collagen proline hydroxylase; hydroxylase, collagen proline; peptidyl proline hydroxylase; proline protocollagen hydroxylase; proline, 2-oxoglutarate dioxygenase; prolyl hydroxylase; protocollagen dioxygenase; protocollagen hydroxylase; protocollagen proline 4-hydroxylase; protocollagen proline dioxygenase; protocollagen proline hydroxylase; protocollagen 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 retic-

ulum, 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: [1777, 2144, 2142, 297, 1924, 2333, 2953, 2143]

[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 + O_2 = uridine + succinate + CO_2

Other name(s): deoxyuridine 2'-dioxygenase; deoxyuridine 2'-hydroxylase; pyrimidine deoxyribonucleoside 2'-

hydroxylase; thymidine 2'-dioxygenase; thymidine 2'-hydroxylase; thymidine 2-oxoglutarate dioxy-

genase; thymidine dioxygenase

Systematic name: 2'-deoxyuridine,2-oxoglutarate:oxygen oxidoreductase (2'-hydroxylating)

Comments: Requires iron(II) and ascorbate. Also acts on thymidine. cf. EC 1.14.11.10, pyrimidine-

deoxynucleoside 1'-dioxygenase.

References: [211, 4076, 4547]

[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 + O_2 = [procollagen]-(2S,5R)-5-hydroxy-L-lysine + succinate

 $+ CO_2$

Other name(s): lysine hydroxylase; lysine,2-oxoglutarate 5-dioxygenase; protocollagen lysine dioxygenase; col-

lagen lysine hydroxylase; lysine-2-oxoglutarate dioxygenase; lysyl hydroxylase; lysylprotocollagen dioxygenase; protocollagen lysyl hydroxylase; peptidyl-lysine, 2-oxoglutarate: oxygen oxidoreductase; peptidyllysine, 2-oxoglutarate:oxygen 5-oxidoreductase; protocollagen 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 Fe^{2+} and ascorbate. **References:** [1567, 3510, 3394, 3395]

[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]

Accepted name: thymine dioxygenase

Reaction: thymine + 2-oxoglutarate + O_2 = 5-hydroxymethyluracil + succinate + CO_2

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: [210, 2511, 4547]

[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 + O_2 = [procollagen]-trans-3-hydroxy-L-proline + succinate

+ CO₂

Other name(s): proline,2-oxoglutarate 3-dioxygenase; prolyl 3-hydroxylase; protocollagen 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: [3527, 3528, 4476, 4282]

[EC 1.14.11.7 created 1981, modified 1983, modified 2017]

EC 1.14.11.8

Accepted name: trimethyllysine dioxygenase

Reaction: N^6, N^6, N^6 -trimethyl-L-lysine + 2-oxoglutarate + $O_2 = (3S)$ -3-hydroxy- N^6, N^6, N^6 -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: N^6, N^6, N^6 -trimethyl-L-lysine,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)

Comments: Requires Fe^{2+} and ascorbate. **References:** [1771, 4238, 2422, 3476]

[EC 1.14.11.8 created 1983]

EC 1.14.11.9

Accepted name: flavanone 3-dioxygenase

Reaction: a (2S)-flavan-4-one + 2-oxoglutarate + O_2 = a (2R,3R)-dihydroflavonol + succinate + CO_2

 $\textbf{Other name}(s) \textbf{:} \quad \text{naringenin 3-hydroxylase; flavanone 3-hydro$

(2S)-flavanone 3-hydroxylase; naringenin,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating);

F₃H; flavanone,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)

Systematic name: (2S)-flavan-4-one,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)

Comments: Requires Fe^{2+} and ascorbate. This plant enzyme catalyses an early step in the flavonoid biosynthesis

pathway, leading to the production of flavanols and anthocyanins. Substrates include (2S)-naringenin, (2S)-eriodictyol, (2S)-dihydrotricetin and (2S)-pinocembrin. Some enzymes are bifuctional and also

catalyse EC 1.14.20.6, flavonol synthase.

References: [1140, 611, 3284, 4584, 1917, 3840]

[EC 1.14.11.9 created 1983, modified 1989, modified 2004, modified 2016]

Accepted name: pyrimidine-deoxynucleoside 1'-dioxygenase

Reaction: 2'-deoxyuridine + 2-oxoglutarate + O_2 = uracil + 2-deoxyribonolactone + succinate + CO_2

Other name(s): deoxyuridine-uridine 1'-dioxygenase

Systematic name: 2'-deoxyuridine,2-oxoglutarate:oxygen oxidoreductase (1'-hydroxylating)

Comments: Requires iron(II) and ascorbate. *cf.* EC 1.14.11.3, pyrimidine-deoxynucleoside 2'-dioxygenase.

References: [4076]

[EC 1.14.11.10 created 1989, modified 2002]

EC 1.14.11.11

Accepted name: hyoscyamine (6S)-dioxygenase

Reaction: L-hyoscyamine + 2-oxoglutarate + O_2 = (6*S*)-hydroxyhyoscyamine + succinate + CO_2 hyoscyamine 6β-hydroxylase; hyoscyamine 6β-dioxygenase; hyoscyamine 6-hydroxylase

Systematic name: L-hyoscyamine,2-oxoglutarate:oxygen oxidoreductase [(6S)-hydroxylating]

Comments: Requires Fe^{2+} and ascorbate.

References: [1551]

[EC 1.14.11.11 created 1989]

EC 1.14.11.12

Accepted name: gibberellin-44 dioxygenase

Reaction: gibberellin 44 + 2-oxoglutarate $+ O_2$ = gibberellin 19 + succinate $+ CO_2$

Other name(s): oxygenase, gibberellin A44 oxidase; (gibberellin-44), 2-oxoglutarate:oxygen oxidoreductase

Systematic name: (gibberellin-44),2-oxoglutarate:oxygen oxidoreductase

Comments: Requires Fe^{2+} .

References: [1327]

[EC 1.14.11.12 created 1990]

EC 1.14.11.13

Accepted name: gibberellin 2β-dioxygenase

Reaction: gibberellin 1 + 2-oxoglutarate + $O_2 = 2\beta$ -hydroxygibberellin 1 + succinate + CO_2

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: [3947]

[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 $+ O_2$ = gibberellin 1 + succinate $+ CO_2$

Other name(s): gibberellin 3β-hydroxylase; (gibberrellin-20),2-oxoglutarate: oxygen oxidoreductase (3β-

hydroxylating)

Systematic name: (gibberellin-20),2-oxoglutarate:oxygen oxidoreductase (3β-hydroxylating)

Comments: Requires Fe^{2+} and ascorbate.

References: [2317]

[EC 1.14.11.15 created 1992]

Accepted name: peptide-aspartate β-dioxygenase

Reaction: peptide-L-aspartate + 2-oxoglutarate + O_2 = peptide-3-hydroxy-L-aspartate + succinate + CO_2

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: [1419]

[EC 1.14.11.16 created 1992]

EC 1.14.11.17

Accepted name: taurine dioxygenase

Reaction: taurine + 2-oxoglutarate + O_2 = sulfite + aminoacetaldehyde + succinate + CO_2 **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-dioxoisoindolin-2-yl)ethanesulfonate, but at lower rates.

References: [1027]

[EC 1.14.11.17 created 2000]

EC 1.14.11.18

Accepted name: phytanoyl-CoA dioxygenase

Reaction: phytanoyl-CoA + 2-oxoglutarate + O_2 = 2-hydroxyphytanoyl-CoA + succinate + CO_2

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: [1886, 1887, 1888, 2800, 2799]

[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

Systematic name:

Accepted name: deacetoxyvindoline 4-hydroxylase

Reaction: deacetoxyvindoline + 2-oxoglutarate + O_2 = deacetylvindoline + succinate + CO_2 desacetoxyvindoline 4-hydroxylase; desacetyoxyvindoline-17-hydroxylase; D17H; desacetoxyvindoline,2-oxoglutarate:oxygen oxidoreductase (4β-hydroxylating)

deacetoxyvindoline,2-oxoglutarate:oxygen oxidoreductase (4β-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: [560, 561, 4426]

[EC 1.14.11.20 created 2002, modified 2005]

EC 1.14.11.21

Accepted name: clavaminate synthase

Reaction: (1) deoxyamidinoproclavaminate + 2-oxoglutarate + O_2 = amidinoproclavaminate + succinate + CO_2

(2) proclavaminate + 2-oxoglutarate + O_2 = dihydroclavaminate + succinate + CO_2 + H_2O

(3) dihydroclavaminate + 2-oxoglutarate + O_2 = clavaminate + succinate + CO_2 + H_2O

Other name(s): clavaminate synthase 2; clavaminic acid synthase

Systematic name: deoxyamidinoproclavaminate,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)

Comments: Contains nonheme iron. Catalyses three separate oxidative reactions in the pathway for the biosythesis of the β -lactamase inhibitor clavulanate in *Streptomyces clavuligerus*. The first step (hydroxy-

sis 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, proclavaminate amidinohydrolase. The three reactions are all catalysed at the same nonheme

iron site.

References: [3649, 4911, 4892, 4913, 4317]

[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 + O_2 = mugineic acid + succinate + CO_2

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: [2986, 2177]

[EC 1.14.11.24 created 2005]

EC 1.14.11.25

Accepted name: mugineic-acid 3-dioxygenase

Reaction: (1) mugineic acid + 2-oxoglutarate + O_2 = 3-epihydroxymugineic acid + succinate + CO_2

(2) 2'-deoxymugineic acid + 2-oxoglutarate + O_2 = 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:** [2986, 3165]

[EC 1.14.11.25 created 2005]

EC 1.14.11.26

Accepted name: deacetoxycephalosporin-C hydroxylase

Reaction: deacetoxycephalosporin C + 2-oxoglutarate $+ O_2 =$ deacetylcephalosporin C + succinate $+ CO_2$ deacetylcephalosporin C synthase; 3'-methylcephem hydroxylase; DACS; DAOC hydroxylase; deacetylcephalosporin C synthase; 3'-methylcephem hydroxylase; deacetylcephalosporin C synthase; C s

toxycephalosporin 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 [190]. In Acremonium chrysogenum, the enzyme forms part of a bifunctional protein along with EC 1.14.20.1, deactoxycephalosporin-C synthase. It is

a separate enzyme in Streptomyces clavuligerus.

References: [956, 190, 733, 1313, 2529, 4682, 2665]

[EC 1.14.11.26 created 2005]

Accepted name: [histone H3]-dimethyl-L-lysine³⁶ demethylase

Reaction: a [histone H3]- N^6 , N^6 -dimethyl-L-lysine N^6 + 2 2-oxoglutarate + 2 N^6 = a [histone H3]-L-lysine N^6 + 2

succinate + 2 formaldehyde + 2 CO₂ (overall reaction)

(1a) a [histone H3]- N^6 , N^6 -dimethyl-L-lysine³⁶ + 2-oxoglutarate + O₂ = a [histone H3]- N^6 -methyl-L-

lysine³⁶ + succinate + formaldehyde + CO₂

(1b) a [histone H3]- N^6 -methyl-L-lysine³⁶ + 2-oxoglutarate + O_2 = a [histone H3]-L-lysine³⁶ + succinate

+ formaldehyde + CO₂

Other name(s): KDM2A (gene name); KDM2B (gene name); JHDM1A (gene name); JHDM1B (gene name); JmjC

domain-containing histone demethylase 1A; H3-K36-specific demethylase (ambiguous); histonelysine (H3-K36) demethylase (ambiguous); histone demethylase (ambiguous); protein-6-*N*,6-*N*-dimethyl-L-lysine,2-oxoglutarate:oxygen oxidoreductase; protein-*N*⁶,*N*⁶-dimethyl-L-lysine,2-

oxoglutarate:oxygen oxidoreductase; [histone-H3]-lysine-36 demethylase

Systematic name: [histone H3]- N^6 , N^6 -dimethyl-L-lysine³⁶,2-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 Lys³⁶. Lysine residues exist in three methylation states (mono-, di- and trimethylated). The enzyme preferentially demethylates the dimethyl form of Lys³⁶ (K36me2), which is its natural substrate, to form the monomethylated and unmethylated forms of Lys³⁶. It can also demethylate monomethylated (but not the trimethylated) Lys³⁶.

cf. EC 1.14.11.69, [histone H3]-trimethyl-L-lysine³⁶ demethylase.

References: [4344]

[EC 1.14.11.27 created 2006, modified 2019]

EC 1.14.11.28

Accepted name: proline 3-hydroxylase

Reaction: L-proline + 2-oxoglutarate + $O_2 = cis$ -3-hydroxy-L-proline + succinate + CO_2

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 [2886]. 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 [2886].

References: [2885, 2886, 703]

[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 $+ O_2 =$ hypoxia-inducible factor-trans-4-

hydroxy-L-proline + succinate + CO_2

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 sub-

unit 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: [1868, 1854, 472, 1058, 3132, 2755]

[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 + O_2 = hypoxia-inducible factor-(3S)-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 hy-

poxia.

References: [2618, 1634, 826, 2338, 2206, 1038]

[EC 1.14.11.30 created 2010]

EC 1.14.11.31

Accepted name: thebaine 6-O-demethylase

Reaction: thebaine + 2-oxoglutarate $+ O_2 =$ neopinone + formaldehyde + succinate $+ CO_2$

Other name(s): T60DM

Systematic name: thebaine, 2-oxoglutarate: oxygen oxidoreductase (6-O-demethylating)

Comments: Requires Fe²⁺. Catalyses a step in morphine biosynthesis. The product neopinione spontaneously re-

arranges to the more stable codeinone. The enzyme also catalyses the 6-O-demethylation of oripavine

to morphinone, with lower efficiency.

References: [1471]

[EC 1.14.11.31 created 2010]

EC 1.14.11.32

Accepted name: codeine 3-O-demethylase

Reaction: codeine + 2-oxoglutarate + O_2 = morphine + formaldehyde + succinate + CO_2

Other name(s): codeine *O*-demethylase; CODM

Systematic name: codeine,2-oxoglutarate:oxygen oxidoreductase (3-*O*-demethylating)

Comments: Requires Fe^{2+} . Catalyses a step in morphine biosynthesis. The enzyme also catalyses the 3-O-

demethylation of thebaine to oripavine, with lower efficiency.

References: [1471]

[EC 1.14.11.32 created 2010]

EC 1.14.11.33

Accepted name: DNA oxidative demethylase

Reaction: DNA-base-CH₃ + 2-oxoglutarate + O_2 = DNA-base + formaldehyde + succinate + CO_2

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: [1081, 4791, 4790]

[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]

Accepted name: 1-deoxypentalenic acid 11β-hydroxylase

Reaction: 1-deoxypentalenate + 2-oxoglutarate + O_2 = 1-deoxy-11 β -hydroxypentalenate + succinate + CO_2

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 iron(II) and ascorbate. Isolated from the bacterium *Streptomyces avermitilis*.

Part of the pathway for pentalenolactone biosynthesis.

References: [4822, 4824]

[EC 1.14.11.35 created 2012]

EC 1.14.11.36

Accepted name: pentalenolactone F synthase

Reaction: pentalenolactone D + 2 2-oxoglutarate + 2 O_2 = pentalenolactone F + 2 succinate + 2 CO_2 + H_2O

(overall reaction)

 $(1a)\ pentalenolactone\ D+2-oxoglutarate+O_2=pentalenolactone\ E+succinate+CO_2+H_2O$

(1b) pentalenolactone E + 2-oxoglutarate + O_2 = pentalenolactone F + succinate + CO_2

Other name(s): *penD* (gene name); *pntD* (gene name); *ptlD* (gene name) **Systematic name:** pentalenolactone-D,2-oxoglutarate:oxygen oxidoreductase

Comments: Requires iron(II) and ascorbate. Isolated from the bacteria Streptomyces exfoliatus, Streptomyces are-

nae and Streptomyces avermitilis. Part of the pentalenolactone biosynthesis pathway.

References: [3801]

[EC 1.14.11.36 created 2012]

EC 1.14.11.37

Accepted name: kanamycin B dioxygenase

Reaction: kanamycin B + 2-oxoglutarate + $O_2 = 2'$ -dehydrokanamycin A + succinate + $NH_3 + CO_2$

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 in-

volved in the conversion of the aminoglycoside antibiotic kanamycin B to kanamycin A.

References: [4089]

[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 +

 H_2O + 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 [4013, 2020]. Involved in the biosynthetic pathways of

several indole alkaloids such as fumitremorgin A.

References: [4013, 2020]

[EC 1.14.11.38 created 2013]

EC 1.14.11.39

Accepted name: L-asparagine hydroxylase

Reaction: L-asparagine + 2-oxoglutarate + $O_2 = (2S,3S)$ -3-hydroxyasparagine + succinate + CO_2

Other name(s): L-asparagine 3-hydroxylase; AsnO

L-asparagine,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating) **Systematic name:**

Requires Fe²⁺. The enzyme is only able to hydroxylate free L-asparagine. It is not active toward D-**Comments:**

asparagine. The β-hydroxylated asparagine produced is incorporated at position 9 of the calciumdependent antibiotic (CDA), an 11-residue non-ribosomally synthesized acidic lipopeptide lactone.

References: [4066]

[EC 1.14.11.39 created 2013]

EC 1.14.11.40

Accepted name: enduracididine β-hydroxylase

> L-enduracididine + 2-oxoglutarate + $O_2 = (3S)$ -3-hydroxy-L-enduracididine + succinate + CO_2 Reaction:

Other name(s): MppO; L-enduracididine,2-oxoglutarate:O₂ oxidoreductase (3-hydroxylating) **Systematic name:** L-enduracididine,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)

Fe²⁺-dependent enzyme. The enzyme is involved in biosynthesis of the nonproteinogenic amino acid **Comments:**

β-hydroxyenduracididine, a component of the mannopeptimycins (cyclic glycopeptide antibiotic),

produced by Streptomyces hygroscopicus NRRL 30439.

References: [1486, 2605]

[EC 1.14.11.40 created 2013]

EC 1.14.11.41

Accepted name: L-arginine hydroxylase

Reaction: L-arginine + 2-oxoglutarate + O_2 = (3S)-3-hydroxy-L-arginine + succinate + CO_2 Other name(s): VioC (ambiguous); L-arginine,2-oxoglutarate:O2 oxidoreductase (3-hydroxylating)

Systematic name: L-arginine,2-oxoglutarate:oxygen oxidoreductase (3-hydroxylating)

Fe²⁺-dependent enzyme. The enzyme is involved in the biosynthesis of the cyclic pentapeptide antibi-**Comments:**

otic 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: [1957, 1621]

[EC 1.14.11.41 created 2013]

EC 1.14.11.42

Accepted name:

tRNA Phe (7-(3-amino-3-carboxypropyl)wyosine 37 - C^2)-hydroxylase 7-(3-amino-3-carboxypropyl)wyosine 37 in tRNA Phe + 2-oxoglutarate + O₂ = 7-(2-hydroxy-3-amino-3-carboxypropyl) **Reaction:**

3-carboxypropyl)wyosine³⁷ in tRNA^{Phe} + succinate + CO₂

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

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

hydroxylating)

Requires Fe^{2+} . The enzyme is not active with wybutosine. **Comments:**

References: [3099, 2017]

[EC 1.14.11.42 created 2013]

EC 1.14.11.43

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

> (1) (S)-2-(4-chloro-2-methylphenoxy)propanoate + 2-oxoglutarate + O_2 = 4-chloro-2-methylphenol + **Reaction:**

pyruvate + succinate + CO_2

(2) (S)-(2,4-dichlorophenoxy)propanoate + 2-oxoglutarate + O_2 = 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 [4595, 2928].

References: [4595, 2928, 2929]

[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 + O_2 = 4-chloro-2-methylphenol

+ pyruvate + succinate + CO₂

(2) (R)-(2,4-dichlorophenoxy)propanoate + 2-oxoglutarate + O_2 = 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 [4595, 2928].

References: [4595, 2928, 2929]

[EC 1.14.11.44 created 2013]

EC 1.14.11.45

Accepted name: L-isoleucine 4-hydroxylase

Reaction: L-isoleucine + 2-oxoglutarate + $O_2 = (4S)$ -4-hydroxy-L-isoleucine + succinate + CO_2

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 hydrox-

ylation 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: [2182, 1636, 1637]

[EC 1.14.11.45 created 2014]

EC 1.14.11.46

Accepted name: 2-aminoethylphosphonate dioxygenase

Reaction: (2-aminoethyl)phosphonate + 2-oxoglutarate + O_2 = (2-amino-1-hydroxyethyl)phosphonate + succi-

nate + CO_2

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: [2757]

[EC 1.14.11.46 created 2014]

Accepted name: [50S ribosomal protein L16]-arginine 3-hydroxylase

Reaction: [50S ribosomal protein L16]-L-Arg⁸¹ + 2-oxoglutarate + O_2 = [50S ribosomal protein L16]-(3R)-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*R*-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: [1294, 4413]

[EC 1.14.11.47 created 2014]

EC 1.14.11.48

Accepted name: xanthine dioxygenase

Reaction: xanthine + 2-oxoglutarate $+ O_2 =$ urate + succinate $+ CO_2$ **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 xan-

thine.

References: [781, 2869, 2451]

[EC 1.14.11.48 created 2015]

EC 1.14.11.49

Accepted name: uridine-5'-phosphate dioxygenase

Reaction: UMP + 2-oxoglutarate + $O_2 = 5'$ -dehydrouridine + succinate + CO_2 + 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 C^7 furanosyl nucleosides such as A-90289s, caprazamycins, liposidomycins, muraymycins and FR-

900453. Requires Fe^{2+} .

References: [4772, 4774]

[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 N^6 -methyladenine demethylase

Reaction: N^6 -methyladenine in DNA + 2-oxoglutarate + O_2 = adenine in DNA + formaldehyde + succinate +

 CO_2

Other name(s): ALKBH1

Systematic name: DNA- N^6 -methyladenosine,2-oxoglutarate:oxygen oxidoreductase (formaldehyde-forming)

Comments: Contains iron(II). Catalyses oxidative demethylation of DNA N^6 -methyladenine, a prevalent modifi-

cation in LINE-1 transposons, which are specifically enriched on the human X chromosome.

References: [4680]

[EC 1.14.11.51 created 2016]

Accepted name: validamycin A dioxygenase

Reaction: validamycin A + 2-oxoglutarate + O_2 = validamycin B + succinate + CO_2

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 hygroscopicus* subsp. *limoneus*. Re-

quires Fe²⁺.

References: [71]

[EC 1.14.11.52 created 2016]

EC 1.14.11.53

Accepted name: mRNA N^6 -methyladenine demethylase

Reaction: N^6 -methyladenine in mRNA + 2-oxoglutarate + O_2 = 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 N^6 -methyladenine. The FTO enzyme from human can also demethylate N^3 -methylthymine from single stranded DNA and N^3 -

methyluridine from single stranded RNA [1914, 1502] with low activity [1913].

References: [1914, 1502, 1913, 4908, 1099, 4703, 42]

[EC 1.14.11.53 created 2016]

EC 1.14.11.54

Accepted name: mRNA N^1 -methyladenine demethylase

Reaction: N^1 -methyladenine in mRNA + 2-oxoglutarate + O_2 = adenine in mRNA + formaldehyde + succinate

 $+ CO_2$

Other name(s): ALKBH3

Systematic name: mRNA-N¹-methyladenine,2-oxoglutarate:oxygen oxidoreductase (formaldehyde-forming)

Comments: Contains iron(II). Catalyses oxidative demethylation of mRNA N^1 -methyladenine. The enzyme is

also involved in alkylation repair in DNA [824].

References: [4125, 824, 2461]

[EC 1.14.11.54 created 2016]

EC 1.14.11.55

Accepted name: ectoine hydroxylase

Reaction: ectoine + 2-oxoglutarate + O_2 = 5-hydroxyectoine + succinate + CO_2

Other name(s): *ectD* (gene name); ectoine dioxygenase

Systematic name: ectoine,2-oxoglutarate:oxygen oxidoreductase (5-hydroxylating)

Comments: Requires Fe^{2+} and ascorbate. The enzyme, found in bacteria, is specific for ectoine.

References: [505, 504, 3505]

[EC 1.14.11.55 created 2017]

EC 1.14.11.56

Accepted name: L-proline *cis*-4-hydroxylase

Reaction: L-proline + 2-oxoglutarate + $O_2 = cis$ -4-hydroxy-L-proline + succinate + CO_2

Systematic name: L-proline,2-oxoglutarate:oxygen oxidoreductase (*cis*-4-hydroxylating)

Comments: Requires Fe^{2+} 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: [1524]

[EC 1.14.11.56 created 2017]

EC 1.14.11.57

Accepted name: L-proline *trans*-4-hydroxylase

Reaction: L-proline + 2-oxoglutarate + O_2 = trans-4-hydroxy-L-proline + succinate + CO_2

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: [2369, 3852]

[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 + O_2 = a 2-hydroxyornithine lipid + succinate + CO_2

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: [3558, 4431]

[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 +

 $O_2 = (2R)-4$,7-dihydroxy-3-oxo-3,4-dihydro-2*H*-1,4-benzoxazin-2-yl β-D-glucopyranoside + succi-

nate + CO_2 + H_2O

Other name(s): BX6 (gene name); DIBOA-Glc dioxygenase

Systematic name: (2R)-4-hydroxy-3-oxo-3,4-dihydro-2H-1,4-benzoxazin-2-yl β-D-glucopyranoside:oxygen oxidoreduc-

tase (7-hydroxylating)

Comments: The enzyme is involved in the biosynthesis of protective and allelophatic benzoxazinoids in some

plants, most commonly from the family of Poaceae (grasses).

References: [1942]

[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 + O_2 = fraxetin + succinate + CO_2

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: [3921, 3439]

[EC 1.14.11.60 created 2018]

EC 1.14.11.61

Accepted name: feruloyl-CoA 6-hydroxylase

Reaction: trans-feruloyl-CoA + 2-oxoglutarate + O₂ = trans-6-hydroxyferuloyl-CoA + succinate + CO₂

Systematic name: feruloyl-CoA,2-oxoglutarate:oxygen oxidoreductase (6-hydroxylating)

Comments: Requires iron(II) and ascorbate. The product spontaneously undergoes *trans*-cis isomerization and

lactonization to form scopoletin, liberating CoA in the process. The enzymes from the plants *Ruta graveolens* and *Ipomoea batatas* also act on *trans*-4-coumaroyl-CoA. *cf.* EC 1.14.11.62, *trans*-4-

coumaroyl-CoA 2-hydroxylase.

References: [1980, 250, 4443, 2702]

[EC 1.14.11.61 created 2019]

EC 1.14.11.62

Accepted name: trans-4-coumaroyl-CoA 2-hydroxylase

Reaction: trans-4-coumaroyl-CoA + 2-oxoglutarate + O_2 = 2,4-dihydroxycinnamoyl-CoA + succinate + CO_2

Other name(s): Diox4 (gene name); C2'H (gene name)

Systematic name: (2*E*)-3-(4-hydroxyphenyl)prop-2-enoyl-CoA,2-oxoglutarate:oxygen oxidoreductase (2-hydroxylating)

Comments: Requires iron(II) and ascorbate. The product spontaneously undergoes *trans*-cis isomerization fol-

lowed by lactonization and cyclization, liberating CoA and forming umbelliferone. The enzymes from the plants *Ruta graveolens* and *Ipomoea batatas* also act on *trans*-feruloyl-CoA (*cf.* EC 1.14.11.61,

feruloyl-CoA 6-hydroxylase).

References: [4443, 2702]

[EC 1.14.11.62 created 2019]

EC 1.14.11.63

Accepted name: peptidyl-lysine (3*S*)-dioxygenase

Reaction: a [protein]-L-lysine + 2-oxoglutarate + O_2 = a [protein]-(3S)-3-hydroxy-L-lysine + succinate + CO_2 **Other name(s):** JMJD7 (gene name); Jumonji domain-containing protein 7; JmjC domain-containing protein 7

Systematic name: [protein]-L-lysine,2-oxoglutarate:oxygen oxidoreductase (3S-hydroxylating)

Comments: Requires iron(II). The enzyme acts on specific lysine residues in its substrates, and is stereo-specific.

The enzyme encoded by the human JMJD7 gene acts specifically on two related members of the

translation factor family of GTPases, DRG1 and DRG2.

References: [2652]

[EC 1.14.11.63 created 2019]

EC 1.14.11.64

Accepted name: glutarate dioxygenase

Reaction: glutarate + 2-oxoglutarate + $O_2 = (S)$ -2-hydroxyglutarate + succinate + CO_2

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

Systematic name: glutarate, 2-oxoglutarate:oxygen oxidoreductase ((S)-2-hydroxyglutarate-forming)

Comments: Requires iron(II). The enzyme, characterized from the bacteria Escherichia coli and Pseudomonas

putida, participates in L-lysine degradation in many bacteria. It provides an alternative route for L-

glutarate degradation that does not proceed via CoA-activated intermediates.

References: [2172, 4883]

[EC 1.14.11.64 created 2019]

EC 1.14.11.65

Accepted name: [histone H3]-dimethyl-L-lysine⁹ demethylase

Reaction: a [histone H3]- N^6 , N^6 -dimethyl-L-lysine + 2 2-oxoglutarate + 2 O_2 = a [histone H3]-L-lysine + 2

succinate + 2 formaldehyde + 2 CO₂ (overall reaction)

(1a) a [histone H3]- N^6 , N^6 -dimethyl-L-lysine + 2-oxoglutarate + O₂ = a [histone H3]- N^6 -methyl-L-

lysine⁹ + succinate + formaldehyde + CO₂

(1b) a [histone H3]- N^6 -methyl-L-lysine⁹ + 2-oxoglutarate + O_2 = a [histone H3]-L-lysine⁹ + succinate

+ formaldehyde + CO₂

Other name(s): KDM3A (gene name); KDM3B (gene name); JMJD1A (gene name); JMJD1B (gene name);

JHDM2A (gene name); JHDM2B (gene name); KDM7B (gene name); PHF8 (gene name); HR (gene

name)

Systematic name: [histone H3]- N^6 , N^6 -dimethyl-L-lysine⁹, 2-oxoglutarate: oxygen oxidoreductase

Comments: Requires iron(II). This entry describes a group of enzymes that demethylate N-methylated Lys-9

residues in the tail of the histone protein H3 (H3K9). This lysine residue can exist in three methylation states (mono-, di- and trimethylated), but this group of enzymes only act on the di- and monomethylated forms. The enzymes are dioxygenases and act by hydroxylating the methyl group, forming an unstable hemiaminal that leaves as formaldehyde. *cf.* EC 1.14.11.66, [histone H3]-trimethyl-L-

lysine⁹ demethylase.

References: [4748, 2533, 1101, 2304, 2518]

[EC 1.14.11.65 created 2019]

EC 1.14.11.66

Accepted name: [histone H3]-trimethyl-L-lysine⁹ demethylase

Reaction: a [histone H3]- N^6 , N^6 , N^6 -trimethyl-L-lysine + 2 2-oxoglutarate + 2 O_2 = a [histone H3]- N^6 -methyl-

L-lysine 9 + 2 succinate + 2 formaldehyde + 2 CO₂ (overall reaction)

(1a) a [histone H3]- N^6 , N^6 , N^6 -trimethyl-L-lysine + 2-oxoglutarate + O₂ = a [histone H3]- N^6 , N^6 -

dimethyl-L-lysine⁹ + succinate + formaldehyde + CO₂

(1b) a [histone H3]- N^6 , N^6 -dimethyl-L-lysine⁹ + 2-oxoglutarate + O₂ = a [histone H3]- N^6 -methyl-L-

lysine⁹ + succinate + formaldehyde + CO₂

Other name(s): KDM4A (gene name); KDM4B (gene name); KDM4C (gene name); KDM4D (gene name);

JHDM3A (gene name); JMJD2 (gene name); JMJD2A (gene name); GASC1 (gene name)

Systematic name: [histone H3]- N^6 , N^6 -trimethyl-L-lysine⁹,2-oxoglutarate:oxygen oxidoreductase

Comments: Requires iron(II). This entry describes a group of enzymes that demethylate *N*-methylated Lys-9

residues in the tail of the histone protein H3 (H3K9). This lysine residue can exist in three methylation states (mono-, di- and trimethylated), but this group of enzymes only act on the the tri- and dimethylated forms. The enzymes are dioxygenases and act by hydroxylating the methyl group, forming an unstable hemiaminal that leaves as formaldehyde. *cf.* EC 1.14.11.65, [histone H3]-dimethyl-L-

lysine⁹ demethylase.

References: [707, 1133, 2158, 4600]

[EC 1.14.11.66 created 2019]

EC 1.14.11.67

Accepted name: [histone H3]-trimethyl-L-lysine⁴ demethylase

Reaction: a [histone H3]- N^6 , N^6 , N^6 -trimethyl-L-lysine + 3 2-oxoglutarate + 3 O_2 = a [histone H3]-L-lysine + 3

succinate + 3 formaldehyde + 3 CO₂ (overall reaction)

(1a) a [histone H3]- N^6 , N^6 -trimethyl-L-lysine⁴ + 2-oxoglutarate + O₂ = a [histone H3]- N^6 , N^6 -

dimethyl-L-lysine 4 + succinate + formaldehyde + CO_2

(1b) a [histone H3]- N^6 , N^6 -dimethyl-L-lysine⁴ + 2-oxoglutarate + O₂ = a [histone H3]- N^6 -methyl-L-

lysine⁴ + succinate + formaldehyde + CO₂

(1c) a [histone H3]- N^6 -methyl-L-lysine⁴ + 2-oxoglutarate + O_2 = a [histone H3]-L-lysine⁴ + succinate

+ formaldehyde + CO₂

Other name(s): KDM5A (gene name); KDM5B (gene name); KDM5C (gene name); KDM5D (gene name);

JARID1A (gene name)

Systematic name: [histone H3]- N^6 , N^6 -trimethyl-L-lysine⁴,2-oxoglutarate:oxygen oxidoreductase

Comments: Requires iron(II). This entry describes a group of enzymes that demethylate N-methylated L-lysine

residues at position 4 of histone H3 (H3K4). The enzymes are dioxygenases and act by hydroxylating the methyl group, forming an unstable hemiaminal that leaves as formaldehyde. They can act on tri-,

di-, and mono-methylated forms.

References: [3812, 2159, 1861, 684]

[EC 1.14.11.67 created 2019]

EC 1.14.11.68

Accepted name: [histone H3]-trimethyl-L-lysine²⁷ demethylase

Reaction: a [histone H3]- N^6 , N^6 , N^6 -trimethyl-L-lysine²⁷ + 2 2-oxoglutarate + 2 O₂ = a [histone H3]- N^6 -methyl-

L-lysine²⁷ + $\mathbf{2}$ succinate + $\mathbf{2}$ formaldehyde + $\mathbf{2}$ CO₂ (overall reaction)

(1a) a [histone H3]- N^6 , N^6 -trimethyl-L-lysine²⁷ + 2-oxoglutarate + O₂ = a [histone H3]- N^6 , N^6 -

dimethyl-L-lysine²⁷ + succinate + formaldehyde + CO₂

(1b) a [histone H3]- N^6 , N^6 -dimethyl-L-lysine²⁷ + 2-oxoglutarate + O₂ = a [histone H3]- N^6 -methyl-L-

lysine²⁷ + succinate + formaldehyde + CO₂

Other name(s): KDM6A (gene name); KDM6C (gene name); UTX (gene name); UTY (gene name); JMJD3 (gene

name)

Systematic name: [histone H3]- N^6 , N^6 , N^6 -trimethyl-L-lysine²⁷, 2-oxoglutarate:oxygen oxidoreductase

Comments: Requires iron(II). This entry describes a group of enzymes that demethylate N-methylated L-lysine

residues at position 27 of histone H3 (H3K27). The enzymes are dioxygenases and act by hydroxylating the methyl group, forming an unstable hemiaminal that leaves as formaldehyde. They can act on

tri- and di-methylated forms, but have no activity with the mono-methylated form.

References: [3659, 1707, 2336, 2389, 4695]

[EC 1.14.11.68 created 2019]

EC 1.14.11.69

Accepted name: [histone H3]-trimethyl-L-lysine³⁶ demethylase

Reaction: a [histone H3]- N^6 , N^6 , N^6 -trimethyl-L-lysine N^6 + 2 2-oxoglutarate + 2 N^6 = a [histone H3]- N^6 -methyl-

L-lysine³⁶ + 2 succinate + 2 formaldehyde + 2 CO₂ (overall reaction)

(1a) a [histone H3]- N^6 , N^6 , N^6 -trimethyl-L-lysine³⁶ + 2-oxoglutarate + O₂ = a [histone H3]- N^6 , N^6 -

dimethyl-L-lysine 36 + succinate + formaldehyde + CO_2

(1b) a [histone H3]- N^6 , N^6 -dimethyl-L-lysine³⁶ + 2-oxoglutarate + O₂ = a [histone H3]- N^6 -methyl-L-

lysine³⁶ + succinate + formaldehyde + CO₂

Other name(s): KDM4A (gene name); KDM4B (gene name); RPH1 (gene name); JHDM3A (gene name); JHDM3B

(gene name); JMJD2A (gene name); JMJD2B (gene name)

Systematic name: [histone H3]- N^6 , N^6 , N^6 -trimethyl-L-lysine³⁶,2-oxoglutarate:oxygen oxidoreductase

Comments: Requires iron(II). This entry describes a group of enzymes that demethylate N-methylated Lys³⁶

residues in the tail of the histone protein H3 (H3K36). This lysine residue can exist in three methylation states (mono-, *di*- and trimethylated), but this group of enzymes only act on the the tri- and dimethylated forms. The enzymes are dioxygenases and act by hydroxylating the methyl group, forming an unstable hemiaminal that leaves as formaldehyde. Since trimethylation of H3K36 enhances transcription, this enzyme acts as a transcription repressor. The enzymes that possess this activity often also catalyse the activity of EC 1.14.11.66, [histone H3]-trimethyl-L-lysine⁹ demethylase. *cf.* EC

1.14.11.27, [histone H3]-dimethyl-L-lysine³⁶ demethylase.

References: [4600, 2158, 2108, 753, 2486, 716]

[EC 1.14.11.69 created 2019]

EC 1.14.11.70

Accepted name: 7-deoxycylindrospermopsin hydroxylase

Reaction: (1) 7-deoxycylindrospermopsin + 2-oxoglutarate + O_2 = cylindrospermopsin + succinate + CO_2

(2) 7-deoxycylindrospermopsin + 2-oxoglutarate + $O_2 = 7$ -epi-cylindrospermopsin + succinate + CO_2

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

Systematic name: 7-deoxycylindrospermopsin,2-oxoglutarate:oxygen oxidoreductase (7-hydroxylating)

Comments: Requires iron(II). The enzyme, found in some cyanobacterial species, catalyses the last step in the

biosynthesis of the toxins cylindrospermopsin and 7-epi-cylindrospermopsin. The ratio of the two

products differs among different strains.

References: [2735, 2736]

[EC 1.14.11.70 created 2019]

EC 1.14.11.71

Accepted name: methylphosphonate hydroxylase

Reaction: methylphosphonate + 2-oxoglutarate + O_2 = hydroxymethylphosphonate + succinate + CO_2

Other name(s): $phnY^*$ (gene name)

Systematic name: methylphosphonate, 2-oxoglutarate: oxygen oxidoreductase (1-hydroxylating)

Comments: Requires iron(II). The enzyme, characterized from the marine bacterium *Gimesia maris*, participates

in a methylphosphonate degradation pathway.

References: [1265]

[EC 1.14.11.71 created 2019]

EC 1.14.11.72

Accepted name: [2-(trimethylamino)ethyl]phosphonate dioxygenase

Reaction: [2-(trimethylamino)ethyl]phosphonate + 2-oxoglutarate + O_2 = [(1R)-1-hydroxy-2-

(trimethylamino)ethyl]phosphonate + succinate + CO₂

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

Systematic name: [2-(trimethylamino)ethyl]phosphonate,2-oxoglutarate:oxygen oxidoreductase (1*R*-hydroxylating)

Comments: Requires Fe^{2+} and ascorbate. The enzyme, found in bacteria, participates in a degradation pathway

for [2-(trimethylamino)ethyl]phosphonate.

References: [3437]

[EC 1.14.11.72 created 2020]

EC 1.14.11.73

Accepted name: [protein]-arginine 3-hydroxylase

Reaction: [protein]-L-arginine + 2-oxoglutarate + O_2 = [protein]-(3R)-3-hydroxy-L-arginine + succinate + CO_2

Other name(s): JMJD5 (gene name)

Systematic name: [protein]-L-arginine,2-oxoglutarate:oxygen oxidoreductase (3*R*-hydroxylating)

Comments: The enzyme, characterized from humans, catalyses the stereoselective formation of the (2S,3R)-

hydroxy-L-arginine stereoisomer. So far the enzyme has been shown to act on two substrates - the 40S ribosomal protein S6 (RPS6), which is hydroxylated at R137, and, at a lower activity, RCCD1, a protein involved in chromatin stability, which is hydroxylated at R141. Even though the same stereoisomer is produced by the bacterial EC 1.14.11.47, [50S ribosomal protein L16]-arginine 3-hydroxylase, the two enzymes do not exhibit any cross-reactivity on their respective ribosomal protein substrates.

References: [4628]

[EC 1.14.11.73 created 2020]

EC 1.14.11.74

Accepted name: L-isoleucine 3¹-dioxygenase

Reaction: L-isoleucine + 2-oxoglutarate + $O_2 = 3^1$ -hydroxy-L-isoleucine + succinate + CO_2

Other name(s): *hilA* (gene name); L-isoleucine 4'-dioxygenase (incorrect)

Systematic name: L-isoleucine,2-oxoglutarate:oxygen oxidoreductase (3¹-hydroxylating)

Comments: Requires Fe²⁺ and ascorbate. The enzyme has been characterized from the bacterium *Pantoea ana*-

natis.

References: [3933]

[EC 1.14.11.74 created 2020]

EC 1.14.11.75

Accepted name: 3¹-hydroxy-L-isoleucine 4-dioxygenase

Reaction: 3^1 -hydroxy-L-isoleucine + 2-oxoglutarate + $O_2 = (4S)-3^1$,4-dihydroxy-L-isoleucine + succinate +

CO₂

Other name(s): *hilB* (gene name); 4'-hydroxy-L-isoleucine 4-dioxygenase (incorrect)

Systematic name: 3¹-hydroxy-L-isoleucine,2-oxoglutarate:oxygen oxidoreductase (4S-hydroxylating)

Comments: Requires Fe²⁺ and ascorbate. The enzyme has been characterized from the bacterium *Pantoea ana*-

natis.

References: [3933]

[EC 1.14.11.75 created 2020]

EC 1.14.11.76

Accepted name: L-glutamate 3(R)-hydroxylase

Reaction: L-glutamate + 2-oxoglutarate + $O_2 = (3R)$ -3-hydroxy-L-glutamate + succinate + CO_2

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

Systematic name: L-glutamate,2-oxoglutarate:oxygen oxidoreductase (3*R*-hydroxylating)

Comments: Requires Fe²⁺ and L-ascorbate. The enzyme, characterized from the basidiomycete mushroom

Amanita muscaria, participates in the biosynthesis of the psychoactive compounds ibotenate and mus-

cimol.

References: [3125]

[EC 1.14.11.76 created 2020]

EC 1.14.11.77

Accepted name: alkyl sulfatase

Reaction: a primary alkyl sulfate ester + 2-oxoglutarate + O_2 = an aldehyde + succinate + CO_2 + sulfate **Other name(s):** atsK (gene name); α -ketoglutarate-dependent sulfate ester dioxygenase; 2-oxoglutarate-dependent

sulfate ester dioxygenase; type II alkyl sulfatase

Systematic name: primary alkyl sulfate ester, 2-oxoglutarate:oxygen oxidoreductase (sulfate-hydrolyzing)

Comments: Sulfatase enzymes are classified as type I, in which the key catalytic residue is 3-oxo-L-alanine, type

II, which are non-heme iron-dependent dioxygenases, or type III, whose catalytic domain adopts a metallo- β -lactamase fold and binds two zinc ions as cofactors. The type II sulfatases oxidize the C-H bond of the carbon next to the sulfate ester, using 2-oxoglutarate and oxygen as substrates. The resulting hemiacetal sulfate ester collapses, liberating inorganic sulfate and an alkyl aldehyde along with carbon dioxide and succinate. The enzymes often desulfate a broad spectrum of linear and branched-chain sulfate esters. The enzyme from *Pseudomonas putida* acts on a range of medium-chain alkyl sulfate esters, with chain lengths ranging from C₄ to C₁₂. *cf.* sulfatase EC 3.1.6.1, arylsulfatase (type I), EC 3.1.6.21, linear primary-alkylsulfatase, and EC 3.1.6.22, branched primary-alkylsulfatase.

References: [1979, 2923, 3950]

[EC 1.14.11.77 created 2021]

EC 1.14.11.78

Accepted name: (*R*)-3-[(carboxymethyl)amino]fatty acid dioxygenase/decarboxylase

Reaction: a (3R)-3-[(carboxylmethyl)amino]fatty acid + 2 2-oxoglutarate + 2 O_2 = a (3R)-3-isocyanyl-fatty acid

+ 2 succinate $+ 3 CO_2 + 2 H_2O$ (overall reaction)

(1a) a (3R)-3-[(carboxylmethyl)amino]fatty acid + 2-oxoglutarate + O_2 = a (3R)-3-

[carboxy(hydroxy)methyl]aminofatty acid + succinate + CO₂

(1b) a (3R)-3-[carboxy(hydroxy)methyl]aminofatty acid + 2-oxoglutarate + O_2 = a (3R)-3-isocyanyl-

fatty acid + succinate + 2 CO₂ + 2 H₂O

Other name(s): scoE (gene name); mmaE (gene name); Rv0097 (locus name)

Systematic name: (3*R*)-3-[(carboxylmethyl)amino]fatty acid,2-oxoglutarate:oxygen oxidoreductase (isonitrile-forming) **Comments:** Requires Fe(II). The enzyme, found in actinobacterial species, participates in the biosynthesis of

isonitrile-containing lipopeptides. The reaction comprises two catalytic cycles, each consuming an oxygen molecule and a 2-oxoglutarate molecule. In the first cycle the substrate is hydroxylated, while in the second cycle the enzyme catalyses a decarboxylation/oxidation reaction that produces an isoni-

trile group.

References: [1537, 1536, 1948]

[EC 1.14.11.78 created 2022]

EC 1.14.11.79

Accepted name: protein-L-histidine (3S)-3-hydroxylase

Reaction: a [protein]-L-histidine + 2-oxoglutarate + O_2 = a [protein]-(3S)-3-hydroxy-L-histidine + succinate +

 CO_2

Other name(s): RIOX1 (gene name); RIOX2 (gene name); protein histidyl hydroxylase

Systematic name: protein-L-histidine,2-oxoglutarate:oxygen oxidoreductase (3S-hydroxylating)

Comments: The human enzymes encoded by the RIOX1 and RIOX2 genes catalyse the hydroxylation of L-

histidine residues in the 60S ribosomal proteins Rpl8 and L27a, respectively. Both proteins contain JmjC and winged helix domains, and both also catalyse histone L-lysine demethylation activities.

References: [1294, 492]

[EC 1.14.11.79 created 2022]

EC 1.14.11.80

Accepted name: methylcytosine dioxygenase

Reaction: (1) 5-methylcytosine in DNA + 2-oxoglutarate + O_2 = 5-hydroxymethylcytosine in DNA + succinate

 $+ CO_2$

(2) 5-hydroxymethylcytosine in DNA + 2-oxoglutarate + O_2 = 5-formylcytosine in DNA + succinate +

 $CO_2 + H_2O$

(3) 5-formylcytosine in DNA + 2-oxoglutarate + O_2 = 5-carboxycytosine in DNA + succinate + CO_2

Other name(s): TET1 (gene name); TET2 (gene name); TET3 (gene name)

Systematic name: 5-methylcytosine in DNA,2-oxoglutarate:oxygen oxidoreductase

Comments: The TET proteins mediate iterative oxidation of 5-methylcytosine in DNA (5mc) to 5-

hydroxymethylcytosine (5hmC), 5-formylcytosine (5fC), and 5-carboxylcytosine (5caC). 5fC and 5caC are recognized by EC 3.2.2.29, thymine-DNA glycosylase (TDG), which excises them, leaving an apyrimidinic site. Coupled with the base excision repair (BER) pathway, these activities result in a

cytosine demethylation pathway.

References: [1848, 1849, 1593, 2623, 4880]

[EC 1.14.11.80 created 2022]

EC 1.14.11.81

Accepted name: (–)-cyclopenine synthase

Reaction: (1) cyclopeptine + 2-oxoglutarate + O_2 = dehydrocyclopeptine + succinate + CO_2 + H_2O

(2) dehydrocyclopeptine + 2-oxoglutarate + O_2 = (-)-cyclopenine + succinate + CO_2

Other name(s): asqJ (gene name)

Systematic name: cyclopeptine,2-oxoglutarate:oxygen oxidoreductase ((-)-cyclopenine-forming)

Comments: This fungal enzyme is involved in the biosynthesis of quinolone compounds. it catalyses two oxida-

tion reactions: the first reaction results in a desaturation; the second reaction is a monooxygenation of the double bond, forming an epoxide. The enzyme is also active with 4'-methoxycyclopeptine.

References: [3110, 1831, 426, 600, 3963, 2472, 2599, 4652, 2447, 4200]

[EC 1.14.11.81 created 2022]

EC 1.14.11.82

Accepted name: 5-dehydro-6-demethoxyfumagillol dioxygenase

Reaction: 5-dehydro-6-demethoxyfumagillol + 2-oxoglutarate + O₂ = 5-dehydro-6-demethoxy-6-

hydroxyfumagillol + succinate + CO₂

Other name(s): *fmaF* (gene name); Fma-C6H

Systematic name: 5-dehydro-6-demethoxyfumagillol,2-oxoglutarate:oxygen oxidoreductase (6-hydroxylating)

Comments: Requires iron(II). The enzyme, characterized from the mold Aspergillus fumigatus, participates in the

biosynthesis of the meroterpenoid fumagillin.

References: [2489]

[EC 1.14.11.82 created 2022]

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 + $\mathbf{2}$ 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 Fe^{2+} . **References:** [2176, 4208]

[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⁺ + $O_2 = cis$ -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: [1321]

[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⁺ + $O_2 = cis$ -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 oxyge-

nase, and no independent ferredoxin. Requires Fe²⁺.

References: [237]

[EC 1.14.12.7 created 1990]

EC 1.14.12.8

Accepted name: 4-sulfobenzoate 3,4-dioxygenase

Reaction: 4-sulfobenzoate + NADH + H⁺ + O_2 = 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 oxyge-

nase, and no independent ferredoxin. Requires Fe²⁺.

References: [2530]

[EC 1.14.12.8 created 1992]

EC 1.14.12.9

Accepted name: 4-chlorophenylacetate 3,4-dioxygenase

Reaction: 4-chlorophenylacetate + NADH + H⁺ + O_2 = 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. Re-

quires Fe²⁺. Also acts on 4-bromophenyl acetate.

References: [2655]

[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⁺ + $O_2 = (1R,6S)$ -1,6-dihydroxycyclohexa-2,4-diene-1-carboxylate + NAD⁺ **Other name(s):** benzoate hydroxylase; benzoate hydroxylase; benzoate dioxygenase; benzoate hydroxylase; benz

zoate, 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 oxy-

genase. Requires Fe²⁺.

References: [4730, 4731, 4732]

 $[EC\ 1.14.12.10\ created\ 1972\ as\ EC\ 1.13.99.2,\ transferred\ 1992\ to\ EC\ 1.14.12.10]$

EC 1.14.12.11

Accepted name: toluene dioxygenase

Reaction: toluene + NADH + H⁺ + O₂ = (1S,2R)-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 oxyge-

nase, and a ferredoxin. Some other aromatic compounds, including ethylbenzene, 4-xylene and some

halogenated toluenes, are converted into the corresponding cis-dihydrodiols.

References: [3499, 4087]

[EC 1.14.12.11 created 1992]

EC 1.14.12.12

Accepted name: naphthalene 1,2-dioxygenase

Reaction: naphthalene + NADH + H⁺ + O₂ = (1R,2S)-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 [1955]. 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: [1056, 1897, 2038, 3236, 1955]

[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⁺ + O_2 = catechol + a halide anion + NAD⁺ + CO_2

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 *Burkholde*.

component. The latter contains FAD. The enzyme, characterized from the bacterium *Burkholde-ria 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 prefer-

ence.

References: [1112, 1113, 1460]

[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⁺ + O_2 = 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: [1962, 1964]

[EC 1.14.12.14 created 1999]

EC 1.14.12.15

Accepted name: terephthalate 1,2-dioxygenase

Reaction: terephthalate + NADH + H^+ + O_2 = (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: [3720]

[EC 1.14.12.15 created 1999]

Accepted name: 2-hydroxyquinoline 5,6-dioxygenase

Reaction: quinolin-2-ol + NADH + H⁺ + O_2 = 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(1*H*)-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: [3697]

[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: [1273, 1274]

[EC 1.14.12.17 created 2000]

EC 1.14.12.18

Accepted name: biphenyl 2,3-dioxygenase

Reaction: biphenyl + NADH + H⁺ + O₂ = (1S,2R)-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: [1466, 1467, 448]

[EC 1.14.12.18 created 2001]

EC 1.14.12.19

Accepted name: 3-phenylpropanoate dioxygenase

Reaction: (1) 3-phenylpropanoate + NADH + H^+ + O_2 = 3-(cis-5,6-dihydroxycyclohexa-1,3-dien-1-

yl)propanoate + NAD⁺

(2) (2E)-3-phenylprop-2-enoate + NADH + H⁺ + O₂ = (2E)-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 catal-

yses 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: [900, 497]

[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: [3004, 1254]

[EC 1.14.12.22 created 2010]

EC 1.14.12.23

Accepted name: nitroarene dioxygenase

Reaction: nitrobenzene + NADH + O_2 = 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 dioxyge-

nases. 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 $\alpha 3\beta 3$ oxygenase. The enzyme forms of 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: [3235, 2423, 2513, 3908]

[EC 1.14.12.23 created 2015]

EC 1.14.12.24

Accepted name: 2,4-dinitrotoluene dioxygenase

Reaction: 2,4-dinitrotoluene + NADH + O_2 = 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 $\alpha3\beta3$ 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: [4091]

[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 = (2R,3S)-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: [861, 4622, 1009, 1007]

[EC 1.14.12.25 created 2016]

EC 1.14.12.26

Accepted name: chlorobenzene dioxygenase

Reaction: chlorobenzene + NADH + H⁺ + O₂ = (1R,2R)-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 ter-

minal 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: [3986, 3959, 273, 274]

[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:** [4139, 4180, 4179, 4743]

[EC 1.14.13.1 created 1972]

EC 1.14.13.2

Accepted name: 4-hydroxybenzoate 3-monooxygenase

Reaction: 4-hydroxybenzoate + NADPH + H^+ + O_2 = 3,4-dihydroxybenzoate + NADP⁺ + H_2O

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 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: [1739, 1745, 3976, 3974, 3975, 3785]

[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]

Accepted name: melilotate 3-monooxygenase

Reaction: 3-(2-hydroxyphenyl)propanoate + NADH + H⁺ + O₂ = 3-(2,3-dihydroxyphenyl)propanoate + NAD⁺

 $+ H_2O$

Other name(s): 2-hydroxyphenylpropionate hydroxylase; melilotate hydroxylase; 2-hydroxyphenylpropionic hydroxylase;

ylase; melilotic hydroxylase

Systematic name: 3-(2-hydroxyphenyl)propanoate,NADH:oxygen oxidoreductase (3-hydroxylating)

Comments: A flavoprotein (FAD). **References:** [2431, 2432, 4063, 4062]

[EC 1.14.13.4 created 1972]

EC 1.14.13.5

Accepted name: imidazoleacetate 4-monooxygenase

Reaction: 4-imidazoleacetate + NADH + H $^+$ + O $_2$ = 5-hydroxy-4-imidazoleacetate + NAD $^+$ + H $_2$ O other name(s): imidazoleacetic hydroxylase; imidazoleacetate hydroxylase; imidazoleacetic monooxygenase

Systematic name: 4-imidazoleacetate, NADH: oxygen oxidoreductase (5-hydroxylating)

Comments: A flavoprotein (FAD).

References: [2626]

[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: [3205]

[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: [2973, 3046, 3047]

[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 [571, 572]. This enzyme is distinct from other monooxygenases in that the enzyme forms a relatively stable hydroperoxy flavin intermediate [572, 1945]. 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) [652, 651]

References: [4930, 652, 571, 572, 1945, 651]

[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

Systematic name: L-kynurenine,NADPH:oxygen oxidoreductase (3-hydroxylating)

Comments: A flavoprotein (FAD). **References:** [843, 3155, 3635]

[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:** [1700, 1701]

[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: [1309]

[EC 1.14.13.14 created 1976]

[1.14.13.15 Transferred entry. cholestanetriol 26-monooxygenase.] Transferred entry. cholestanetriol 26-monooxygenase.]

[EC 1.14.13.15 created 1976, modified 2005, modified 2012, deleted 2016]

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: [1408, 1409]

[EC 1.14.13.16 created 1976]

[1.14.13.17] Transferred entry. cholesterol 7\alpha-monooxygenase. Now EC 1.14.14.23, cholesterol 7\alpha-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: [1532]

[EC 1.14.13.18 created 1976]

EC 1.14.13.19

Accepted name: taxifolin 8-monooxygenase

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: [1896]

[EC 1.14.13.19 created 1976]

EC 1.14.13.20

Accepted name: 2,4-dichlorophenol 6-monooxygenase

Reaction: 2,4-dichlorophenol + NADPH + H $^+$ + O₂ = 3,5-dichlorocatechol + NADP $^+$ + H₂O

Other name(s): 2,4-dichlorophenol hydroxylase; 2,4-dichlorophenol monooxygenase 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: [252]

[EC 1.14.13.20 created 1983]

[1.14.13.21 Transferred entry. flavonoid 3'-monooxygenase. Now EC 1.14.14.82, flavonoid 3'-monooxygenase.]

[EC 1.14.13.21 created 1983, deleted 2018]

EC 1.14.13.22

Accepted name: cyclohexanone monooxygenase

Reaction: cyclohexanone + NADPH + H⁺ + O₂ = hexano-6-lactone + NADP⁺ + H₂O

Other name(s): cyclohexanone 1,2-monooxygenase; cyclohexanone oxygenase; cyclohexanone:NADPH:oxygen oxi-

doreductase (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 [3843]. This enzyme is able to catalyse a wide range of oxidative reactions, including enantioselective Baeyer-Villiger reactions [4026], sulfoxidations [628],

amine oxidations [3209] and epoxidations [718].

References: [950, 3843, 4026, 628, 3209, 718]

[EC 1.14.13.22 created 1984, modified 2004]

EC 1.14.13.23

Accepted name: 3-hydroxybenzoate 4-monooxygenase

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: [2790, 3374]

[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: [1420]

[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 alka-

nes can also be hydroxylated, but more slowly.

References: [710, 1780, 4035, 4307]

[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]

Accepted name: 4-aminobenzoate 1-monooxygenase

Reaction: 4-aminobenzoate + NAD(P)H + $\mathbf{2}$ 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: [4342]

[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: [2832]

[EC 1.14.13.29 created 1989]

[1.14.13.30 Transferred entry. leukotriene-B₄ 20-monooxygenase. Now EC 1.14.14.94, leukotriene-B₄ 20-monooxygenase]

[EC 1.14.13.30 created 1989, deleted 2018]

EC 1.14.13.31

Accepted name: 2-nitrophenol 2-monooxygenase

Reaction: 2-nitrophenol + 2 NADPH + 2 H⁺ + O_2 = catechol + nitrite + 2 NADP⁺ + H_2O

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: [4872]

[EC 1.14.13.31 created 1989]

EC 1.14.13.32

Accepted name: albendazole monooxygenase

Reaction: albendazole + NADPH + H⁺ + O₂ = albendazole S-oxide + NADP⁺ + H₂O

Other name(s): albendazole oxidase (misleading); albendazole sulfoxidase (ambiguous); FMO3 (gene name); albendazole

dazole monooxygenase (flavin-containing)

Systematic name: albendazole, NADPH: oxygen oxidoreductase (sulfoxide-forming)

Comments: A microsomal flavin-containing monooxygenase. A similar conversion is also carried out by some

microsomal cytochrome P-450 enzymes [EC 1.14.14.73, albendazole monooxygenase (sulfoxide-

forming)]. It is estimated that cytochrome *P*-450s are responsible for 70% of the activity.

References: [1088, 2898, 3463]

[EC 1.14.13.32 created 1989, modified 2018]

Accepted name: 4-hydroxybenzoate 3-monooxygenase [NAD(P)H]

Reaction: 4-hydroxybenzoate + NAD(P)H + H $^+$ + O₂ = 3,4-dihydroxybenzoate + NAD(P) $^+$ + H₂O

Other name(s): 4-hydroxybenzoate 3-monooxygenase (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-monooxygenase). It is less specific for NADPH than EC 1.14.13.2.

References: [1203, 3785]

[EC 1.14.13.33 created 1989, modified 1999]

EC 1.14.13.34

Accepted name: leukotriene-E₄ 20-monooxygenase

Reaction: (7E,9E,11Z,14Z)-(5S,6R)-6-(cystein-S-yl)-5-hydroxyicosa-7,9,11,14-tetraenoate + NADPH + H⁺ +

 $O_2 = 20$ -hydroxyleukotriene $E_4 + NADP^+ + H_2O$

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: [3192]

[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: [3367, 4088]

[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^+ + O_2 = 12-dehydrotetracycline + NADP⁺ + H_2O

Other name(s): ATC oxygenase; anhydrotetracycline oxygenase; oxyS (gene name); anhydrotetracycline monooxyge-

nase

Systematic name: anhydrotetracycline, NADPH: oxygen oxidoreductase (6-hydroxylating)

Comments: The enzyme, characterized from the bacterium *Streptomyces rimosus*, participates in the biosyn-

thesis of tetracycline antibiotics. It can also catalyse EC 1.14.13.234, 12-dehydrotetracycline 5-

monooxygenase.

References: [270, 335, 4419, 4522]

[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 (over-

all 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

 H_2O

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: [431, 4080, 4079, 31, 1139]

[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⁺ + O_2 = 2-amino-5-oxocyclohex-1-enecarboxyl-CoA + H_2O +

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: [488, 489, 2348]

[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. hydroxyphenylacetonitrile 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⁺ + O_2 = 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: [1202]

[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: [2197]

[EC 1.14.13.44 created 1992]

[1.14.13.45 Transferred entry. CMP-N-acetylneuraminate monooxygenase. Now EC 1.14.18.2, CMP-N-acetylneuraminate 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: [2602]

[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^+ + O_2 = 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⁺ +

 H_2O

Other name(s): pcpB (gene name); pentachlorophenol dechlorinase; pentachlorophenol dehalogenase; pen-

tachlorophenol 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 [4714]. If C-4 carries a halogen substituent, reaction 1 is catalysed; if C-4 is unsubstituted, reaction 2 is catal-

ysed.

References: [3709, 4714, 4713, 2346, 2984, 633, 1676, 3593]

[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^+ + O_2 = 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(3H)-one.

References: [4631]

[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^+ + O_2 = a steroid ester/lactone + NADP⁺ + H_2O (general reaction)

(1) progesterone + NADPH + H^+ + O_2 = testosterone acetate + NADP⁺ + H_2O (2) androstenedione + NADPH + H^+ + O_2 = testololactone + NADP⁺ + H_2O

(3) 17α -hydroxyprogesterone + NADPH + H⁺ + O₂ = androstenedione + acetate + NADP⁺ + H₂O

Other name(s): steroid-ketone monooxygenase; progesterone, NADPH₂:oxygen oxidoreductase (20-hydroxylating,

ester-producing); 17α-hydroxyprogesterone, NADPH₂:oxygen oxidoreductase (20-hydroxylating, side-chain cleaving); androstenedione, NADPH₂:oxygen oxidoreductase (17-hydroxylating, lactoniz-

ing)

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 oxida-

tion) reaction. The oxidative esterification of a number of derivatives of progesterone to produce the corresponding 17α -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-secoandrosteno- $17,13\alpha$ -lactone, such as testololactone, is shown in Reaction (2). The oxidative cleavage of the 17β -side-chain of 17α -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: [2008, 1842, 1843]

[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^+ + O_2 = 3-hydroxybenzoyl-CoA + NADP⁺ + H_2O

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 reac-

tion (FAD or FMN). Benzoate is not a substrate.

References: [3069]

[EC 1.14.13.58 created 1999]

EC 1.14.13.59

Accepted name: L-lysine N^6 -monooxygenase (NADPH)

Reaction: L-lysine + NADPH + H⁺ + O₂ = N^6 -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: [3334, 2591, 4251, 851, 2659, 1350]

[EC 1.14.13.59 created 1999, modified 2001, modified 2012]

[1.14.13.60 Transferred entry. 27-hydroxycholesterol 7\alpha-monooxygenase. Now classified as EC 1.14.14.29, 25/26-hydroxycholesterol 7\alpha-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(1H)-one tautomer.

References: [3572]

[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: [361]

[EC 1.14.13.62 created 1999]

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: [4396]

[EC 1.14.13.63 created 1999]

EC 1.14.13.64

Accepted name: 4-hydroxybenzoate 1-hydroxylase

Reaction: 4-hydroxybenzoate + NAD(P)H + $\mathbf{2}$ 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: [4397]

[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^+ + O_2 = 6-hydroxyhexan-6-olide + NADP⁺ + H_2O

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: [837]

[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-hydroxyphenylacetaldehyd 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 $^+$ + O $_2$ = 1,2-epoxypropane + NAD $^+$ + H $_2$ O **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 X anthobacter sp. strain Py2 contains an additional small protein of unknown function that is essential for activity. In general, the enzyme oxygenates C_2 to C_6 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: [3929, 1258, 4915, 591, 590]

[EC 1.14.13.69 created 2001]

	[EC 1.14.13.09 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-methylcoclaurine 3'-monooxygenase. Now EC 1.14.14.102, N-methylcoclaurine 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 10β-hydroxylase. Now EC 1.14.14.105, taxane 10β-hydroxylase]
	[EC 1.14.13.76 created 2002, deleted 2018]
[1.14.13.77	Transferred entry. taxane 13α-hydroxylase. Now EC 1.14.14.106, taxane 13α-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 magnesium-protoporphyrin IX 13-monomethyl ester + 3 NADPH + 3 H⁺ + 3 O₂ = 3,8-divinyl pro-

tochlorophyllide a + 3 NADP⁺ + 5 H₂O (overall reaction)

(1a) magnesium-protoporphyrin IX 13-monomethyl ester + NADPH + H^+ + O_2 = 13^1 -hydroxy-magnesium-protoporphyrin IX 13-monomethyl ester + NADP⁺ + H_2O

(1b) 13^1 -hydroxy-magnesium-protoporphyrin IX 13-monomethyl ester + NADPH + H⁺ + O₂ = 13^1 -oxo-magnesium-protoporphyrin IX 13-monomethyl ester + NADP⁺ + **2** H₂O

(1c) 13^{1} -oxo-magnesium-protoporphyrin IX 13-monomethyl ester + NADPH + H⁺ + O₂ = 3,8-divinyl

protochlorophyllide $a + \text{NADP}^+ + 2 \text{ H}_2\text{O}$

Other name(s): Mg-protoporphyrin IX monomethyl ester (oxidative) cyclase

Systematic name: magnesium-protoporphyrin-IX 13-monomethyl ester,NADPH:oxygen oxidoreductase (hydroxylating)

Comments: Requires iron(II) for activity. The enzyme participates in the biosynthesis of chlorophyllide a in aero-

bic 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: [4495, 379, 3329, 4315]

[EC 1.14.13.81 created 2003, modified 2017]

EC 1.14.13.82

Accepted name: vanillate monooxygenase

Reaction: vanillate + O_2 + 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: [475, 3379]

[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 biosythesis 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: [858, 3771, 4550]

[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^+ + O_2 = 4-hydroxyphenyl acetate + NADP⁺ + H_2O

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 [1984]. In the absence of substrate, the

enzyme can act as an NAD(P)H oxidase (EC 1.6.3.1).

References: [1984, 1985]

[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] Transferred entry. flavanoid 3,5-hydroxylase. Now EC 1.14.14.81, flavanoid 3,5-hydroxylase] [1.14.13.88 [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 phenylacetone + NADPH + H^+ + O_2 = benzyl acetate + NADP⁺ + H_2O Reaction: 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 alipatic ketones (e.g. dodecan-2-one) and sulfides (e.g. 1-methyl-4-(methylsulfanyl)benzene). **References:** [2631, 1159] [EC 1.14.13.92 created 2005] Transferred entry. (+)-abscisic acid 8-hydroxylase. Now EC 1.14.14.137, (+)-abscisic acid 8-hydroxylase] [1.14.13.93 [EC 1.14.13.93 created 2005, deleted 2018] [1.14.13.94 Transferred entry. lithocholate 6β-hydroxylase. Now EC 1.14.148, lithocholate 6β-hydroxylase] [EC 1.14.13.94 created 2005, deleted 2018] [1.14.13.95 Transferred entry. 7α-hydroxycholest-4-en-3-one 12α-hydroxylase. Now included with EC 1.14.14.139, 5βcholestane- 3α , 7α -diol 12α -hydroxylase] [EC 1.14.13.95 created 2005, deleted 2015] *[1.14.13.96]* Transferred entry. 5β -cholestane- 3α , 7α -diol 12α -hydroxylase. Now EC 1.14.14.139, 5β -cholestane- 3α , 7α -diol 12α-hydroxylase] [EC 1.14.13.96 created 2005, deleted 2018] [1.14.13.97 Transferred entry. taurochenodeoxycholate 6α-hydroxylase. Now EC 1.14.14.57, taurochenodeoxycholate 6αhydroxylase] [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]

Transferred entry. 24-hydroxycholesterol 7α-hydroxylase. Now EC 1.14.14.26, 24-hydroxycholesterol 7α-

[1.14.13.99

hydroxylase]

[EC 1.14.13.99 created 2005, deleted 2016]

[1.14.13.100 Transferred entry. 25/26-hydroxycholesterol 7\alpha-hydroxylase. Now classified as EC 1.14.14.29, 25/26-hydroxycholesterol 7α-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

> senecionine + NADPH + H^+ + O_2 = senecionine N-oxide + NADP $^+$ + H_2O **Reaction:**

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. senkirkine) as substrates [2498]. 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: [2498, 3022]

[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 1.14.143, (+)-menthofuran synthase]

[EC 1.14.13.104 created 2008, deleted 2018]

EC 1.14.13.105

Accepted name: monocyclic monoterpene ketone monooxygenase

(1) (-)-menthone + NADPH + H⁺ + O₂ = (4R,7S)-7-isopropyl-4-methyloxepan-2-one + NADP⁺ + Reaction:

(2) dihydrocarvone + NADPH + H^+ + O_2 = 4-isopropenyl-7-methyloxepan-2-one + NADP⁺ + H_2O

(3) (iso)-dihydrocarvone + NADPH + H^+ + O_2 = 6-isopropenyl-3-methyloxepan-2-one + NADP⁺ +

(4a) 1-hydroxymenth-8-en-2-one + NADPH + H^+ + O_2 = 7-hydroxy-4-isopropenyl-7-methyloxepan-

2-one + NADP⁺ + H₂O

(4b) 7-hydroxy-4-isopropenyl-7-methyloxepan-2-one = 3-isopropenyl-6-oxoheptanoate (spontaneous)

1-hydroxy-2-oxolimonene 1,2-monooxygenase; dihydrocarvone 1,2-monooxygenase; MMKMO Other name(s): **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 [4588]. Both

(1R,4S)- and (1S,4R)-1-hydroxymenth-8-en-2-one are metabolized, with the lactone product sponta-

neously rearranging to form 3-isopropenyl-6-oxoheptanoate [4404].

[4404, 4588, 4403] **References:**

[EC 1.14.13.105 created 2008]

[1.14.13.106 Transferred entry. epi-isozizaene 5-monooxygenase, now classified as EC 1.14.15.39, epi-isozizaene 5-monooxygenase.]

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: [4404]

[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.

lase]

[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; methanesul-

fonic 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 [853]. 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: [853, 1646]

[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 $^+$ + O $_2$ = 5-hydroxyisourate + NAD $^+$ + H $_2$ O **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 pneu-*

moniae. 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: [3167]

[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) [2989]. The reaction is involved in the aerobic catabolism of nicotinic acid.

References: [2989, 1915]

[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]

[1.14.13.116] Transferred entry, geranylhydroquinone 3-hydroxylase, Now EC 1.14.14.174, geranylhydroquinone 3-hydroxylase,]

[EC 1.14.13.116 created 2010, deleted 2020]

[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. premnaspirodiene oxygenase. Now EC 1.14.14.151, premnaspirodiene oxygenase]

[EC 1.14.13.121 created 2011, deleted 2018]

EC 1.14.13.122

Accepted name: chlorophyllide-*a* oxygenase

Reaction: chlorophyllide $a + 2 O_2 + 2 NADPH + 2 H^+ = chlorophyllide <math>b + 3 H_2O + 2 NADP^+$ (overall reac-

tion)

(1a) chlorophyllide $a + O_2 + NADPH + H^+ = 7^1$ -hydroxychlorophyllide $a + H_2O + NADP^+$ (1b) 7^1 -hydroxychlorophyllide $a + O_2 + NADPH + H^+ =$ chlorophyllide $b + 2 H_2O + NADP^+$

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 chloro-

plast of green algae, cyanobacteria and plants [3199, 1024]. Contains a mononuclear iron centre [1024]. 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 chlorophyl-

lide *b* [3199]. Chlorophyll *a* and protochlorophyllide *a* are not substrates [3199].

References: [1064, 3199, 1024, 3355]

[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^+ + O_2 = 3-(2,3-dihydroxyphenyl)propanoate +

 $H_2O + NAD^+$

(2) (2E)-3-(3-hydroxyphenyl)prop-2-enoate + NADH + H⁺ + O₂ = (2E)-3-(2,3-dihydroxyphenyl)prop-

2-enoate + H_2O + 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 bac-

terium Escherichia coli for the degradation of various phenylpropanoid compounds.

References: [497, 498, 1106, 900]

[EC 1.14.13.127 created 2011]

EC 1.14.13.128

Accepted name: 7-methylxanthine demethylase

Reaction: 7-methylxanthine + O_2 + $NAD(P)H + H^+$ = xanthine + $NAD(P)^+$ + H_2O + 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 [4113]. Forms part of the caffeine degra-

dation pathway.

References: [4114, 4113]

[EC 1.14.13.128 created 2011]

[1.14.13.129 Transferred entry. \(\beta\)-carotene 3-hydroxylase. Now EC 1.14.15.24, \(\beta\)-carotene 3-hydroxylase.]

[EC 1.14.13.129 created 2011, deleted 2017]

Accepted name: pyrrole-2-carboxylate monooxygenase

Reaction: pyrrole-2-carboxylate + NADH + H^+ + O_2 = 5-hydroxypyrrole-2-carboxylate + NAD⁺ + H_2O

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: [1731, 262]

[EC 1.14.13.130 created 2011]

EC 1.14.13.131

Accepted name: dissimilatory dimethyl sulfide monooxygenase

Reaction: dimethyl sulfide + O_2 + NADH + H⁺ = methanethiol + formaldehyde + NAD⁺ + H₂O

Other name(s): dmoAB (gene names); dimethyl sulfide C-monooxygenase; dimethylsulfide monooxygenase (ambigu-

ous); 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 Mg^{2+} and Fe^{2+} . 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: [387, 365]

[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. \(\beta\)-amyrin 11-oxidase. Now EC 1.14.14.152, \(\beta\)-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

[3028].

References: [891, 3028]

[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 9α -monooxygenase. Now EC 1.14.15.30, 3-ketosteroid 9α -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\beta-pimara-7,15-diene oxidase.] Transferred entry. 9\beta-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 14β-hydroxylase

Reaction: 10β -hydroxytaxa-4(20),11-dien- 5α -yl acetate + O_2 + NADPH + H^+ = 10β , 14β -dihydroxytaxa-

4(20), 11-dien- 5α -yl acetate + NADP⁺ + H₂O

Systematic name: 10β-hydroxytaxa-4(20),11-dien-5α-yl-acetate,NADPH:oxygen 14-oxidoreductase

Comments: Requires cytochrome P450. From the yew Taxus cuspidata. Also acts on taxa-4(20),11-dien- 5α -yl

acetate.

References: [1899]

[EC 1.14.13.146 created 2012]

[1.14.13.147 Transferred entry. taxoid 7β-hydroxylase. Now EC 1.14.14.182, taxoid 7β-hydroxylase]

[EC 1.14.13.147 created 2012, deleted 2022]

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 car-

bon and energy [2353, 638]. The mammalian enzyme is involved in detoxification of trimethylamine. Mutations in the human enzyme cause the inheritable disease known as trimethylaminuria (fish odor

syndrome) [939, 4325].

References: [2353, 939, 4325, 638]

[EC 1.14.13.148 created 2012]

Accepted name: phenylacetyl-CoA 1,2-epoxidase

Reaction: phenylacetyl-CoA + NADPH + H^+ + O_2 = 2-(1,2-epoxy-1,2-dihydrophenyl)acetyl-CoA + NADP+ +

 H_2O

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: [4250, 1414, 1413]

[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⁺ + O_2 = (+)-cis-sabinol + NADP⁺ + H_2O

Systematic name: (+)-sabinene,NADPH:oxygen oxidoreductase (3-hydroxylating)

Comments: Requires cytochrome *P*-450. The enzyme has been characterized from *Salvia officinalis* (sage).

References: [1995]

[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 alter-

native substrate erythromycin B [2332].

References: [2332, 3680, 2868]

[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: [717]

[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: [(1R)-2,2,3-trimethyl-5-oxocyclopent-3-enyl]acetyl-CoA + O₂ + NADPH + H⁺ = [(2R)-3,3,4-

trimethyl-6-oxo-3,6-dihydro-1H-pyran-2-yl]acetyl-CoA + NADP⁺ + H₂O

Other name(s): $2-\cos(-\Delta^3-4.5.5)$ -trimethylcyclopentenylacetyl-CoA monooxygenase; $2-\cos(-\Delta^3-4.5.5)$ -

trimethylcyclopentenylacetyl-CoA 1,2-monooxygenase; OTEMO

Systematic name: [(1R)-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: [3215, 2412, 1969]

[EC 1.14.13.160 created 2012]

EC 1.14.13.161

Accepted name: (+)-camphor 6-exo-hydroxylase

Reaction: (+)-camphor + NADPH + H^+ + O_2 = (+)-6-exo-hydroxycamphor + NADP+ + H_2O

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: [1231, 1229]

[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: $4-(6-\text{hydroxypyridin-}3-\text{yl})-4-\text{oxobutanoate} + 2 \text{ NADH} + 2 \text{ H}^+ + \text{O}_2 = 2,5-\text{dihydroxypyridine} + \text{succi-}$

nate semialdehyde + 2 NAD^+ + H_2O

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 [4203].

References: [4202, 4203]

[EC 1.14.13.163 created 2012]

[1.14.13.164 Transferred entry. carotenoid isomerooxygenase. The enzyme was discovered at the public-review stage to have been misclassified and so was withdrawn. See EC 1.13.11.65, carotenoid isomerooxygenase]

[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 [1967]. 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 [1967, 2133] while the enzyme from *Pseudomonas* sp. WBC-3 was shown to also catalyse EC 1.14.13.167, 4-nitrophenol 4-

monooxygenase [4878].

References: [1967, 2133, 4878]

[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: [4878]

[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^+ + O_2 = (indol-3-yl)acetate + NADP⁺ + H_2O + CO_2

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: [2681, 4906]

[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^+ + O_2 = pentalenolactone D + NADP+ + H_2O

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 pentaleno-

lactone biosynthesis.

References: [3801]

[EC 1.14.13.170 created 2012]

EC 1.14.13.171

Accepted name: neopentalenolactone D synthase

> 1-deoxy-11-oxopentalenate + NADPH + H^+ + O_2 = neopentalenolactone D + NADP⁺ + H_2O Reaction:

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 un-

dergoes a biological Baeyer-Villiger reaction.

References: [3801]

[EC 1.14.13.171 created 2012]

EC 1.14.13.172

salicylate 5-hydroxylase Accepted name:

> salicylate + NADH + H⁺ + O_2 = 2,5-dihydroxybenzoate + NAD⁺ + H_2O **Reaction:**

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: [1201]

[EC 1.14.13.172 created 2013]

Transferred entry. 11-oxo-β-amyrin 30-oxidase. Now EC 1.14.14.115, 11-oxo-β-amyrin 30-oxidase.] [1.14.13.173

[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

methylxanthine N^1 -demethylase Accepted name:

> (1) caffeine + O_2 + NAD(P)H + H⁺ = theobromine + NAD(P)⁺ + H₂O + formaldehyde **Reaction:**

> > (2) the ophylline + O_2 + NAD(P)H + H⁺ = 3-methylxanthine + NAD(P)⁺ + H₂O + formaldehyde

(3) paraxanthine + O_2 + NAD(P)H + H⁺ = 7-methylxanthine + NAD(P)⁺ + H₂O + formaldehyde

ndmA (gene name) Other name(s):

caffeine:oxygen oxidoreductase (N^1 -demethylating) **Systematic name:**

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 N^3 -demethylase, and has a 5-fold higher activity with NADH than with NADPH [4113]. Also demethylate 1-methylxantine

with lower efficiency. Forms part of the degradation pathway of methylxanthines.

References: [4114, 4113]

[EC 1.14.13.178 created 2013]

EC 1.14.13.179

Accepted name: methylxanthine N^3 -demethylase

Reaction: (1) theobromine + O_2 + NAD(P)H + H⁺ = 7-methylxanthine + NAD(P)⁺ + H₂O + formaldehyde

(2) 3-methylxanthine + O_2 + NAD(P)H + H⁺ = xanthine + NAD(P)⁺ + H₂O + formaldehyde

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

Systematic name: the obromine: 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 [4114]. Also demethylates caffeine and theophylline

with lower efficiency. Forms part of the degradation pathway of methylxanthines.

References: [4114, 4113]

[EC 1.14.13.179 created 2013]

EC 1.14.13.180

Accepted name: aklavinone 12-hydroxylase

Reaction: aklavinone + NADPH + H⁺ + O₂ = ε -rhodomycinone + 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 purpuras*-

cens participate in the biosynthesis of daunorubicin, doxorubicin and rhodomycins. The enzyme from

Streptomyces purpurascens is an FAD monooxygenase.

References: [1122, 3070]

[EC 1.14.13.180 created 2013]

EC 1.14.13.181

Accepted name: 13-deoxydaunorubicin hydroxylase

Reaction: (1) 13-deoxydaunorubicin + NADPH + H^+ + O_2 = 13-dihydrodaunorubicin + NADP⁺ + H_2O

(2) 13-dihydrodaunorubicin + NADPH + H^+ + O_2 = daunorubicin + NADP⁺ + $\mathbf{2}$ H_2O

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: [4493, 904]

[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: [3713]

[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-monooxygenase. Now EC 1.14.15.34, 20-oxo-5-O-mycaminosyltylactone 23-monooxygenase]

[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) $dTDP-\beta-L$ -evernosamine + NADPH + H⁺ + O₂ = dTDP-N-hydroxy- $\beta-L$ -evernosamine + NADP⁺

 $+ H_2O$

(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: [1748, 4442]

[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^+ + O_2 = 3-hydroxy-5-methyl-1-naphthoate + NADP⁺ + H_2O

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 of the the antitumor antibiotic azinomycin B.

References: [919]

[EC 1.14.13.189 created 2014]

[1.14.13.190 Transferred entry. ferruginol synthase. Now EC 1.14.14.175, ferruginol synthase]

[EC 1.14.13.190 created 2014, modified 2015, deleted 2020]

[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, phylloquinone ω-hydroxylase. Now EC 1.14.14.78, phylloquinone 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 (N⁵-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: [1293, 2769, 3341, 3534]

[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 desferriferricrocin, 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 [3566]. *cf.* EC 1.14.13.195, L-ornithine

 N^5 -monooxygenase (NADPH).

References: [670, 1161, 3566, 3049]

[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 \omega-hydroxylase. Now EC 1.14.14.79, docosahexaenoic acid \omega-hydroxylase]

[EC 1.14.13.199 created 2014, deleted 2018]

EC 1.14.13.200

Accepted name: tetracenomycin A2 monooxygenase-dioxygenase

Reaction: tetracenomycin A2 + $\mathbf{2}$ O₂ + $\mathbf{2}$ NAD(P)H + $\mathbf{2}$ H⁺ = tetracenomycin C + $\mathbf{2}$ 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 bac-

terium *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 hy-

droxy group.

References: [3839, 3423, 324]

[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 \omega-monooxygenase. Now EC 1.14.14.129, long-chain acyl-CoA \omega-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^+ + O_2 = 2,3-epoxy-2,3-dihydrobenzoyl-CoA + NADP⁺ + H_2O **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 [4849].

References: [4849, 1308, 2857, 3455]

[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: [1835]

[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⁺ + O_2 = 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: [1478, 2425]

[EC 1.14.13.210 created 2016]

EC 1.14.13.211

Accepted name: rifampicin monooxygenase

Reaction: rifampicin + NAD(P)H + O_2 = 2-hydroxy-2,27-secorifampicin + NAD(P)⁺ + H_2O

Other name(s): RIF-O; ROX; RIFMO; rifampicin:NAD(P)H:oxygen oxidoreductase (2'-N-hydroxyrifampicin-

forming) (incorrect)

Systematic name: rifampicin:NAD(P)H:oxygen oxidoreductase (2-hydroxy-2,27-secorifampicin-forming; ring-cleaving)

Comments: The enzyme has been found in a variety of environmental bacteria, notably *Rhodococcus*, *Nocardia*,

and Streptomyces. It hydroxylates C-2 of rifampicin leading to its macro-ring cleaving.

References: [92, 1737, 2246, 2519]

[EC 1.14.13.211 created 2016, modified 2022]

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: [2858, 4115]

[EC 1.14.13.212 created 2016]

[1.14.13.213 Transferred entry. bursehernin 5-monooxygenase. Now EC 1.14.14.131, bursehernin 5-monooxygenase]

[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-monooxygenase

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: [3602]

[EC 1.14.13.215 created 2016]

EC 1.14.13.216

Accepted name: asperlicin C monooxygenase

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 en-

zyme 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: [1583]

[EC 1.14.13.216 created 2016]

EC 1.14.13.217

Accepted name: protodeoxyviolaceinate monooxygenase

Reaction: protodeoxyviolaceinate + NAD(P)H + O_2 = protoviolaceinate + NAD(P)⁺ + H_2O

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: [199, 3887]

[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 + O_2 = pyocyanin + NAD⁺ + CO_2 + H_2O

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 biosyn-

thesis 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: [2727, 3247, 1401]

[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: [1757]

[EC 1.14.13.219 created 2016]

EC 1.14.13.220

Accepted name: resorcinol 4-hydroxylase (NADH)

Reaction: resorcinol + NADH + H⁺ + O_2 = hydroxyquinol + NAD⁺ + H_2O

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 hy-

droxylase. 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: [2004]

[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 + $NAD(P)^+$ + H_2O (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-dihydroxyireno[2,3-b]quinolin-[(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 C_2 - C_3 double bond of aurachin C, which is followed by a semipinacol rearrangement, causing migration

of the farnesyl group from C_3 to C_4 .

References: [2028]

[EC 1.14.13.222 created 2016]

Accepted name: 3-hydroxy-4-methylanthranilyl-[aryl-carrier protein] 5-monooxygenase

3-hydroxy-4-methylanthranilyl-[aryl-carrier protein] + NADH + H^+ + O_2 = 3,5-dihydroxy-4-**Reaction:**

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: [1324]

[EC 1.14.13.223 created 2016]

EC 1.14.13.224

Accepted name: violacein synthase

> Reaction: (1) protoviolaceinate + NAD(P)H + O_2 = violaceinate + NAD(P)⁺ + H_2O

> > (2) protodeoxyviolaceinate + NAD(P)H + O_2 = deoxyviolaceinate + NAD(P)⁺ + H_2O

Other name(s): proviolaceinate monooxygenase; *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, un-

dergo non-enzymic autooxidation into violacein and deoxyviolacein, respectively.

References: [199, 3887]

[EC 1.14.13.224 created 2016]

EC 1.14.13.225

Accepted name: F-actin monooxygenase

> **Reaction:** [F-actin]-L-methionine + NADPH + O_2 + H^+ = [F-actin]-L-methionine-(R)-S-oxide + NADP+ + H_2O

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 oxidoreduc-

> tase 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 [1775]. Free methionine is not a substrate [1773]. The reaction is stereospecific and generates the (R)-sulfoxide [1774]. In the absence of substrate, the enzyme can act as an NAD(P)H oxidase (EC 1.6.3.1) [4939, 4454].

References: [1775, 1773, 1774, 4939, 4454]

[EC 1.14.13.225 created 2016]

EC 1.14.13.226

Accepted name: acetone monooxygenase (methyl acetate-forming)

acetone + NADPH + H^+ + O_2 = methyl acetate + NADP⁺ + H_2O **Reaction:**

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 monooxygenase and participates in a propane utilization pathway.

References: [2245]

[EC 1.14.13.226 created 2016]

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: [2244, 3829, 1240]

[EC 1.14.13.227 created 2016]

EC 1.14.13.228

Accepted name: jasmonic acid 12-hydroxylase

Reaction: (-)-jasmonate + NADPH + H⁺ + O_2 = trans-12-hydroxyjasmonate + NADP⁺ + H_2O

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: [3262]

[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 *Aquincola 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: [3699, 3760]

[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 C_3 - C_6 linear and branched aliphatic alkanes with

lower activity.

References: [3928, 976, 958, 725]

[EC 1.14.13.230 created 2016]

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: [4766, 2875, 4467]

[EC 1.14.13.231 created 2016]

EC 1.14.13.232

Accepted name: 6-methylpretetramide 4-monooxygenase

Reaction: 6-methylpretetramide + NADPH + H^+ + O_2 = 4-hydroxy-6-methylpretetramide + NADP⁺ + H_2O

Systematic name: 6-methylpretetramide,NADPH:oxygen oxidoreductase (4-hydroxylating)

Comments: The enzyme, characterized from the bacterium *Streptomyces rimosus*, participates in the biosynthe-

sis 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.

tion is EC 1.14.13.233, 4-hydroxy-6-methylpretetramide 12a-monooxygenase.

References: [4886, 4524]

[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^+ + O_2 = 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: [4886]

[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-dehydrooxytetracycline + 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-

dehydrooxytetracycline, which, following the action of OxyR, becomes oxytetracycline.

References: [335, 2810, 4419, 4522]

[EC 1.14.13.234 created 2016]

Accepted name: indole-3-acetate monooxygenase

Reaction: (indol-3-yl)acetate + NADH + H⁺ + O₂ = (2-hydroxy-1H-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: [2428, 3774]

[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): TMC

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 oxi-

doreductase, a Rieske-type [2Fe-2S] ferredoxin, and an effector protein.

References: [4606, 1624, 3765, 184, 1741]

[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 + $NADP^+$ + H_2O

Other name(s): ω-(methylthio)alkylglucosinolate S-oxygenase; GS-OX1 (gene name); ω-(methylthio)alkylglucosinolate S-oxygenase; ω-(methylthio)alkylglucosinolate S-oxygenase; ω-(methylthio)alkylglucosinolate S-oxygenase; ω-(methylthio)alkylglucosinolate S-oxygena

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: [1510, 2445]

[EC 1.14.13.237 created 2017]

EC 1.14.13.238

Accepted name: dimethylamine monooxygenase

Reaction: dimethylamine + NADPH + H^+ + O_2 = methylamine + formaldehyde + NADP⁺ + H_2O

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: [1001, 999, 59, 2479]

[EC 1.14.13.238 created 2017]

Accepted name: carnitine monooxygenase

Reaction: L-carnitine + NAD(P)H + H⁺ + O₂ = (3R)-3-hydroxy-4-oxobutanoate + trimethylamine + NAD(P)⁺

 $+ H_2O$

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 re-

ductase 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: [923, 4928, 2191]

[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 +

 $NADP^+ + H_2O$

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 hydroxyla-

tion 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: [625, 3285]

[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^+ + O_2 = 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 B_6). 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: [3973, 3040, 587]

[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 (decy-

clizing); 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 *Mesorhizo*-

bium 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: [3973, 588, 3187, 4840, 2745, 4284, 4283]

[EC 1.14.13.242 created 2018 (EC 1.14.12.4 created 1972, incorporated 2018)]

EC 1.14.13.243

Accepted name: toluene 2-monooxygenase

Reaction: (1) toluene + NADH + H⁺ + O₂ = 2-methylphenol + NAD⁺ + H₂O

(2) 2-methylphenol + NADH + H⁺ + O₂ = 3-methylcatechol + NAD⁺ + H₂O

Other name(s): *tomA1/2/3/4/5* (gene names); toluene *ortho*-monooxygenase **Systematic name:** toluene,NADH:oxygen oxidoreductase (2,3-dihydroxylating)

Comments: The enzyme, characterized from the bacterium *Burkholderia cepacia*, belongs to a class of nonheme,

oxygen-dependent diiron enzymes. It contains a hydroxylase component with two binuclear iron centers, an NADH-oxidoreductase component containing FAD and a [2Fe-2S] iron-sulfur cluster, and a third component involved in electron transfer between the hydroxylase and the reductase. The enzyme dihydroxylates its substrate in two sequential hydroxylations, initially forming 2-methylphenol, which

is hydroxylated to 3-methylcatechol.

References: [3055, 4784, 543]

[EC 1.14.13.243 created 2019]

EC 1.14.13.244

Accepted name: phenol 2-monooxygenase (NADH)

Reaction: phenol + NADH + H⁺ + O₂ = catechol + NAD⁺ + H₂O

Other name(s): dmpLMNOP (gene names)

Systematic name: phenol,NADH:oxygen oxidoreductase (2-hydroxylating)

Comments: The enzyme, characterized from the bacteria *Pseudomonas* sp. CF600 and *Acinetobacter radiore*-

sistens, consists of a multisubunit oxygenease component that contains the active site and a dinuclear iron center, a reductase component that contains FAD and one iron-sulfur cluster, and a regulatory component. The reductase component is responsible for transferring electrons from NADH to the din-

uclear iron center.

References: [3106, 3366, 3365, 3398, 517]

[EC 1.14.13.244 created 2019]

EC 1.14.13.245

Accepted name: assimilatory dimethylsulfide S-monooxygenase

Reaction: (1) dimethyl sulfide + NADH + H⁺ + O_2 = dimethyl sulfoxide + NAD⁺ + H_2O

(2) dimethyl sulfoxide + NADH + H^+ + O_2 = dimethyl sulfone + NAD⁺ + H_2O

Other name(s): dsoBCDEF (gene names)

Systematic name: dimethyl sulfide,NADH:oxygen oxidoreductase (S-oxidizing)

Comments: The enzyme, studied from the bacterium *Acinetobacter* sp. strain 20B, is very similar to EC

1.14.13.244, phenol 2-monooxygenase (NADH). It consists of a multisubunit oxygenease component that contains the active site and a dinuclear iron center, a reductase component that contains FAD and one iron-sulfur cluster, and a regulatory component. The three components comprise five different polypeptides. The enzyme catalyses the first two steps of a dimethyl sulfide oxidation pathway in this

organism.

References: [1724, 1725]

[EC 1.14.13.245 created 2019]

EC 1.14.13.246

Accepted name: 4β -methylsterol monooxygenase

Reaction: a 3β -hydroxy-4,4-dimethylsteroid + **3** NADH + **3** H⁺ + **3** O₂ = a 3β -hydroxy-4 α -methylsteroid-4 β -

carboxylate + 3 NAD^+ + $4 \text{ H}_2\text{O}$ (overall reaction)

(1a) a 3 β -hydroxy-4,4-dimethylsteroid + NADH + H⁺ + O₂ = a 3 β -hydroxy-4 β -hydroxymethyl-4 α -

methylsteroid + NAD^+ + H_2O

(1b) a 3 β -hydroxy-4 β -hydroxymethyl-4 α -methylsteroid + NADH + H⁺ + O₂ = a 3 β -hydroxy-4 β -

formyl- 4α -methylsteroid + NAD⁺ + 2 H₂O

(1c) a 3 β -hydroxy-4 β -formyl-4 α -methylsteroid + NADH + H⁺ + O₂ = a 3 β -hydroxy-4 α -methylsteroid-

 4β -carboxylate + NAD⁺ + H₂O

Other name(s): sdm

sdmA (gene name)

Systematic name: 3β-hydroxy-4,4-dimethylsteroid,NADH:oxygen oxidoreductase (*C*-4mβ-hydroxylating)

Comments: Contains a Rieske [2Fe-2S] iron-sulfur cluster. This bacterial enzyme (SdmA) participates in the

biosynthesis of bacterial sterols. Together with SdmB it forms an enzyme system that removes one methyl group from the C-4 position of 4,4-dimethylated steroid molecules. SdmA catalyses three successive oxidations of the C-4 β methyl group, turning it into a carboxylate group; the second enzyme, SdmB, is a bifunctional enzyme that catalyses two different activities. As EC 1.1.1.417, 3 β -hydroxysteroid-4 β -carboxylate 3-dehydrogenase (decarboxylating), it catalyses an oxidative decarboxylation that results in reduction of the 3 β -hydroxy group at the C-3 carbon to an oxo group. As EC 1.1.270, 3 β -hydroxysteroid 3-dehydrogenase, it reduces the 3-oxo group back to a 3 β -hydroxyl. Unlike the animal/fungal enzyme EC 1.14.18.9, 4 α -methylsterol monooxygenase, and the plant enzymes EC 1.14.18.10, plant 4,4-dimethylsterol C-4 α -methyl-monooxygenase, and EC 1.14.18.11, plant 4 α -monomethylsterol monooxygenase, this enzyme acts preferentially on the 4 β -methyl group. Since no epimerization of the remaining C-4 α methyl group occurs, the enzyme can only remove one methyl

group, leaving a 4α -monomethylated product. Known substrates include 4,4-dimethyl- 5α -cholest-8-en- 3β -ol and 14-demethyllanosterol.

References: [2376]

[EC 1.14.13.246 created 2019]

EC 1.14.13.247

Accepted name: stachydrine *N*-demethylase

Reaction: L-proline betaine + NAD(P)H + H⁺ + O₂ = N-methyl-L-proline + formaldehyde + NAD(P)⁺ + H₂O

Other name(s): L-proline betaine N-demethylase; stc2 (gene name)

Systematic name: L-proline betaine,NAD(P)H:oxygen oxidoreductase (formaldehyde-forming)

Comments: The enzyme, characterized from the bacterium *Sinorhizobium meliloti* 1021, consists of three different

types of subunits. The catalytic unit contains a Rieske [2Fe-2S] iron-sulfur cluster, and catalyses the monooxygenation of a methyl group. The resulting N-methoxyl group is unstable and decomposes spontaneously to form formaldehyde. The other subunits are involved in the transfer of electrons from

NAD(P)H to the catalytic subunit.

References: [835, 2283]

[EC 1.14.13.247 created 2017]

Accepted name: L-aspartate *N*-monooxygenase (nitrosuccinate-forming)

L-aspartate + 3 NADPH + 3 H⁺ + 3 O₂ = (2S)- 2-nitrobutanedioate + 3 NADP⁺ + 4 H₂O **Reaction:**

(1a) L-aspartate + NADPH + H^+ + O_2 = N-hydroxy-L-aspartate + NADP⁺ + H_2O

(1b) N-hydroxy-L-aspartate + NADPH + H^+ + $O_2 = N$, N-dihydroxy-L-aspartate + NADP+ + H_2O

(1c) N,N-dihydroxy-L-aspartate = (2S)-2-nitrosobutanedioate + H₂O (spontaneous)

(1d) (2S)-2-nitrosobutanedioate + NADPH + H^+ + O_2 = (2S)-2-nitrobutanedioate + NADP⁺ + H_2O

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

L-aspartate, NADPH: oxygen oxidoreductase [(2S)-2-nitrobutanedioate-forming] **Systematic name:**

Comments: The enzyme, found in some Actinobacteria, is involved in a pathway that forms nitrite, which is sub-

sequently used to generate a diazo group in some secondary metabolites. Requires an FAD cofactor.

References: [4092, 1475]

[EC 1.14.13.248 created 2021]

EC 1.14.13.249

Accepted name: 3-amino-4-hydroxybenzoate 2-monooxygenase

Reaction: 3-amino-4-hydroxybenzoate + NADPH + H $^+$ + O₂ = 3-amino-2,4-dihydroxybenzoate + NADP $^+$ +

Other name(s): creL (gene name); ptmB3 (gene name); ptnB3 (gene name)

Systematic name: 3-amino-4-hydroxybenzoate,NADPH:oxygen oxidoreductase (2-hydroxylating)

Comments: Requires FAD. The CreL enzyme from the bacterium Streptomyces cremeus participates in the

biosynthesis of cremeomycin. The PrmB3 and PtnB3 enzymes from Streptomyces platensis are in-

volved in the biosynthesis of platensimycin and platencin, respectively.

[3931, 4494, 4092, 948] **References:**

[EC 1.14.13.249 created 2021]

EC 1.14.13.250

Accepted name: nitrosourea synthase

> N^{ω} -methyl-L-arginine + 2 NADH + 2 H⁺ + 3 O₂ = N^{δ} -hydroxy- N^{ω} -methyl- N^{ω} -nitroso-L-citrulline + **Reaction:**

> > 2 NAD $^+$ + 3 H₂O (overall reaction)

(1a) N^{ω} -methyl-L-arginine + NADH + H⁺ + O₂ = N^{δ} -hydroxy- N^{ω} -methyl-L-arginine + NAD⁺ + H₂O (1b) N^{δ} -hydroxy- N^{ω} -methyl-L-arginine + NADH + H⁺ + O₂ = N^{δ} , $N^{\omega'}$ -dihydroxy- N^{ω} -methyl-L-

arginine + NAD^+ + H_2O

(1c) N^{δ} , $N^{\omega\prime}$ -dihydroxy- N^{ω} -methyl-L-arginine + $O_2 = N^{\delta}$ -hydroxy- N^{ω} -methyl- N^{ω} -nitroso-L-citrulline

+ H₂O

sznF (gene name); StzF Other name(s):

 N^{ω} -methyl-L-arginine,NADH:oxygen oxidoreductase (N^{δ} -hydroxy- N^{ω} -methyl- N^{ω} -nitroso-L-**Systematic name:**

citrulline-forming)

Comments: The enzyme, characterized from the bacterium *Streptomyces achromogenes subsp. streptozoticus*,

> catalyses a complex multi-step reaction during the biosynthesis of the glucosamine-nitrosourea antibiotic streptozotocin. The overall reaction is an oxidative rearrangement of the guanidine group of N^{ω} -methyl-L-arginine, generating an N-nitrosourea product. The enzyme hydroxylates its substrate at the N^{δ} position, followed by a second hydroxylation at the $N^{\omega'}$ position. It then catalyses an oxidative rearrangement to form N^{δ} -hydroxy- N^{ω} -methyl- N^{ω} -nitroso-L-citrulline. This product is unstable, and degrades non-enzymically into nitric oxide and the denitrosated product N^{δ} -hydroxy- N^{ω} -methyl-L-citrulline. The enzyme contains two active sites, each of which utilizes a different iron-containing

cofactor.

[3057, 1588, 2740, 2739, 4517] **References:**

[EC 1.14.13.250 created 2021]

Accepted name: glycine betaine monooxygenase

Reaction: glycine betaine + NADH + H⁺ + O₂ = N,N-dimethylglycine + formaldehyde + NAD⁺ + H₂O

Other name(s): glycine betaine dioxygenase (incorrect); bmoAB (gene names); gbcAB (gene names)

Systematic name: glycine betaine,NADH:oxygen oxidoreductase (demethylating)

Comments: The enzyme, characterized from the bacteria *Pseudomonas aeruginosa* and *Chromohalobacter salexi-*

gens, is involved in a degradation pathway of glycine betaine. It is composed of two subunits - a ferredoxin reductase component that contains FAD, and a terminal oxygenase component that contains a

[2Fe-2S] Rieske-type iron-sulfur cluster and a nonheme iron centre.

References: [4543, 2456, 3823]

[EC 1.14.13.251 created 2022]

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] + O_2 = 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 xeno-

biotics, steroids, fatty acids, vitamins and prostaglandins; reactions catalysed include hydroxylation, epoxidation, N-oxidation, sulfooxidation, 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: [390, 1213, 1564, 1805, 1930, 2297, 2343, 2344, 2417, 2549, 2830, 2831, 3009, 3033, 4106, 4254,

4265]

[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 + hv

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 oxidore-

ductase (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 lu-

ciferase.

References: [1554, 1553, 1555, 3032, 4137, 2300]

[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 + O_2 = an aldehyde + FMN + sulfite + H_2O

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 C_1 - to C_{14} -sulfonates as well as substituted C_2 -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: [1028]

[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 H_2O 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 ri-

way 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: [2525]

[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 [4712]. FADH₂ is provided by EC 1.5.1.36, flavin

reductase (NADH) [1256, 2545].

References: [12, 3381, 3380, 4712, 1256, 2545]

[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: [4370, 2169, 4708]

[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: [3208, 4296]

[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 + O_2 = 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: [965]

[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: $4-(\gamma-L-glutamylamino)$ butanoyl-[BtrI acyl-carrier protein] + FMNH₂ + O₂ = $4-(\gamma-L-glutamylamino)$ -

(2S)-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. $FMNH_2$ 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 pro-

tein is mandatory. Octanoyl-S-[BtrI acyl-carrier protein] is also accepted.

References: [2465]

[EC 1.14.14.13 created 2012]

EC 1.14.14.14

Accepted name: aromatase

Reaction: (1) testosterone + $3 O_2 + 3$ [reduced NADPH—hemoprotein reductase] = 17β -estradiol + formate + 4

 $H_2O + 3$ [oxidized NADPH—hemoprotein reductase] (overall reaction)

(1a) testosterone + O_2 + [reduced NADPH—hemoprotein reductase] = 19-hydroxytestosterone + H_2O

+ [oxidized NADPH—hemoprotein reductase]

(1b) 19-hydroxytestosterone + O_2 + [reduced NADPH—hemoprotein reductase] = 19-oxotestosterone

+ 2 H₂O + [oxidized NADPH—hemoprotein reductase]

(1c) 19-oxotestosterone + O_2 + [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 + for-

mate + $4 \text{ H}_2\text{O} + 3$ [oxidized NADPH—hemoprotein reductase] (overall reaction)

(2a) androst-4-ene-3,17-dione + O_2 + [reduced NADPH—hemoprotein reductase] = 19-

hydroxyandrost-4-ene-3,17-dione + H₂O + [oxidized NADPH—hemoprotein reductase]

(2b) 19-hydroxyandrost-4-ene-3,17-dione + O_2 + [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: testosteronel,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: [4270, 1128, 2060, 1315]

[EC 1.14.14.14 created 2013]

EC 1.14.14.15

Accepted name: (3S)-3-amino-3-(3-chloro-4-hydroxyphenyl)propanoyl-[peptidyl-carrier protein SgcC2] monooxyge-

nase

Reaction: (3S)-3-amino-3-(3-chloro-4-hydroxyphenyl)propanoyl-[peptidyl-carrier protein SgcC2] + FADH₂ +

O₂ = (3S)-3-amino-3-(3-chloro-4,5-dihydroxyphenyl)propanoyl-[peptidyl-carrier protein SgcC2] +

 $FAD + H_2O$

Other name(s): SgcC

Systematic name: (3S)-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: [2493]

[EC 1.14.14.15 created 2014]

Accepted name: steroid 21-monooxygenase

Reaction: a C_{21} steroid + [reduced NADPH—hemoprotein reductase] + O_2 = a 21-hydroxy- C_{21} -steroid + [oxi-

dized 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: [1577, 3333, 3611, 2214, 2669, 124]

[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] + $O_2 = (3S)-2,3$ -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

[3186, 690].

References: [735, 4230, 4414, 4741, 3186, 3673, 690, 1587]

[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 O_2 = biliverdin + Fe²⁺ + CO + 3 [oxi-

dized NADPH—hemoprotein reductase] + 3 H₂O

Other name(s): ORP33 proteins; haem oxygenase (ambiguous); heme oxygenase (decyclizing) (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, hydroxy-

lating)

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 [3096]. 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 reduc-

tase. cf. EC 1.14.15.20, heme oxygenase (biliverdin-producing, ferredoxin).

References: [2622, 4124, 4812, 3096, 2324]

[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 17α-monooxygenase

Reaction: a C_{21} -steroid + [reduced NADPH—hemoprotein reductase] + O_2 = a 17α -hydroxy- C_{21} -steroid + [oxi-

dized NADPH—hemoprotein reductase] + H₂O

Other name(s): steroid 17α-hydroxylase; cytochrome P-450 17α; cytochrome P-450 (P-450 17α,lyase); 17α-

hydroxylase-C17,20 lyase; CYP17; CYP17A1 (gene name)

Systematic name: steroid,NADPH—hemoprotein reductase:oxygen oxidoreductase (17α-hydroxylating)

Comments: Requires NADPH and EC 1.6.2.4, NADPH—hemoprotein reductase. A microsomal hemoprotein that

catalyses two independent reactions at the same active site - the 17α -hydroxylation of pregnenolone and progesterone, which is part of glucocorticoid hormones biosynthesis, and the conversion of the 17α -hydroxylated products via a 17,20-lyase reaction to form androstenedione and dehydroepiandrosterone, leading to sex hormone biosynthesis (EC 1.14.14.32, 17α -hydroxyprogesterone deacetylase). The ratio of the 17α -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: [2571, 4809, 1326, 2210, 3273]

[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 2015 to EC 1.14.14.19]

EC 1.14.14.20

Accepted name: phenol 2-monooxygenase (FADH₂)

Reaction: phenol + FADH₂ + O₂ = catechol + FAD + H₂O

Other name(s): *pheA*1 (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 [2125] as well as 4-nitrophenol, 3-nitrophenol, and resorcinol [3618]. 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

[2125, 3618]. cf. EC 1.14.13.7, phenol 2-monooxygenase (NADPH).

References: [2125, 4401, 3618]

[EC 1.14.14.20 created 2016]

EC 1.14.14.21

Accepted name: dibenzothiophene monooxygenase

Reaction: dibenzothiophene + 2 FMNH₂ + 2 O_2 = dibenzothiophene-5,5-dioxide + 2 FMN + 2 O_2 = dibenzothiophene

reaction)

(1a) dibenzothiophene + $FMNH_2 + O_2 = dibenzothiophene-5-oxide + <math>FMN + H_2O$

(1b) dibenzothiophene-5-oxide + $FMNH_2 + O_2 = dibenzothiophene-5,5-dioxide + <math>FMN + H_2O$

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 dibenzothio-

phenes, 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, dibenzothio-

phene sulfone monooxygenase.

References: [1391, 2523, 1435]

[EC 1.14.14.21 created 2016]

EC 1.14.14.22

Accepted name: dibenzothiophene sulfone monooxygenase

Reaction: dibenzothiophene-5,5-dioxide + FMNH₂ + NADH + $O_2 = 2'$ -hydroxybiphenyl-2-sulfinate + $O_2 = 2'$ -hydroxybiphenyl-2-sulfinate

FMN + NAD⁺ + H⁺ (overall reaction) (1a) FMNH₂ + O₂ = FMN- N^5 -peroxide

(1b) dibenzothiophene-5,5-dioxide + FMN- N^5 -peroxide = 2'-hydroxybiphenyl-2-sulfinate + FMN- N^5 -

oxide

(1c) FMN- N^5 -oxide + NADH = FMN + H_2O + NAD⁺ + H^+ (spontaneous)

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. The flavin- N^5 -oxide that is formed by the enzyme reacts spontaneously with NADH

to give oxidized flavin, releasing a water molecule.

References: [1391, 3146, 2222, 3145, 18, 19, 2723]

[EC 1.14.14.22 created 2016, modified 2019]

EC 1.14.14.23

Accepted name: cholesterol 7α-monooxygenase

Reaction: cholesterol + [reduced NADPH—hemoprotein reductase] + $O_2 = 7\alpha$ -hydroxycholesterol + [oxidized

NADPH—hemoprotein reductase] + H₂O

Other name(s): cholesterol 7α-hydroxylase; CYP7A1 (gene name)

Systematic name: cholesterol,NADPH—hemoprotein reductase:oxygen oxidoreductase (7α-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: [2835, 412, 3134, 3060, 3059]

[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: calciol + 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: calciol,NADPH—hemoprotein reductase:oxygen oxidoreductase (25-hydroxylating)

Comments: A microsomal enzyme isolated from human and mouse liver that bioactivates vitamin D_3 . While mul-

tiple 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* [4921]. The di-

rect electron donor to the enzyme is EC 1.6.2.4, NADPH—hemoprotein reductase.

References: [642, 3886, 4075, 4921]

[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] + O_2 = (24*S*)-cholest-5-ene-3 β ,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 [371]. 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 [2689]. The direct electron

donor to the enzyme is EC 1.6.2.4, NADPH—hemoprotein reductase [2689].

References: [2562, 371, 2689, 2564, 3607]

[EC 1.14.14.25 created 2005 as EC 1.14.13.98, transferred 2016 to EC 1.14.14.25]

Accepted name: 24-hydroxycholesterol 7α-hydroxylase

Reaction: (24S)-cholest-5-ene-3 β ,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: (24*S*)-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 epithe-

lium [1792]. The enzyme is specific for (24S)-cholest-5-ene-3 β ,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: [2469, 1792, 3607]

[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 -resorcylate and resorcinol. *cf.* EC 1.14.13.220, resorcinol 4-hydroxylase (NADH), and EC 1.14.13.219, resorcinol 4-hydroxylase

(NADPH).

References: [3148, 4810]

[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 C_{15} to C_{36} into their corresponding primary alcohols [1100, 2449].

The FMNH₂ cofactor is provided by an FMN reductase [949].

References: [1100, 2449, 949]

[EC 1.14.14.28 created 2016]

EC 1.14.14.29

Accepted name: 25/26-hydroxycholesterol 7α-hydroxylase

Reaction: (1) cholest-5-ene-3 β ,25-diol + [reduced NADPH—hemoprotein reductase] + O₂ = cholest-5-ene-

 3β , 7α ,25-triol + [oxidized NADPH—hemoprotein reductase] + H_2O

(2) (25R)-cholest-5-ene-3 β ,26-diol + [reduced NADPH—hemoprotein reductase] + O₂ = (25R)-

cholest-5-ene-3 β ,7 α ,26-triol + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): 25-hydroxycholesterol 7α-monooxygenase; CYP7B1; CYP7B1 oxysterol 7α-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-3β,25/26-diol, [NADPH—hemoprotein reductase]: oxygen oxidoreductase (7α-

hydroxylating)

Comments: A *P*-450 (heme-thiolate) protein. Unlike EC 1.14.14.26, 24-hydroxycholesterol 7α-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 [4302].

The direct electron donor to the enzyme is EC 1.6.2.4, NADPH—hemoprotein reductase.

References: [2285, 4302, 2469, 3498, 3607]

[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 + $O_2 = N$ -(2-methylpropyl)hydroxylamine + FAD + H₂O

(2) 2-methylpropan-1-amine + FMNH₂ + $O_2 = N$ -(2-methylpropyl)hydroxylamine + FMN + H_2O

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: [3244, 3245, 3243]

[EC 1.14.14.30 created 2016, modified 2017]

EC 1.14.14.31

Accepted name: ipsdienol synthase

Reaction: myrcene + [reduced NADPH—hemoprotein reductase] + $O_2 = (R)$ -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: [3656, 3962]

[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: 17α-hydroxyprogesterone deacetylase

Reaction: (1) 17α -hydroxyprogesterone + [reduced NADPH—hemoprotein reductase] + O_2 = androstenedione

+ acetate + [oxidized NADPH—hemoprotein reductase] + H₂O

(2) 17α -hydroxypregnenolone + [reduced NADPH—hemoprotein reductase] + O_2 = 3β -

hydroxyandrost-5-en-17-one + acetate + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): C-17/C-20 lyase; 17α-hydroxyprogesterone acetaldehyde-lyase; CYP17; CYP17A1 (gene name);

17α-hydroxyprogesterone 17,20-lyase

Systematic name: 17α-hydroxyprogesterone,NADPH—hemoprotein reductase:oxygen oxidoreductase (17α-

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 gluco-corticoid 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 [153, 3906]. 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 [1326]. **References:** [1326, 153, 2624, 3906, 328]

[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 FMNH_2 + 2 O_2 = ethylenediamine-N,N'-diacetate + $2 \text{ glyoxylate} + 2 \text{ o}_2$

FMN + 2 H₂O (overall reaction)

(1a) ethylenediaminetetraacetate + FMNH₂ + O₂ = ethylenediaminetriacetate + glyoxylate + FMN +

 H_2O

(1b) ethylenediaminetriacetate + FMNH $_2$ + O $_2$ = 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: [4647, 3268, 374]

[EC 1.14.14.33 created 2016]

EC 1.14.14.34

Accepted name: methanesulfonate monooxygenase (FMNH₂)

Reaction: methanesulfonate + FMNH₂ + O_2 = formaldehyde + FMN + sulfite + H_2O

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 methanesul-

fonate 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: [2072, 1046]

[EC 1.14.14.34 created 2016]

EC 1.14.14.35

Accepted name: dimethylsulfone monooxygenase

Reaction: dimethyl sulfone + FMNH₂ + O_2 = methanesulfinate + formaldehyde + FMN + H_2O

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 sponta-

neously to methanesulfonate in the presence of dioxygen and FMNH₂.

References: [1045, 4616]

[EC 1.14.14.35 created 2016]

EC 1.14.14.36

Accepted name: tyrosine *N*-monooxygenase

Reaction: L-tyrosine + 2 O_2 + 2 [reduced NADPH—hemoprotein reductase] = (E)-[4-

hydroxyphenylacetaldehyde oxime] + 2 [oxidized NADPH—hemoprotein reductase] + CO₂ + 3

H₂O (overall reaction)

(1a) L-tyrosine + O_2 + [reduced NADPH—hemoprotein reductase] = N-hydroxy-L-tyrosine + [oxidized

NADPH—hemoprotein reductase] + H₂O

(1b) N-hydroxy-L-tyrosine + O_2 + [reduced NADPH—hemoprotein reductase] = N, N-dihydroxy-L-

tyrosine + [oxidized NADPH—hemoprotein reductase] + H₂O

(1c) N,N-dihydroxy-L-tyrosine = (E)-[4-hydroxyphenylacetaldehyde oxime] + CO_2 + H_2O

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 biosynthe-

sis of the cyanogenic glucoside dhurrin. In Sinapis alba (white mustard) the enzyme is involved in the

biosynthesis of the glucosinolate sinalbin.

References: [1481, 3897, 289, 1978, 187, 3068, 510, 2265, 699]

[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] + $O_2 = (S)$ -4-

hydroxymandelonitrile + [oxidized NADPH—hemoprotein reductase] + $2 \text{ H}_2\text{O}$ (overall reaction) (1a) (*E*)-4-hydroxyphenylacetaldehyde oxime = (*Z*)-4-hydroxyphenylacetaldehyde oxime

(1b) (Z)-4-hydroxyphenylacetaldehyde oxime = 4-hydroxyphenylacetonitrile + H_2O

(1c) 4-hydroxyphenylacetonitrile + [reduced NADPH—hemoprotein reductase] + O_2 = (S)-4-

hydroxymandelonitrile + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): 4-hydroxybenzeneacetaldehyde oxime monooxygenase; cytochrome P450II-dependent monooxyge-

nase; NADPH-cytochrome P450 reductase (CYP71E1); CYP71E1; 4-hydroxyphenylacetaldehyde

oxime,NADPH:oxygen oxidoreductase

Systematic name: (E)-4-hydroxyphenylacetaldehyde oxime, [reduced NADPH—hemoprotein reductase]: oxygen oxi-

doreductase

Comments: This cytochrome P-450 (heme thiolate) enzyme is involved in the biosynthesis of the cyanogenic glu-

coside dhurrin in sorghum. It catalyses three different activities - isomerization of the (E) isomer to

the (*Z*) isomer, dehydration, and C-hydroxylation.

References: [2590, 3863, 510, 2265, 699]

[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] + $2 O_2 = (E)$ -2-methylpropanal oxime + 2

[oxidized NADPH—hemoprotein reductase] + CO₂ + 3 H₂O (overall reaction)

(1a) L-valine + [reduced NADPH—hemoprotein reductase] + $O_2 = N$ -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 + CO_2 + H_2O

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: [90, 1150]

[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 $O_2 = (1E,2S)$ -2-methylbutanal

oxime + 2 [oxidized NADPH—hemoprotein reductase] + CO_2 + 3 H_2O (overall reaction)

(1a) L-isoleucine + [reduced NADPH—hemoprotein reductase] + $O_2 = N$ -hydroxy-L-isoleucine + [ox-

idized NADPH—hemoprotein reductase] + H₂O

(1b) N-hydroxy-L-isoleucine + [reduced NADPH—hemoprotein reductase] + $O_2 = N$, N-dihydroxy-L-

isoleucine + [oxidized NADPH—hemoprotein reductase] + H₂O

(1c) N,N-dihydroxy-L-isoleucine = (1E,2S)-2-methylbutanal oxime + CO_2 + H_2O (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: [90, 1150]

[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 $O_2 = (E)$ -phenylacetaldoxime +

2 [oxidized NADPH—hemoprotein reductase] + CO₂ + 3 H₂O (overall reaction)

(1a) L-phenylalanine + [reduced NADPH—hemoprotein reductase] + $O_2 = N$ -hydroxy-L-phenylalanine

+ [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) N-hydroxy-L-phenylalanine + [reduced NADPH—hemoprotein reductase] + $O_2 = N$, N-dihydroxy-

L-phenylalanine + [oxidized NADPH—hemoprotein reductase] + H₂O

(1c) N,N-dihydroxy-L-phenylalanine = (E)-phenylacetaldoxime + CO_2 + H_2O

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: [4648, 4734]

[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] + O_2 = 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 + H_2O

(1c) 2-methylbutanenitrile + [reduced NADPH—hemoprotein reductase] + O_2 = 2-hydroxy-2-

methylbutanenitrile + [oxidized NADPH—hemoprotein reductase] + H₂O

(2) (E)-2-methylpropanal oxime + [reduced NADPH—hemoprotein reductase] + O_2 = 2-hydroxy-2-

methylpropanenitrile + [oxidized NADPH—hemoprotein reductase] + $2 H_2O$ (overall reaction)

(2a) (*E*)-2-methylpropanal oxime = (*Z*)-2-methylpropanal oxime (2b) (*Z*)-2-methylpropanal oxime = 2-methylpropanenitrile + H_2O

(2c) 2-methylpropanenitrile + [reduced NADPH—hemoprotein reductase] + O_2 = 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 glu-

cosides lotaustralin and linamarin. It catalyses three different activities - isomerization of its substrate,

the (E) isomer, to the (Z) isomer, dehydration, and C-hydroxylation.

References: [1949]

[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 O_2 = an (E)- ω -

(methylsulfanyl)alkanal oxime + 2 [oxidized NADPH—hemoprotein reductase] + CO₂ + 3 H₂O

(overall reaction)

(1a) an L-polyhomomethionine + [reduced NADPH—hemoprotein reductase] + O_2 = an L-N-

hydroxypolyhomomethionine + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) an L-N-hydroxypolyhomomethionine + [reduced NADPH—hemoprotein reductase] + O_2 = an

L-N,N-dihydroxypolyhomomethionine + [oxidized NADPH—hemoprotein reductase] + H₂O

(1c) an L-N,N-dihydroxypolyhomomethionine = an (E)- ω -(methylsulfanyl)alkanal oxime + CO_2 + H_2O

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 glu-

cosinolates 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: [1511, 636]

[EC 1.14.14.42 created 2017]

Accepted name: (methylsulfanyl)alkanaldoxime *N*-monooxygenase

Reaction: an (E)-ω-(methylsulfanyl)alkanal oxime + [reduced NADPH—hemoprotein reductase] + glutathione

+ O_2 = an S-[(1E)-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-[(1E)-1-(hydroxyimino)-ω-

(methylsulfanyl)alkyl]-L-glutathione + H₂O

Other name(s): CYP83A1 (gene name); (methylthio)alkanaldoxime N-monooxygenase; (E)-ω-

(methylthio)alkananaldoxime,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase

(*N*-hydroxylating)

Systematic name: (E)-ω-(methylsulfanyl)alkananal oxime, [reduced NADPH—hemoprotein reductase]: oxygen oxidore-

ductase (*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: [188, 3024, 699]

[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] + $O_2 = (R)$ -

mandelonitrile + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)

(1a) (*E*)-phenylacetaldehyde oxime = (*Z*)-phenylacetaldehyde oxime (1b) (*Z*)-phenylacetaldehyde oxime = phenylacetonitrile + H_2O

(1c) phenylacetonitrile + [reduced NADPH—hemoprotein reductase] + $O_2 = (R)$ -mandelonitrile + [ox-

idized 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 glu-

cosides (R)-prunasin and (R)-amygdalin. It catalyses three different activities - isomerization of the

(E) isomer to the (Z) isomer, dehydration, and C-hydroxylation.

References: [4734]

[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 +

 $O_2 = S-[(E)-N-hydroxy(indol-3-yl)acetimidoyl]-L-glutathione + [oxidized NADPH—hemoprotein]$

reductase] + 2 H₂O (overall reaction)

(1a) (E)-indol-3-ylacetaldehyde oxime + [reduced NADPH—hemoprotein reductase] + $O_2 = 1-(1H-1)$

indol-3-yl)-2-aci-nitroethane + [oxidized NADPH—hemoprotein reductase] + H₂O

 $(1b) \ 1 - (1H-\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl})\text{acetimidoyl}] - L-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} = S - [(E)-N-\text{hydroxy}(\text{indol-}3-\text{yl}) - 2 - aci-\text{nitroethane} + \text{glutathione} + \text{glutath$

glutathione + H_2O (spontaneous)

(2) (E)-phenylacetaldehyde oxime + [reduced NADPH—hemoprotein reductase] + glutathione + O_2 =

S-[(Z)-N-hydroxy(phenyl)acetimidoyl]-L-glutathione + [oxidized NADPH—hemoprotein reductase] +

2 H₂O (overall reaction)

(2a) (E)-phenylacetaldehyde oxime + [reduced NADPH—hemoprotein reductase] + O_2 = 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 oxidore-

ductase (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: [188, 3024, 1311]

[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 O_2 = pimeloyl-[acyl-carrier pro-

tein] + an n-alkanal + 2 oxidized flavodoxin + 3 H_2O (overall reaction)

(1a) a long-chain acyl-[acyl-carrier protein] + reduced flavodoxin + O_2 = 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 + O_2 = 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): biol (gene name); P450Biol; 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 [780].

References: [4045, 780, 779, 777]

[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 L-arginine + 3 reduced flavodoxin + 4 O₂ = 2 L-citrulline + 2 nitric oxide + 3 oxidized flavodoxin +

4 H₂O (overall reaction)

(1a) 2 L-arginine + 2 reduced flavodoxin + 2 $O_2 = 2 N^{\omega}$ -hydroxy-L-arginine + 2 oxidized flavodoxin +

2 H₂O

(1b) 2 N^{ω} -hydroxy-L-arginine + reduced flavodoxin + 2 O_2 = 2 L-citrulline + 2 nitric oxide + oxidized

flavodoxin + $2 H_2O$

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: [3233, 17, 4540, 31, 1692]

[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] + O_2 = a 12-

hydroxyjasmonoyl-L-amino acid + [oxidized NADPH—hemoprotein reductase] + H₂O

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: [2225, 2136, 1615, 2135, 2226, 4619]

[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 O_2 = a 12-

hydroxy-12-oxojasmonoyl-L-amino acid + 2 [oxidized NADPH—hemoprotein reductase] + 3 H₂O

(overall reaction)

(1a) a 12-hydroxyjasmonoyl-L-amino acid + [reduced NADPH—hemoprotein reductase] + O₂ = a 12-

oxojasmonoyl-L-amino acid + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1b) a 12-oxojasmonoyl-L-amino acid + [reduced NADPH—hemoprotein reductase] + O₂ = a 12-

hydroxy-12-oxojasmonoyl-L-amino acid + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP94C1 (gene name)

Systematic name: 12-hydroxyjasmonoyl-L-amino acid,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreduc-

tase (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: [1615, 4619, 465]

[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] + $O_2 = (3R)$ -3-hydroxy-

16-methoxy-1,2-didehydro-2,3-dihydrotabersonine + [oxidized NADPH—hemoprotein reductase] +

 H_2O

(2) tabersonine + [reduced NADPH—hemoprotein reductase] + $O_2 = (3R)$ -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 biosynthe-

sis 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: [3407]

[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] + $O_2 = (-)$ -trans-carveol + [oxidized

NADPH—hemoprotein reductase] + H₂O

Other name(s): (-)-limonene 6-hydroxylase; (-)-limonene 6-monooxygenase; (-)-limonene,NADPH:oxygen oxidore-

ductase (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: [1996]

[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] + $O_2 = (-)$ -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: [1996, 2726, 1217]

[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] + O_2 = (+)-trans-carveol + [oxidized

NADPH—hemoprotein reductase] + H_2O

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: [407, 408]

[EC 1.14.14.53 created 2003 as EC 1.14.13.80, transferred 2017 to EC 1.14.14.53]

Accepted name: phenylacetate 2-hydroxylase

Reaction: phenylacetate + [reduced NADPH—hemoprotein reductase] + O_2 = (2-hydroxyphenyl)acetate + [oxi-

dized 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: [2818, 3549]

[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: [3494, 4873, 4904, 4905]

[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] + O_2 = 2-exo-hydroxy-1,8-cineole + [oxi-

dized 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 micro-

somes, 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: [2845, 2844, 2846]

[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 6α-hydroxylase

Reaction: (1) taurochenodeoxycholate + [reduced NADPH—hemoprotein reductase] + O_2 = taurohyocholate +

[oxidized NADPH—hemoprotein reductase] + H₂O

(2) lithocholate + [reduced NADPH—hemoprotein reductase] + O_2 = hyodeoxycholate + [oxidized

NADPH—hemoprotein reductase] + H_2O

Other name(s): CYP3A4; CYP4A21; taurochenodeoxycholate 6α-monooxygenase

Systematic name: taurochenodeoxycholate, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase (6α-

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 [2566].

References: [127, 126, 2257, 2565, 2566, 3607]

[EC 1.14.14.57 created 2005 asEC 1.14.13.97, transferred 2018 to EC 1.14.14.57]

Accepted name: trimethyltridecatetraene synthase

Reaction: (6E,10E)-geranyllinalool + [reduced NADPH—hemoprotein reductase] + $O_2 = (3E,7E)$ -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: (6E,10E)-geranyllinalool,[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 C_{16} homoterpene in response to herbivore attack. In vitro some variants of the enzyme also convert (3S,6E)-nerolidol to (3E)-4,8-dimethylnona-1,3,7-triene

(see EC 1.14.14.59, dimethylnonatriene synthase).

References: [2391, 3515]

[EC 1.14.14.58 created 2018]

EC 1.14.14.59

Accepted name: dimethylnonatriene synthase

Reaction: (3S,6E)-nerolidol + [reduced NADPH—hemoprotein reductase] + $O_2 = (3E)$ -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: (3S,6E)-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 C_{11} homoterpene in response to herbivore attack. In vitro the enzyme also converts (6E,10E)-geranyllinalool to (3E,7E)-4,8,12-trimethyltrideca-1,3,7,11-

tetraene (see EC 1.14.14.58, trimethyltridecatetraene synthase).

References: [2391, 3515]

[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] + H_2O

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 antioxi-

dant.

References: [1790, 3707, 1444]

[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 O_2 = carnosic acid + 3 [ox-

idized 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: [1790, 3707]

[EC 1.14.14.61 created 2018]

Accepted name: salviol synthase

Reaction: ferruginol + [reduced NADPH—hemoprotein reductase] + O_2 = 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: [1790]

[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 (baloon

flower). The enzyme is also able to oxidize oleanolic acid to cochalic acid.

References: [4191]

[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] + O_2 = daturadiol + [oxidized NADPH—

hemoprotein reductase] + H_2O

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: [4780]

[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] + $3 H_2O$

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 fer-

ruginol (EC 1.14.14.60 ferruginol monooxygenase).

References: [1444]

[EC 1.14.14.65 created 2018]

EC 1.14.14.66

Accepted name: marmesin synthase

Reaction: demethylsuberosin + [reduced NADPH—hemoprotein reductase] + O_2 = (+)-marmesin + [oxidized

NADPH—hemoprotein reductase] + H₂O

Systematic name: demethylsuberosin, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase

Comments: A *P*-450 monoxygenase involved in psoralen biosynthesis, see EC 1.14.13.102, psoralen synthase.

References: [1493]

[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] + O_2 = 11,20-dihydroxysugiol + [ox-

idized 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: [1444]

[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] + $O_2 = 9\beta$ -pimara-7,15-diene-

 3β -ol + [oxidized NADPH—hemoprotein reductase] + H_2O

Other name(s): CYP701A8

Systematic name: 9β-pimara7,15-diene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (9β-pimara-

7,15-diene-3 β -ol-forming)

Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from rice, *Oryza sativa*.

References: [2137]

[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** $O_2 = ent$ -3 β -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-2 β -ol + [reduced NADPH—hemoprotein reductase] + O_2 = ent-cassa-12,15-

dien-2-one + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1b') ent-cassa-12,15-dien-2 β -ol + [reduced NADPH—hemoprotein reductase] + O₂ = ent-cassa-12,15-

diene- 2β , 3β -diol + [oxidized NADPH—hemoprotein reductase] + H_2O

(1c) ent-cassa-12,15-dien-2-one + [reduced NADPH—hemoprotein reductase] + O₂ = ent-3β-

 $hydroxycassa-12,15-dien-2-one + [oxidized NADPH—hemoprotein\ reductase] + H_2O$

(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*-3β-

hydroxycassa-12,15-dien-2-one-forming)

Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Oryza sativa* (rice) that is in-

volved 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-2β,3β-diol as an intermediate.

References: [2137]

[EC 1.14.14.69 created 2018]

Accepted name: ent-sandaracopimaradiene 3-hydroxylase

Reaction: *ent*-sandaracopimaradiene + [reduced NADPH—hemoprotein reductase] + O₂ = *ent*-

sandaracopimaradien-3β-ol + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP701A; OsKOL4

Systematic name: ent-sandaracopimaradiene, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase (ent-

sandaracopimaradien-3β-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 9β -pimara-7,15-diene as substrate (*cf.* EC 1.14.14.68, *syn*-pimaradiene 3-monooxygenase).

References: [4527, 4684]

[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] + O_2 = 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: [4875]

[EC 1.14.14.71 created 2018]

EC 1.14.14.72

Accepted name: drimenol monooxygenase

Reaction: drimenol + [reduced NADPH—hemoprotein reductase] + O_2 = 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: [1627]

[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 + [oxi-

dized NADPH—hemoprotein reductase] + H₂O

(2) fenbendazole + [reduced NADPH—hemoprotein reductase] + O_2 = fenbendazole S-oxide + [oxi-

dized 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: [2898, 3463, 150, 2379, 4685]

[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: [4685]

[EC 1.14.14.74 created 2018]

EC 1.14.14.75

Accepted name: fenbendazole monooxygenase (4'-hydroxylating)

Reaction: fenbendazole + [reduced NADPH—hemoprotein reductase] + $O_2 = 4'$ -hydroxyfenbendazole + [oxi-

dized 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, al-

bendazole monooxygenase (hydroxylating). CYP2C19 does not act on albendazole.

References: [4685]

[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-2 β ,3 β -diol +

[oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)

(1a) ent-isokaurene + O_2 + [reduced NADPH—hemoprotein reductase] = ent-isokauren-2 β -ol + [oxi-

dized NADPH—hemoprotein reductase] + H_2O

(1b) ent-isokauren- 2β -ol + O₂ + [reduced NADPH—hemoprotein reductase] = ent-isokaurene- 2β ,3 β -

diol + [oxidized NADPH—hemoprotein reductase] + H_2O

Other name(s): CYP71Z6; *ent*-isokaurene C2-hydroxylase

Systematic name: *ent-*isokaurene,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (*ent-*isokaurene-

 2β , 3β -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: [4683, 2137]

[EC 1.14.14.76 created 2012 as EC 1.14.13.143, transferred 2018 to EC 1.14.14.76]

Accepted name: phenylacetonitrile α -monooxygenase

Reaction: phenylacetonitrile + [reduced NADPH—hemoprotein reductase] + $O_2 = (R)$ -mandelonitrile + [oxi-

dized 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 hualienen*-

sis. 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 sub-

strates at a lower rate.

References: [4733]

[EC 1.14.14.77 created 2018]

EC 1.14.14.78

Accepted name: phylloquinone ω-hydroxylase

Reaction: phylloquinone + [reduced NADPH—hemoprotein reductase] + $O_2 = \omega$ -hydroxyphylloquinone + [oxi-

dized NADPH—hemoprotein reductase] + H_2O

Other name(s): vitamin K_1 ω -hydroxylase; CYP4F2; CYP4F11

Systematic name: phylloquinone, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase (ω-

hydroxyphylloquinone-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 [1916].

References: [1916, 4205, 1020]

[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] + O_2 = 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: [2991]

[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] + O_2 = an ω -hydroxy-long-

chain fatty acid + [oxidized NADPH—hemoprotein reductase] + H_2O

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 arachido-

nate (20:4).

References: [292, 1679, 935, 1752]

[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

> a flavanone + 2 [reduced NADPH—hemoprotein reductase] + 2 O_2 = a 3',5'-dihydroxyflavanone + 2 **Reaction:**

> > [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)

(1a) a flavanone + [reduced NADPH—hemoprotein reductase] + O_2 = a 3'-hydroxyflavanone + [oxi-

dized NADPH—hemoprotein reductase] + H₂O

(1b) a 3'-hydroxyflavanone + [reduced NADPH—hemoprotein reductase] + O_2 = a 3',5'-

dihydroxyflavanone + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): flavonoid 3',5'-hydroxylase

Systematic name: flavanone, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase (3',5'-dihydroxylating)

A cytochrome P-450 (heme-thiolate) protein found in plants. The 3',5'-dihydroxyflavanone is formed **Comments:**

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 catal-

yses the hydroxylation of 3,5,7,3',4'-pentahydroxyflavanone (taxifolin) at the 5' position, forming ampelopsin.

[2772, 3865, 854] **References:**

[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] + O_2 = a 3'-hydroxyflavonoid + [oxidized

> > NADPH—hemoprotein reductase] + H₂O

CYP75B1 (gene name); flavonoid 3'-hydroxylase; flavonoid 3-hydroxylase (incorrect); Other name(s):

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, includ-

ing the flavanone naringenin and the flavone apigenin. Does not act on 4-coumarate or 4-coumaroyl-

CoA.

References: [1140, 470, 3741]

[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] + O_2 = (6E)-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 citronel-

lol, *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) [4129].

References: [715, 4516, 4129]

[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 = (6E)-8-oxolinalool + 2 [oxidized

NADPH—hemoprotein reductase] + 3 H₂O (overall reaction)

(1a) linalool + [reduced NADPH—hemoprotein reductase] + O_2 = (6E)-8-hydroxylinalool + [oxidized

NADPH—hemoprotein reductase] + H₂O

(1b) (6E)-8-hydroxylinalool + [reduced NADPH—hemoprotein reductase] + $O_2 = (6E)$ -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 spe-

cific [2Fe-2S] ferredoxin from the same bacterial strain.

References: [4372, 3570]

[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 monoterpenoid in-

dole alkaloids.

References: [2010, 2797]

[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** O_2 = ent-kaur-16-en-19-oate + **3**

 $[oxidized\ NADPH--hemoprotein\ reductase] + 4\ H_2O\ (overall\ reaction)$

(1a) ent-kaur-16-ene + [reduced NADPH—hemoprotein reductase] + O_2 = ent-kaur-16-en-19-ol + [ox-

idized NADPH—hemoprotein reductase] + H₂O

(1b) ent-kaur-16-en-19-ol + [reduced NADPH—hemoprotein reductase] + $O_2 = ent$ -kaur-16-en-19-al

+ [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1c) ent-kaur-16-en-19-al + [reduced NADPH—hemoprotein reductase] + $O_2 = ent$ -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: [146, 128, 1620]

[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 + O_2 + [reduced NADPH—hemoprotein reductase] = 2,4',7-trihydroxyisoflavanone

+ H₂O + [oxidized NADPH—hemoprotein reductase]

(2) (2S)-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: [2181, 1549, 4009, 3685, 3684]

[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: [1661]

[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] + $O_2 = 2'$ -hydroxyformononetin + [oxi-

dized 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 medi-

carpin and maackiain. EC 1.14.14.90, isoflavone 2'-hydroxylase, is less specific and acts on other

isoflavones as well as 4'-methoxyisoflavones.

References: [1661, 49, 2512]

[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] + O_2 = a 2'-hydroxyisoflavone + [oxi-

dized 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 re-

quires a 4'-methoxyisoflavone.

References: [49]

[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 + [oxi-

dized 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: [3359, 3608, 3320]

[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] + O_2 = 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: [3473, 1077]

[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 6a-monooxygenase

Reaction: (6aR,11aR)-3,9-dihydroxypterocarpan + [reduced NADPH—hemoprotein reductase] + O₂ =

(6aS,11aS)-3,6a,9-trihydroxypterocarpan + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): 3,9-dihydroxypterocarpan 6a-hydroxylase; 3,9-dihydroxypterocarpan 6α-monooxygenase (erro-

neous); CYP93A1 (gene name)

Systematic name: (6aR,11aR)-3,9-dihydroxypterocarpan,[reduced NADPH—hemoprotein reductase]:oxygen oxidore-

ductase (6a-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: [1476, 3744]

[EC 1.14.14.93 created 1989 as EC 1.14.13.28, transferred 2018 to EC 1.14.14.93]

Accepted name: leukotriene-B₄ 20-monooxygenase

Reaction: (6*Z*,8*E*,10*E*,14*Z*)-(5*S*,12*R*)-5,12-dihydroxyicosa-6,8,10,14-tetraenoate + [reduced NADPH—

hemoprotein reductase] + $O_2 = (6Z, 8E, 10E, 14Z) - (5S, 12R) - 5, 12, 20 - trihydroxyicosa - 6, 8, 10, 14 -$

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-dihydroxyicosa-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: [3563, 3815, 3949]

[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 O_2 = germacra-1(10),4,11(13)-

trien-12-oate + 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)

(1a) (+)-germacrene A + O_2 + [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: [3058, 2522]

[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-quinate 3'-monooxygenase

Reaction: trans-5-O-(4-coumaroyl)-D-quinate + [reduced NADPH—hemoprotein reductase] + $O_2 = trans-5-O$ -

caffeoyl-D-quinate + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): 5-*O*-(4-coumaroyl)-D-quinate/shikimate 3'-hydroxylase; coumaroylquinate(coumaroylshikimate) 3'-

monooxygenase; CYP98A3 (gene name)

Systematic name: trans-5-O-(4-coumaroyl)-D-quinate,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreduc-

tase (3'-hydroxylating)

Comments: A cytochrome P-450 (heme-thiolate) protein, found in plants. It also acts on trans-5-O-(4-

coumaroyl)shikimate.

References: [2279, 3740, 1166, 2709]

[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-monooxygenase

Reaction: (S)-N-methylcanadine + [reduced NADPH—hemoprotein reductase] + O_2 = allocryptopine + [oxi-

dized NADPH—hemoprotein reductase] + H₂O

Other name(s): methyltetrahydroprotoberberine 14-hydroxylase; (S)-cis-N-methyltetrahydroberberine 14-

monooxygenase; (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: [3596, 259]

[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] + O_2 = 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: [4193, 4181]

[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] + $O_2 = (-)$ -trans-isopiperitenol + [oxi-

dized 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: [1996, 2569, 4687]

[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] + O_2 = 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: [844]

[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] + O_2 = 12-

hydroxydihydrochelirubine + [oxidized NADPH—hemoprotein reductase] + H_2O

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: [1986]

[EC 1.14.14.101 created 1999 as EC 1.14.13.57, transferred 2018 to EC 1.14.14.101]

Accepted name: *N*-methylcoclaurine 3'-monooxygenase

Reaction: (S)-N-methylcoclaurine + [reduced NADPH—hemoprotein reductase] + $O_2 = (S)-3'$ -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 benzylisoquinoline alkaloid synthesis in

higher plants.

References: [3265]

[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: [3993, 322]

[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 (21α-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: [1080]

[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 10β-hydroxylase

Reaction: taxa-4(20),11-dien- 5α -yl acetate + [reduced NADPH—hemoprotein reductase] + $O_2 = 10\beta$ -

hydroxytaxa-4(20),11-dien-5α-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-5α-yl acetate, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase

(10β-hydroxylating)

Comments: This microsomal cytochrome-*P*-450 (heme-thiolate) enzyme from the plant *Taxus cuspidata* is in-

volved in the biosynthesis of the diterpenoid antineoplastic drug taxol (paclitaxel).

References: [4597, 1900, 3742]

 $[EC\ 1.14.14.105\ created\ 2002\ as\ EC\ 1.14.13.76,\ transferred\ 2018\ to\ EC\ 1.14.14.105]$

EC 1.14.14.106

Accepted name: taxane 13α-hydroxylase

Reaction: taxa-4(20),11-dien- 5α -ol + [reduced NADPH—hemoprotein reductase] + O_2 = taxa-4(20),11-dien-

5α,13α-diol + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP725A2 (gene name)

Systematic name: taxa-4(20),11-dien-5α-ol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (13α-

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: [4597, 1900]

[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 O_2 = gibberellin A_{12} + 3

[oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)

(1a) ent-kaur-16-en-19-oate + [reduced NADPH—hemoprotein reductase] + O_2 = ent-7\alpha-hydroxykaur-

16-en-19-oate + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) ent- 7α -hydroxykaur-16-en-19-oate + [reduced NADPH—hemoprotein reductase] + O_2 = gib-

berellin A₁₂ aldehyde + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1c) gibberellin A_{12} aldehyde + [reduced NADPH—hemoprotein reductase] + O_2 = gibberellin A_{12} +

[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 (hydroxy-

lating)

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 pump-

kin (Cucurbita maxima) ent-6α,7α-dihydroxykaur-16-en-19-oate is also formed.

References: [1619]

[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 + O_2 = (+)-5-oxo-1,2-campholide + FMN + H_2O

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)] [723, 4831, 4227]. Can accept several bicyclic ketones including (+)- and (-)-camphor [1970] and adamantanone [3795]. The prod-

uct spontaneously converts to [(1R)-2,2,3-trimethyl-5-oxocyclopent-3-enyl] acetate.

References: [723, 4831, 4227, 3795, 1946, 1970, 1858]

[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] + O_2 = 2-hydroxy-2*H*-1,4-

benzoxazin-3(4H)-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 protec-

tive and allelophatic benzoxazinoids in some plants, most commonly from the family of Poaceae

(grasses).

References: [1341, 1175, 3987]

[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-2H-1,4-benzoxazin-3(4H)-one + [reduced NADPH—hemoprotein reductase] + O₂ = 2,4-

dihydroxy-2H-1,4-benzoxazin-3(4H)-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 oxi-

doreductase (*N*-hydroxylating)

Comments: A cytochrome P-450 (heme-thiolate) protein. The enzyme is involved in the biosynthesis of protec-

tive and allelophatic benzoxazinoids in some plants, most commonly from the family of Poaceae

(grasses).

References: [182, 1341]

[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 + $3 O_2 + 3$ [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 + O_2 + [reduced NADPH—hemoprotein reductase] = 9β -pimara-7,15-dien-

19-ol + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) 9 β -pimara-7,15-dien-19-ol + O₂ + [reduced NADPH—hemoprotein reductase] = 9 β -pimara-7,15-

dien-19-al + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1c) 9β-pimara-7,15-dien-19-al + O_2 + [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: [4526]

[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-11 β -hydroxycassa-

12,15-diene + [oxidized NADPH—hemoprotein reductase] + H_2O

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: [4148]

 $[EC\ 1.14.14.112\ created\ 2012\ as\ EC\ 1.14.13.145,\ transferred\ 2018\ to\ EC\ 1.14.14.112]$

Accepted name: α-humulene 10-hydroxylase

Reaction: α -humulene + O₂ + [reduced NADPH—hemoprotein reductase] = 10-hydroxy- α -humulene + [oxi-

dized 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: [4833]

[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 [oxi-

dized 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 + [oxi-

dized 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 worm-

wood). Part of the biosynthetic pathway of artemisinin.

References: [4242]

[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 + $3 O_2 + 3$ [reduced NADPH—hemoprotein reductase] = glycyrrhetinate + 3 [oxi-

dized 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] = gly-

cyrrhetaldehyde + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1c) glycyrrhetaldehyde + O_2 + [reduced NADPH—hemoprotein reductase] = glycyrrhetinate + [oxi-

dized 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: [3790]

[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] + $O_2 = (1'S, 5'S)-5'-$

hydroxyaverantin + [oxidized NADPH—hemoprotein reductase] + H₂O

(2) (1'S)-averantin + [reduced NADPH—hemoprotein reductase] + $O_2 = (1'S, 5'R) - 5'$ -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 parasiti*-

cus. Involved in aflatoxin biosynthesis. Does not react with (1'R)-averantin.

References: [4717, 4835]

[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 O_2 = aflatoxin

B₁ + 2 [oxidized NADPH—hemoprotein reductase] + H₂O + methanol + CO₂

(2) 8-O-methyldihydrosterigmatocystin + 2 [reduced NADPH—hemoprotein reductase] + 2 O₂ = afla-

toxin 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: [327, 4836, 4363]

[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] + O_2 = 6-hydroxytryprostatin B + [oxi-

dized 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: [2019]

[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 $O_2 = 12\alpha$, 13α -

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 (12α , 13α -

dihydroxyfumitremorgin *C*-forming)

Comments: A cytochrome *P*-450 (heme-thiolate) protein. Involved in the biosynthetic pathway of the indole alka-

loid verruculogen.

References: [2019]

[EC 1.14.14.119 created 2013 as EC 1.14.13.177, transferred 2018 to EC 1.14.14.119]

Accepted name: dammarenediol 12-hydroxylase

Reaction: dammarenediol-II + [reduced NADPH—hemoprotein reductase] + O_2 = protopanaxadiol + [oxidized

NADPH—hemoprotein reductase] + H_2O

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: [1499]

[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] + O_2 = 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: [4844, 1498]

[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] + O_2 = 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: [4684]

[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] + O_2 = 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: [4684]

 $[EC\ 1.14.14.123\ created\ 2014\ as\ EC\ 1.14.13.193,\ transferred\ 2018\ to\ EC\ 1.14.14.123]$

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 + O_2 + [reduced NADPH—hemoprotein reductase] = 3α -hydroxy-3,5-

dihydromonacolin L acid + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) 3α -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 3α-hydroxy-3,5-dihydromonacolin

L acid is believed to be spontaneous [4327, 2983]. The enzyme from fungi also catalyses the reaction

of EC 1.14.14.125, monacolin L hydroxylase [225].

References: [4327, 2983, 225]

[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 + O_2 + [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: [225]

[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 + O_2 + [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 biosyn-

thesis 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: [1226, 1500, 2906]

[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 (2E,6E)-farnesoate + [reduced NADPH—hemoprotein reductase] + O_2 = 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)

[1622, 811].

References: [1622, 811]

[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: (2E,6E)-farnesoate + [reduced NADPH—hemoprotein reductase] + O_2 = juvenile-hormone-III car-

boxylate + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP15C1

Systematic name: (2E,6E)-farnesoate, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase

Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme, found in Lepidoptera (moths and butter-

flies), is specific for farnesoate (cf. EC 1.14.14.127, methyl farnesoate epoxidase) [810, 811]. It is

involved in the synthesis of juvenile hormone.

References: [810, 811]

[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] + O_2 = 18-hydroxyoleoyl-CoA + [oxi-

dized NADPH—hemoprotein reductase] + H₂O

(2) linoleoyl-CoA + [reduced NADPH—hemoprotein reductase] + O₂ = 18-hydroxylinoleoyl-CoA +

[oxidized NADPH—hemoprotein reductase] + H_2O

Other name(s): long-chain acyl-CoA ω-hydroxylase; CYP86A₂2 (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: [1496]

[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] + O_2 = 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 (C_{10}) , myristate (C_{14}) , and palmitate (C_{16}) 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: [2879]

[EC 1.14.14.130 created 2015 as EC 1.14.13.206, transferred 2018 to EC 1.14.14.130]

Accepted name: bursehernin 5'-monooxygenase

Reaction: (-)-bursehernin + [reduced NADPH—hemoprotein reductase] + O_2 = (-)-5'-demethylyatein + [oxi-

dized NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP71CU1 (gene name); bursehernin 5'-hydroxylase

Systematic name: (-)-bursehernin, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase (5'-

hydroxylating)

Comments: A cytochrome P-450 (heme-thiolate) protein characterized from the plant Sinopodophyllum hexan-

drum. The enzyme is involved in the biosynthetic pathway of podophyllotoxin, a non-alkaloid toxin

lignan whose derivatives are important anticancer drugs.

References: [2365]

[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] + $O_2 = (-)-4'$

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 hexan*-

drum. The enzyme produces the direct precursor to etoposide, a potent anticancer drug. It can also act

on (-)-deoxypodophyllotoxin with lower efficiency.

References: [2365]

[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] + O_2 = 2-endo-hydroxy-1,8-cineole + [oxidized flavodoxin] + O_2 + O_2 = 1,8-cineole + [oxidized flavodoxin] + O_3 + O_4 = 1,8-cineole + [oxidized flavodoxin] + O_4 = 1,8-cineole + [oxidized f

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: [1568, 2761, 2119, 2762]

[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] + O_2 = 24-hydroxy- β -amyrin + [oxidized

NADPH—hemoprotein reductase] + H_2O

(2) sophoradiol + [reduced NADPH—hemoprotein reductase] + O_2 = 24-hydroxysophoradiol + [oxi-

dized 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: [3854]

[EC 1.14.14.134 created 2011 as EC 1.14.99.43, transferred 2018 to EC 1.14.14.134]

Accepted name: glyceollin synthase

Reaction: (1) (6aS,11aS)-3,6a,9-trihydroxy-2-prenylpterocarpan + [reduced NADPH—hemoprotein reductase] +

O₂ = glyceollin II + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(2) (6aS,11aS)-3,6a,9-trihydroxy-2-prenylpterocarpan + [reduced NADPH—hemoprotein reductase] +

 O_2 = glyceollin III + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(3) (6aS,11aS)-3,6a,9-trihydroxy-4-prenylpterocarpan + [reduced NADPH—hemoprotein reductase] +

 O_2 = glyceollin I + [oxidized NADPH—hemoprotein reductase] + 2 H_2O

Other name(s): dimethylallyl-3,6a,9-trihydroxypterocarpan cyclase

Systematic name: (6aS,11aS)-3,6a,9-trihydroxy-2-prenylpterocarpan,[reduced NADPH—hemoprotein reduc-

tase]:oxygen oxidoreductase (cyclizing)

Comments: A cytochrome *P*-450 (heme-thiolate) protein purified from soybean.

References: [4580]

[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 cytohrome *P*-450 (heme-thiolate) protein isolated from the plant *Rauvolfia serpentina*.

References: [4830]

[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] + $O_2 = 8'$ -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 oxida-

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 [792]. CO inhibits the reaction, but its effects can be reversed by the presence of blue light [792]. The 8'-hydroxyabscisate formed can be converted into (–)-phaseic

acid, most probably spontaneously.

References: [792, 2266, 3633]

[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] + $O_2 = 6\beta$ -hydroxylithocholate + [oxidized

NADPH—hemoprotein reductase] + H_2O

Other name(s): lithocholate 6β-monooxygenase; CYP3A10; 6β-hydroxylase; cytochrome P450 3A10; lithocholic

acid 6β-hydroxylase

 $\textbf{Systematic name:} \quad \text{lithocholate,} [\text{reduced NADPH---hemoprotein reductase}] : oxygen \ oxidoreductase \ (6\beta - \text{hydroxylating})$

Comments: A cytochrome *P*-450 (heme-thiolate) protein from *Mesocricetus auratus* (golden hamster). Expres-

sion of the gene for this enzyme is 50-fold higher in male compared to female hamsters [4237].

References: [4237, 598, 4086, 3607]

Accepted name: 5 β -cholestane-3 α ,7 α -diol 12 α -hydroxylase

Reaction: (1) 5 β -cholestane-3 α ,7 α -diol + [reduced NADPH—hemoprotein reductase] + O₂ = 5 β -cholestane-

 3α , 7α , 12α -triol + [oxidized NADPH—hemoprotein reductase] + H₂O

(2) 7α -hydroxycholest-4-en-3-one + [reduced NADPH—hemoprotein reductase] + $O_2 = 7\alpha$, 12α -

dihydroxycholest-4-en-3-one + [oxidized NADPH—hemoprotein reductase] + H₂O

(3) chenodeoxycholate + [reduced NADPH—hemoprotein reductase] + O₂ = cholate + [oxidized

NADPH—hemoprotein reductase] + H₂O

Other name(s): 5β -cholestane- 3α , 7α -diol 12α -monooxygenase; sterol 12α -hydroxylase (ambiguous); CYP8B1; cy-

tochrome P450 8B1; 7α-hydroxycholest-4-en-3-one 12α-hydroxylase; 7α-hydroxy-4-cholesten-3-one

 12α -monooxygenase; chenodeoxycholate 12α monooxygenase

Systematic name: 5β-cholestane-3α,7α-diol,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (12α-

hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein found in mammals. This is the key enzyme in the

biosynthesis of the bile acid cholate. The enzyme can also hydroxylate 5β -cholestane- 3α , 7α -diol at

the 25 and 26 position, but to a lesser extent [1516].

References: [1515, 1516, 1828, 1023, 2566, 869, 4770, 3607, 1085]

[EC 1.14.14.139 created 2005 as EC 1.14.13.96, transferred 2018 to EC 1.14.14.139 (EC 1.14.18.8 created 2005 as EC 1.14.13.95, transferred 2015 to EC 1.14.18.8, incorporated 2020), modified 2020]

[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, al-

though 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 sub-

strate.

References: [2351]

[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] + O_2 = leachianone G + [oxidized

NADPH—hemoprotein reductase] + H_2O

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 endoplas-

mic reticulum [4738, 4901]. 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: [4738, 4901]

Accepted name: (+)-menthofuran synthase

Reaction: (+)-pulegone + [reduced NADPH—hemoprotein reductase] + O_2 = (+)-menthofuran + [oxidized

NADPH—hemoprotein reductase] + H₂O

Other name(s): menthofuran synthase; (+)-pulegone 9-hydroxylase; (+)-MFS; cytochrome P450 menthofuran syn-

thase

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 (C_9), intramolecular cyclization to the hemiketal and dehydration to the furan [310]. 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

[310].

References: [310, 2617]

[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 + [oxi-

dized 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 abi-

etic 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

[1232].

References: [1230, 1232]

[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** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** [reduced NADPH—hemoprotein reductase] + **2** O_2 = abieta-7,13-dien-18-ol + **2** O_2 = abieta-7,13-dien-18-ol

oate + 2 [oxidized NADPH—hemoprotein reductase] + $3 H_2O$ (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] + H_2O

(1b) abieta-7,13-dien-18,18-diol = abieta-7,13-dien-18-al + H_2O (spontaneous)

(1c) abieta-7,13-dien-18-al + [reduced NADPH—hemoprotein reductase] + O_2 = abieta-7,13-dien-18-

oate + [oxidized NADPH—hemoprotein reductase] + H_2O

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 abi-

etic acid biosynthesis. The activity has been demonstrated in cell-free stem extracts of *Abies grandis* (grand fir) and *Pinus contorta* (lodgepole pine) [1230], and the gene encoding the enzyme has been identified in *Pinus taeda* (loblolly pine) [3531]. The recombinant enzyme catalyses the oxidation of multiple diterpene alcohol and aldehydes, including levopimaradienol, isopimara-7,15-dienol, isopimara-7,15-dienol, dehydroabietadienol and dehydroabietadienal. It is not able to oxidize abieta-

diene.

References: [1230, 1232, 3531]

Accepted name: geranylgeraniol 18-hydroxylase

Reaction: geranylgeraniol + [reduced NADPH—hemoprotein reductase] + O_2 = 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: [4214]

[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: 22α-hydroxysteroid 23-monooxygenase

Reaction: (1) 3-epi-6-deoxocathasterone + [reduced NADPH—hemoprotein reductase] + O_2 = 6-

deoxotyphasterol + [oxidized NADPH—hemoprotein reductase] + H₂O

(2) (22S,24R)-22-hydroxy-5 α -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; 3-epi-6-deoxocathasterone,[reduced NADPH—

hemoprotein reductase]:oxygen oxidoreductase (C-23-hydroxylating); 3-epi-6-deoxocathasterone

23-monooxygenase

Systematic name: 22α-hydroxysteroid,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (C-23-

hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein involved in brassinosteroid biosynthesis in plants. The

enzyme has a relaxed substrate specificity, and C-23 hydroxylation can occur at different stages in the pathway. In *Arabidopsis thaliana* two isozymes, encoded by the CYP90C1 and CYP90D1 genes,

have redundant activities.

References: [2092, 3142]

[EC 1.14.14.147 created 2010 as EC 1.14.13.112, transferred 2018 to EC 1.14.14.147, modified 2022]

EC 1.14.14.148

Accepted name: angelicin synthase

Reaction: (+)-columbianetin + [reduced NADPH—hemoprotein reductase] + O_2 = 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: [2350]

[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: [3440, 4172]

[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] + $O_2 = 6\alpha$ -hydroxygermacra-1(10),4,11(13)-trien-12-oate + [oxidized NADPH—hemoprotein reductase] + $O_2 = 6\alpha$ -hydroxygermacra-1(10),4,11(13)-trien-12-oate + [oxidized NADPH—hemoprotein reductase] + $O_2 = 6\alpha$ -hydroxygermacra-1(10),4,11(13)-trien-12-oate = (+)-costunolide + $O_2 = 6\alpha$ -hydroxygermacra-1(10),4,11(10)-trien-12-oate = (+)-costunolide + $O_2 = 6\alpha$ -hydroxygermacra-1(10),4,11(10)-trien-12-oate = (+)-costunolide + $O_2 = 6\alpha$ -hyd

Other name(s): CYP71BL2

Systematic name: germacra-1(10),4,11(13)-trien-12-oate, [reduced NADPH—hemoprotein reductase]: oxygen oxidore-

ductase (6α-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 6α-hydroxygermacra-1(10),4,11(13)-trien-12-

oate, which spontaneously cyclises to form the lactone ring.

References: [848]

[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 O_2 = solavetivone + 2 [oxi-

dized 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] + $2 \text{ H}_2\text{O}$

Other name(s): HPO; *Hyoscymus muticus* premnaspirodiene oxygenase; CYP71D55

Systematic name: (-)-vetispiradiene,[reduced NADPH—hemoprotein reductase]:oxygen 2α-oxidoreductase

Comments: A cytochrome *P*-450 (heme-thiolate) protein. The enzyme from the plant *Hyoscymus 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 2β -hydroxy

derivatives that are not oxidized further.

References: [4171]

[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 O_2 = 11-oxo- β -amyrin + 2 [oxidized

NADPH—hemoprotein reductase] + 3 H₂O (overall reaction)

(1a) β -amyrin + [reduced NADPH—hemoprotein reductase] + O_2 = 11α -hydroxy- β -amyrin + [oxi-

dized NADPH—hemoprotein reductase] + H₂O

(1b) 11α -hydroxy- β -amyrin + [reduced NADPH—hemoprotein reductase] + O_2 = 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 11α ,30-dihydroxy- β -amyrin but this is not thought to be part of glycyrrhizin

biosynthesis.

References: [3789]

[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 protec-

tive and allelophatic benzoxazinoids in some plants, most commonly from the family of Poaceae

(grasses).

References: [1175, 1341]

[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 14α -demethylase

Reaction: a 14α -methylsteroid + 3 [reduced NADPH—hemoprotein reductase] + 3 O_2 = a Δ^{14} -steroid + formate

+ 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)

(1a) a 14α -methylsteroid + [reduced NADPH—hemoprotein reductase] + O_2 = a 14α -

hydroxymethylsteroid + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) a 14α -hydroxysteroid + [reduced NADPH—hemoprotein reductase] + O_2 = a 14α -formylsteroid

+ [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(1c) a 14α -formylsteroid + [reduced NADPH—hemoprotein reductase] + O_2 = a Δ^{14} -steroid + formate

+ [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): obtusufoliol 14-demethylase; lanosterol 14-demethylase; lanosterol 14α-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 14α -methyl group, followed by a second hydroxylation, resulting in the elimination of formate and forma-

tion of a 14(15) double bond.

References: [65, 4813, 116, 114, 115, 186]

[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 + O_2 + 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)] [1858, 1841]. The product spon-

taneously converts to [(1R)-2,2,3-trimethyl-5-oxocyclopent-3-enyl]acetate.

References: [1858, 1841]

Accepted name: tryptophan *N*-monooxygenase

Reaction: L-tryptophan + 2 [reduced NADPH—hemoprotein reductase] + 2 $O_2 = (E)$ -indol-3-ylacetaldoxime +

2 [oxidized NADPH—hemoprotein reductase] + CO_2 + 3 H_2O (overall reaction)

(1a) L-tryptophan + [reduced NADPH—hemoprotein reductase] + $O_2 = N$ -hydroxy-L-tryptophan +

[oxidized NADPH—hemoprotein reductase] + H₂O

(1b) N-hydroxy-L-tryptophan + [reduced NADPH—hemoprotein reductase] + $O_2 = N$, N-dihydroxy-L-

tryptophan + [oxidized NADPH—hemoprotein reductase] + H₂O

(1c) N,N-dihydroxy-L-tryptophan = (E)-indol-3-ylacetaldoxime + CO_2 + H_2O

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 catal-

yses 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 decarboxy-

lation is spontaneous or catalysed by the enzyme.

References: [2804, 1770, 4907, 3023]

[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] + O_2 = 3-hydroxyindolin-2-one + [oxi-

dized 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 protec-

tive and allelophatic benzoxazinoids in some plants, most commonly from the family of Poaceae

(grasses).

References: [1175, 1341]

[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] + $O_2 = \alpha$ -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: [3339, 4285, 4030, 595, 3474]

[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 + O_2 + [reduced NADPH—hemoprotein reductase] = 15,16-epoxydolabrene + H_2O

+ [oxidized NADPH—hemoprotein reductase]

(2) 15,16-epoxydolabrene + O_2 + [reduced NADPH—hemoprotein reductase] = 3β -hydroxy-15,16-

epoxydolabrene + H₂O + [oxidized NADPH—hemoprotein reductase]

Other name(s): CYP71Z16 (gene name)

Systematic name: dolabradiene, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase (3β-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: [2604]

[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]

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-yl

carbaldehyde + 2 H₂O + [oxidized NADPH—hemoprotein reductase]

(1c) (4S)-4-(5,5-dimethylcyclohex-1-en-1-yl)cyclohex-1-ene-1-carbaldehyde + O_2 + [reduced NADPH—hemoprotein reductase] = zealexin A1 + H_2O + [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: [2641]

[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 O_2 = 7-deoxyloganetate

+ 3 [oxidized NADPH—hemoprotein reductase] + 4 H₂O (overall reaction)

(1a) (+)-cis,trans-nepetalactol + [reduced NADPH—hemoprotein reductase] + O_2 = 7-deoxyloganetic

alcohol + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) 7-deoxyloganetic alcohol + [reduced NADPH—hemoprotein reductase] + O₂ = iridotrial + [oxi-

dized 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 (hy-

droxylating)

Comments: The enzyme, characterized from the plant Catharanthus roseus, is a cytochrome P-450 (heme thio-

late) protein. It catalyses three successive reactions in the pathway leading to biosynthesis of monoter-

penoid indole alkaloids.

References: [2797]

[EC 1.14.14.161 created 2018]

Accepted name: flavanone 2-hydroxylase

Reaction: a flavanone + [reduced NADPH—hemoprotein reductase] + O_2 = a 2-hydroxyflavanone + [oxidized

NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP93G2 (gene name); CYP93B1 (gene name); (2S)-flavanone 2-hydroxylase; licodione synthase 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 fla-

vanones 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: [3204, 48, 972]

[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] + O_2 = (13S,14R)-

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: [819, 2467, 2464]

[EC 1.14.14.163 created 2018]

EC 1.14.14.164

Accepted name: fraxetin 5-hydroxylase

Reaction: fraxetin + [reduced NADPH—hemoprotein reductase] + O_2 = 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: [3439]

[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] + O_2 = 4-hydroxyindole-3-

carbonyl nitrile + [oxidized NADPH—hemoprotein reductase] + H_2O

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*. In-

volved in biosynthesis of small cyanogenic compounds that take part in pathogen defense. The en-

zyme also catalyses the 5-hydroxylation of xanthotoxin [2268].

References: [2268, 3438]

[EC 1.14.14.165 created 2018]

Accepted name: (S)-N-methylcanadine 1-hydroxylase

Reaction: (S)-N-methylcanadine + [reduced NADPH—hemoprotein reductase] + $O_2 = (S)-1$ -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: [821, 2464]

[EC 1.14.14.166 created 2018]

EC 1.14.14.167

Accepted name: (13S,14R)-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]

 $+ O_2 = (13S, 14R) - 13 - O$ -acetyl-1,8-dihydroxy-*N*-methylcanadine + [oxidized NADPH—hemoprotein

reductase] + H₂O

Other name(s): CYP82X1 (gene name)

Systematic name: (13S,14R)-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: [819, 2467, 2464]

[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] + $O_2 = 8\beta$ -

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 oxidore-

ductase (8β-hydroxylating)

Comments: A cytochrome P-450 (heme-thiolate) protein from the plant Helianthus annuus (common sun-

flower). The cyclisation of 8β -hydroxygermacra-1(10),4,11(13)-triene-12-oate to inunolide (12,8 β) 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: [1177, 1373]

[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] + O_2

= eupatolide + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)

(1a) 8β -hydroxygermacra-1(10),4,11(13)-trien-12-oate + [reduced NADPH—hemoprotein reductase] + $O_2 = 6\alpha$,8 β -dihydroxygermacra-1(10),4,11(13)-trien-12-oate + [oxidized NADPH—hemoprotein reductase]

ductase] + H₂O

(1b) 6α , 8β -dihydroxygermacra-1(10), 4, 11(13)-trien-12-oate = eupatolide + H_2O (spontaneous)

Other name(s): CYP71DD6; HaES

Systematic name: 8β-hydroxygermacra-1(10),4,11(13)-trien-12-oate,[reduced NADPH—hemoprotein reduc-

tase]:oxygen oxidoreductase (6α -hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein from the plant *Helianthus annuus* (common sunflower).

References: [1177]

[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] + $O_2 = 8$ -epi-

inunolide + [oxidized NADPH—hemoprotein reductase] + 2 H₂O (overall reaction)

(1a) germacra-1(10),4,11(13)-trien-12-oate + [reduced NADPH—hemoprotein reductase] + O_2 = 8 α -hydroxygermacra-1(10),4,11(13)-trien-12-oate + [oxidized NADPH—hemoprotein reductase] + H_2O (1b) 8 α -hydroxygermacra-1(10),4,11(13)-trien-12-oate = 8-*epi*-inunolide + H_2O (spontaneous)

Other name(s): CYP71BL1

Systematic name: germacra-1(10),4,11(13)-trien-12-oate, [reduced NADPH—hemoprotein reductase]: oxygen oxidore-

ductase (8α-hydroxylating)

Comments: A cytochrome P-450 (heme-thiolate) protein from the plant *Inula hupehensis*. The enzyme also pro-

duces 8β-hydroxygermacra-1(10),4,11(13)-triene-12-oate (EC 1.14.14.168, germacrene A acid 8β-

hydroxylase).

References: [1373]

[EC 1.14.14.170 created 2018]

EC 1.14.14.171

Accepted name: β -amyrin 16α -hydroxylase

Reaction: β -amyrin + [reduced NADPH—hemoprotein reductase] + $O_2 = 16\alpha$ -hydroxy- β -amyrin + [oxidized

NADPH—hemoprotein reductase] + H₂O

Other name(s): CYP87D16

Systematic name: β-amyrin,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (16α-hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein isolated from the plant *Maesa lanceolata* (false assegai).

Involved in the biosynthesis of maesasaponins. It also acts on some derivatives of β-amyrin such as

erythrodiol or oleanolic acid.

References: [2905, 2906]

[EC 1.14.14.171 created 2019]

EC 1.14.14.172

Accepted name: 3,5,6-trichloropyridin-2-ol monooxygenase

Reaction: (1) 3,5,6-trichloropyridin-2-ol + FADH₂ + O_2 = 3,6-dichloropyridine-2,5-dione + Cl^- + FAD + H_2O

 $(2)\ 3, 6-dichloropyridine - 2, 5-diol + FADH_2 + O_2 = 6-chloro - 3-hydroxypyridine - 2, 5-dione + Cl^- + FADH_2 + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + FADH_3 + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + Cl^- + O_3 = 6-chloropyridine - 2, 5-dione + O$

+ H₂O

(3) 6-chloropyridine-2,3,5-triol + FADH₂ + O₂ = 3,6-dihydroxypyridine-2,5-dione + $C1^-$ + FAD + H₂O

Other name(s): tcpA (gene name)

Systematic name: 3,5,6-trichloropyridin-2-ol,FADH₂:oxygen oxidoreductase (dechlorinating)

Comments: The enzyme, characterized from a number of bacterial species, participates in the degradation of

3,5,6-trichloropyridin-2-ol (TCP), a metabolite of the common organophosphorus insecticide chlor-pyrifos. The enzyme is a multifunctional flavin-dependent monooxygenase that displaces three chlorine atoms by attacking three different positions in the substrate. Each reaction catalysed by the enzyme displaces a single chlorine and results in formation of a dione, which must be reduced by FADH₂ before the monooxygenase could catalyse the next step. The large amount of FADH₂ that is required is generated by a dedicated flavin reductase (TcpX). *cf.* EC 1.14.14.173, 2,4,6-

trichlorophenol monooxygenase.

References: [2446, 1086]

[EC 1.14.14.172 created 2020]

EC 1.14.14.173

Accepted name: 2,4,6-trichlorophenol monooxygenase

Reaction: 2,4,6-trichlorophenol + FADH₂ + O₂ = 6-chloro-2-hydroxy-1,4-benzoquinone + 2 Cl⁻ + FAD (over-

all reaction)

(1b) 2,6-dichloro-1,4-benzoquinone + H_2O = 6-chloro-2-hydroxy-1,4-benzoquinone + Cl^-

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

Systematic name: 2,4,6-trichlorophenol,FADH₂:oxygen oxidoreductase (dechlorinating)

Comments: The enzyme, characterized from *Cupriavidus pinatubonensis*, participates in the degradation of 2,4,6-

trichlorophenol, a compound that has been used for decades as a wood preservative. The enzyme is a multifunctional flavin-dependent monooxygenase that catalyses two different reactions to displace two chlorine atoms, a monooxygenase reaction followed by a hydrolysis reaction that takes advantage of the reactivity of the product of the first reaction, 2,6-dichloro-1,4-benzoquinone [4716]. The large amount of FADH₂ that is required is generated by a dedicated flavin reductase (TcpB). *cf.* EC

1.14.14.172, 3,5,6-trichloropyridin-2-ol monooxygenase.

References: [2544, 4716, 1582]

[EC 1.14.14.173 created 2020, modified 2022]

EC 1.14.14.174

Accepted name: geranylhydroquinone 3"-hydroxylase

Reaction: geranylhydroquinone + [reduced NADPH—hemoprotein reductase] + $O_2 = 3''$ -

hydroxygeranylhydroquinone + [oxidized NADPH—hemoprotein reductase] + H₂O

Other name(s): GHQ 3"-hydroxylase; CYP76B74 (gene name); geranylhydroquinone,NADPH:oxygen oxidoreduc-

tase (3"-hydroxylating)

Systematic name: geranylhydroquinone,[reduced NADPH—hemoprotein reductase]:oxygen oxidoreductase (3"-

hydroxylating)

Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants, where it is part of the biosynthesis path-

way of the red naphthoquinone pigment shikonin.

References: [4735, 4532]

[EC 1.14.14.174 created 2010 as EC 1.14.13.116, transferred 2020 to EC 1.14.14.174]

EC 1.14.14.175

Accepted name: ferruginol synthase

Reaction: abieta-8,11,13-triene + [reduced NADPH—hemoprotein reductase] + O₂ = ferruginol + [oxidized

NADPH—hemoprotein reductase] + H₂O

Other name(s): miltiradiene oxidase (incorrect); CYP76AH1; miltiradiene,NADPH:oxygen oxidoreductase (ferrugi-

nol forming) (incorrect)

Systematic name: abieta-8,11,13-triene,[reduced NADPH—hemoprotein reductase]:oxygen 12-oxidoreductase

(ferruginol-forming)

Comments: A cytochrome P-450 (heme thiolate) enzyme found in some members of the Lamiaceae (mint fam-

ily). 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 bioac-

tive components found in the plant.

References: [1445, 4929, 414]

[EC 1.14.14.175 created 2014 as EC 1.14.13.190, modified 2015, transferred 2020 to EC 1.14.14.175]

Accepted name: taxadiene 5α -hydroxylase

Reaction: taxa-4,11-diene + [reduced NADPH—hemoprotein reductase] + $O_2 = taxa-4(20),11$ -dien- 5α -ol +

[oxidized NADPH—hemoprotein reductase] + H₂O

Systematic name: taxa-4,11-diene, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase (5α-

hydroxylating)

Comments: This microsomal cytochrome-P-450 (heme-thiolate) 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: [1604]

[EC 1.14.14.176 created 2002 as 1.14.99.37, transferred 2020 to EC 1.14.14.176]

EC 1.14.14.177

Accepted name: ultra-long-chain fatty acid ω-hydroxylase

Reaction: an ultra-long-chain fatty acid + [reduced NADPH—hemoprotein reductase] + O_2 = an ultra-long-

chain ω -hydroxy fatty acid + [oxidized NADPH—hemoprotein reductase] + H_2O

Other name(s): CYP4F22 (gene name)

Systematic name: ultra-long-chain fatty acid, [reduced NADPH—hemoprotein reductase]: oxygen oxidoreductase (ω-

hydroxylating)

Comments: The enzyme, which is expressed in the epidermis of mammals, catalyses the ω -hydroxylation of ultra-

long-chain fatty acids (C_{28} to C_{36}). The products are incorporated into acylceramides, epidermis-

specific ceramide species that are very important for skin barrier formation.

References: [3144]

[EC 1.14.14.177 created 2021]

EC 1.14.14.178

Accepted name: steroid 22*S*-hydroxylase

Reaction: (1) a C_{27} -steroid + O_2 + [reduced NADPH—hemoprotein reductase] = a (22S)-22-hydroxy- C_{27} -

steroid + 2 H₂O + [oxidized NADPH—hemoprotein reductase]

(2) a C_{28} -steroid + O_2 + [reduced NADPH—hemoprotein reductase] = a (22S)-22-hydroxy- C_{28} -steroid

+ 2 H₂O + [oxidized NADPH—hemoprotein reductase]

(3) a C₂₉-steroid + O₂ + [reduced NADPH—hemoprotein reductase] = a (22S)-22-hydroxy-C₂₉-steroid

+ 2 H₂O + [oxidized NADPH—hemoprotein reductase]

Other name(s): CYP90B1 (gene name); DWF4 (gene name); steroid *C*-22 hydroxylase

Systematic name: steroid,NADPH—hemoprotein reductase:oxygen 22S-oxidoreductase (hydroxylating)

Comments: This plant cytochrome *P*-450 (heme thiolate) enzyme participates in the biosynthesis of brassinos-

teroids. While *in vivo* substrates include C_{28} -steroids such as campestanol, campesterol, and 6-oxocampestanol, the enzyme is able to catalyse the C-22 hydroxylation of a variety of C_{27} , C_{28} and

 C_{29} steroids.

References: [139, 671, 140, 1212, 3143]

[EC 1.14.14.178 created 2022]

EC 1.14.14.179

Accepted name: brassinosteroid 6-oxygenase

Reaction: 6-deoxocastasterone + $2 O_2$ + 2 [reduced NADPH—hemoprotein reductase] = castasterone + $3 H_2O$ +

2 [oxidized NADPH—hemoprotein reductase] (overall reaction)

(1a) 6-deoxocastasterone + O_2 + [reduced NADPH—hemoprotein reductase] = 6α -hydroxy-6-

deoxocastasterone + H₂O + [oxidized NADPH—hemoprotein reductase]

(1b) 6α -hydroxy-6-deoxocastasterone + O_2 + [reduced NADPH—hemoprotein reductase] = castas-

terone + 2 H₂O + [oxidized NADPH—hemoprotein reductase]

Other name(s): CYP85A1 (gene name); CYP85A2 (gene name); brassinosteroid 6-oxidase

Systematic name: 6-deoxocastasterone, NADPH—hemoprotein reductase: oxygen 6-oxidoreductase (castasterone-

forming)

Comments: This cytochrome *P*-450 (heme thiolate) plant enzyme catalyses the C-6 hydoxylation of several

brassinosteroid biosynthesis intermediates, and the further oxidation of the hydroxyl group to an oxo group. Substrates include 6-deoxocastasterone, 6-deoxotyphasterol, 3-dehydro-6-deoxoteasterone, and 6-deoxoteasterone. The CYP85A2 isozyme of *Arabidopsis thaliana* (but not the CYP85A1

isozyme) also catalyses the activity of EC 1.14.14.180, brassinolide synthase.

References: [3864, 3291]

[EC 1.14.14.179 created 2022]

EC 1.14.14.180

Accepted name: brassinolide synthase

Reaction: castasterone + O_2 + [reduced NADPH—hemoprotein reductase] = brassinolide + $2 H_2O$ + [oxidized

NADPH—hemoprotein reductase]

Other name(s): CYP85A2 (gene name); CYP85A3 (gene name)

Systematic name: castasterone, NADPH—hemoprotein reductase: oxygen oxidoreductase (lactonizing, brassinolide-

forming)

Comments: This cytochrome *P*-450 (heme thiolate) plant enzyme catalyses the lactonization of several brassinos-

teroids, including castasterone, teasterone, and typhasterol. The CYP85A2 enzyme of Arabidopsis

thaliana also catalyses the activity of EC 1.14.14.179, brassinosteroid 6-oxygenase.

References: [3102, 2109, 2027]

[EC 1.14.14.180 created 2022]

EC 1.14.14.181

Accepted name: sulfoquinovose monooxygenase

Reaction: 6-sulfo-D-quinovose + FMNH $_2$ + O $_2$ = 6-dehydro-D-glucose + FMN + sulfite + H $_2$ O **Other name(s):** 6-deoxy-6-sulfo-D-glucose monooxygenase; smoC (gene name); squD (gene name)

Systematic name: 6-sulfo-D-quinovose,FMNH₂:oxygen oxidoreductase

Comments: The enzyme, characterized from the bacteria Agrobacterium fabrum and Rhizobium oryzae, is in-

volved in a D-sulfoquinovose degradation pathway. FMNH2 is provided by an associated FMN re-

ductase [SmoA, EC 1.5.1.42, FMN reductase (NADH)].

References: [2516, 3827]

[EC 1.14.14.181 created 20022]

EC 1.14.14.182

Accepted name: taxoid 7β-hydroxylase

Reaction: (1) taxusin + [reduced NADPH—hemoprotein reductase] + $O_2 = 7\beta$ -hydroxytaxusin + [oxidized

NADPH—hemoprotein reductase] + H₂O

(2) 2α -hydroxytaxusin + [reduced NADPH—hemoprotein reductase] + $O_2 = 2\alpha$, 7β -dihydroxytaxusin

+ [oxidized NADPH—hemoprotein reductase] + H₂O

Systematic name: taxusin, [reduced NADPH—hemoprotein reductase]:oxygen 7-oxidoreductase

Comments: A cytochrome P-450 (heme-thiolate) protein from the yew tree Taxus cuspidata. Does not act on ear-

lier intermediates in taxol biosynthesis.

References: [616, 615]

[EC 1.14.14.182 created 2012 as EC 1.14.13.147, transferred 2022 to EC 1.14.14.182]

Accepted name: taxoid 2α -hydroxylase

Reaction: (1) taxusin + [reduced NADPH—hemoprotein reductase] + $O_2 = 2\alpha$ -hydroxytaxusin + [oxidized

NADPH—hemoprotein reductase] + H₂O

(2) 7β -hydroxytaxusin + [reduced NADPH—hemoprotein reductase] + $O_2 = 2\alpha$, 7β -dihydroxytaxusin

+ [oxidized NADPH—hemoprotein reductase] + H₂O

Systematic name: taxusin, [reduced NADPH—hemoprotein reductase]:oxygen 2-oxidoreductase

Comments: A cytochrome P-450 (heme-thiolate) protein from the yew tree Taxus cuspidata. Does not act on ear-

lier intermediates in taxol biosynthesis.

References: [616, 615]

[EC 1.14.14.183 created 2022]

EC 1.14.14.184

Accepted name: 5-dehydro-6-demethoxyfumagillol synthase

Reaction: (+)-exo- β -bergamotene + 2 [reduced NADPH—hemoprotein reductase] + 3 O₂ = 5-dehydro-6-

demethoxyfumagillol + 2 [oxidized NADPH—hemoprotein reductase] + 3 H_2O (overall reaction) (1a) (+)-exo- β -bergamotene + [reduced NADPH—hemoprotein reductase] + O_2 = (5R)-hydroxy-(+)-

exo-β-bergamotene + [oxidized NADPH—hemoprotein reductase] + H₂O

(1b) (5R)-hydroxy-(+)-exo- β -bergamotene + $O_2 = (3S)$ -3-[2-methyl-3-(3-methylbut-2-en-1-yl)oxiran-

2-yl]-4-methylidenecyclohexan-1-one + H₂O

(1c) (3S)-3-[2-methyl-3-(3-methylbut-2-en-1-yl)oxiran-2-yl]-4-methylidenecyclohexan-1-one + [reduced NADPH—hemoprotein reductase] + O_2 = 5-dehydro-6-demethoxyfumagillol + [oxidized

NADPH—hemoprotein reductase] + H₂O

Other name(s): fumagillin multifunctional cytochrome *P*450 monooxygenase; Fma-*P*450; *fmaG* (gene name)

Systematic name: (+)-exo-β-bergamotene,[reduced NADPH—hemoprotein reductase] oxidoreductase (5-dehydro-6-

demethoxyfumagillol-producing)

Comments: The enzyme, characterized from the mold *Aspergillus fumigatus*, catalyses a complex transforma-

tion comprising hydroxylation, bicyclic ring-opening, and two epoxidations, generating the sesquiter-

penoid core skeleton of fumagillin.

References: [2489]

[EC 1.14.14.184 created 2022]

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 + $O_2 = (+)-exo-5$ -hydroxycamphor + oxidized putidaredoxin +

 H_2O

Other name(s): camphor 5-exo-methylene hydroxylase; 2-bornanone 5-exo-hydroxylase; bornanone 5-exo-

hydroxylase; camphor 5-exo-hydroxylase; camphor 5-exohydroxylase; 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: [1600, 4358]

[EC 1.14.15.1 created 1972, modified 1986]

[1.14.15.2 Transferred entry. camphor 1,2-monooxygenase.] Transferred entry. camphor 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 + O_2 + 2 H^+ = 1-octanol + 2 oxidized rubredoxin + H_2O **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: [554, 2752, 3301]

[EC 1.14.15.3 created 1972]

EC 1.14.15.4

Accepted name: steroid 11β-monooxygenase

Reaction: a steroid + 2 reduced adrenodoxin + O_2 + 2 H^+ = an 11 β -hydroxysteroid + 2 oxidized adrenodoxin +

 H_2O

Other name(s): steroid 11β-hydroxylase; steroid 11β/18-hydroxylase

Systematic name: steroid, reduced-adrenodoxin: oxygen oxidoreductase (11β-hydroxylating)

Comments: A heme-thiolate protein (*P*-450). Also hydroxylates steroids at the 18-position, and converts 18-

hydroxycorticosterone into aldosterone.

References: [1383, 1578, 4306, 4761, 4940]

[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 1.14.1.5.4, modified 1989, modified 2014]

EC 1.14.15.5

Accepted name: corticosterone 18-monooxygenase

Reaction: corticosterone + 2 reduced adrenodoxin + O_2 + 2 H^+ = 18-hydroxycorticosterone + 2 oxidized adren-

odoxin + H_2O

Other name(s): corticosterone 18-hydroxylase; corticosterone methyl oxidase

Systematic name: corticosterone,reduced-adrenodoxin:oxygen oxidoreductase (18-hydroxylating)

References: [3445]

[EC 1.14.15.5 created 1972]

EC 1.14.15.6

Accepted name: cholesterol monooxygenase (side-chain-cleaving)

Reaction: cholesterol + 6 reduced adrenodoxin + $3 O_2$ + 6 H⁺ = pregnenolone + 4-methylpentanal + 6 oxidized

 $adrenodoxin + 4 H_2O$ (overall reaction)

(1a) cholesterol + 2 reduced adrenodoxin + O_2 + 2 H^+ = (22R)-22-hydroxycholesterol + 2 oxidized

adrenodoxin + H₂O

(1b) (22R)-22-hydroxycholesterol + **2** reduced adrenodoxin + O_2 + **2** H⁺ = (20R,22R)-20,22-

dihydroxycholesterol + 2 oxidized adrenodoxin + H₂O

(1c) (20R,22R)-20,22-dihydroxy-cholesterol + 2 reduced adrenodoxin + O_2 + 2 H⁺ = pregnenolone +

4-methylpentanal + 2 oxidized adrenodoxin + 2 H₂O

Other name(s): cholesterol desmolase; cytochrome P-450 $_{scc}$; C₂₇-side chain cleavage enzyme; cholesterol 20-22-

 $desmolase; cholesterol \ C_{20-22} \ desmolase; cholesterol \ side-chain \ cleavage \ enzyme; cholesterol \ enzyme; ch$

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 hydrox-

ylations 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,

 $adrenodoxin\hbox{-}NADP^+\ reductase.$

References: [503, 1520, 1518, 4074, 2688]

[EC 1.14.15.6 created 1983, modified 2013, modified 2014]

EC 1.14.15.7

Accepted name: choline monooxygenase

Reaction: choline + O_2 + 2 reduced ferredoxin + 2 H⁺ = betaine aldehyde hydrate + H_2O + 2 oxidized ferre-

doxin

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) [4485]. 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: [456, 500, 3456, 3606, 3116, 3117, 4485]

[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 15β-monooxygenase

Reaction: progesterone + 2 reduced [2Fe-2S] ferredoxin + $O_2 = 15\beta$ -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 (15β-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 [294].

References: [295, 294, 2507, 1359, 2508]

[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 O_2 + 4 H^+ = spheroiden-2-one + 4

oxidized ferredoxin [iron-sulfur] cluster + 3 H₂O (overall reaction)

(1a) spheroidene + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 2 H⁺ = 2-hydroxyspheroidene + 2 oxidized ferredoxin [iron-sulfur] cluster + H_2O

(1b) 2-hydroxyspheroidene + $\mathbf{2}$ reduced ferredoxin [iron-sulfur] cluster + O_2 + $\mathbf{2}$ H⁺ = 2,2-dihydroxyspheroidene + $\mathbf{2}$ oxidized ferredoxin [iron-sulfur] cluster + O_2 + O_3 + O_4 + O_5 cluster + O_4 + O_5 cluster + O_5 + O_5 cluster + O_5 + O_5 cluster + O_5 clust

(1c) 2,2-dihydroxyspheroidene = spheroiden-2-one + H_2O (spontaneous)

(2) spirilloxanthin + 4 reduced ferredoxin [iron-sulfur] cluster + 2 O_2 + 4 H^+ = 2-oxospirilloxanthin +

4 oxidized ferredoxin [iron-sulfur] cluster + 3 H_2O (overall reaction) (2a) spirilloxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 2 H^+ = 2-hydroxyspirilloxanthin

+ 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O

(2b) 2-hydroxyspirilloxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 2 H⁺ = 2,2-dihydroxyspirilloxanthin + 2 oxidized ferredoxin [iron-sulfur] cluster + H_2O

(2c) 2,2-dihydroxyspirilloxanthin = 2-oxospirilloxanthin + H_2O (spontaneous)

(3) 2-oxospirilloxanthin + 4 reduced ferredoxin [iron-sulfur] cluster + 2 O_2 + 4 H^+ = 2,2′-dioxospirilloxanthin + 4 oxidized ferredoxin [iron-sulfur] cluster + 3 H_2O (overall reaction)

(3a) 2-oxospirilloxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 2 H⁺ = 2'-hydroxy-2-oxospirilloxanthin + 2 oxidized ferredoxin [iron-sulfur] cluster + H_2O

(3b) 2'-hydroxy-2-oxospirilloxanthin + reduced ferredoxin [iron-sulfur] cluster + O_2 + 2 H⁺ = 2',2'-dihydroxy-2-oxospirilloxanthin + oxidized ferredoxin [iron-sulfur] cluster + H_2O

(3c) 2',2'-dihydroxy-2-oxospirilloxanthin = 2,2'-dioxospirilloxanthin + H₂O (spontaneous)

Other name(s): CrtA; acyclic carotenoid 2-ketolase; spirilloxanthin monooxygenase; 2-oxo-spirilloxanthin monooxy-

genase

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 [2390].

References: [2390, 1304]

[EC 1.14.15.9 created 2012, modified 2016]

EC 1.14.15.10

Accepted name: (+)-camphor 6-endo-hydroxylase

Reaction: (+)-camphor + reduced putidaredoxin + O_2 = (+)-6-endo-hydroxycamphor + oxidized putidaredoxin

 $+ H_2O$

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: [1418]

[EC 1.14.15.10 created 2012]

EC 1.14.15.11

Accepted name: pentalenic acid synthase

Reaction: 1-deoxypentalenate + reduced ferredoxin + O_2 = pentalenate + oxidized ferredoxin + O_2 = pentalenate + oxidized ferredoxin + O_2 = pentalenate + oxidized ferredoxin + O_2 oxidoreductase CYP105D7; sav7469 (gene name); 1-deoxypentalenate, reduced ferredoxin: O_2 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: [4176]

[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: $\text{cyclo}(\text{L-leucyl-L-leucyl}) + 6 \text{ reduced ferredoxin} + 3 O_2 = \text{pulcherriminic acid} + 6 \text{ oxidized ferredoxin}$

+ **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. Pulcherrimic acid spontaneously forms an iron chelate with Fe(3+) to

form the red pigment pulcherrimin [778].

References: [2588, 778]

[EC 1.14.15.13 created 2013]

EC 1.14.15.14

Accepted name: methyl-branched lipid ω-hydroxylase

Reaction: a methyl-branched lipid + O_2 + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ = an ω -hydroxy-

methyl-branched lipid + $H_2O + 2$ 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 (2*E*,6*E*)-farnesol, phytanate, geranylgeraniol, 15-methylpalmitate and (2*E*,6*E*)-farnesyl diphosphate. It is a

P-450 heme-thiolate enzyme.

References: [1939]

[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 = (25R)- 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 = (25R)- 5β -cholestane-

 $3\alpha,7\alpha,12\alpha,26$ -tetraol + 2 oxidized adrenodoxin + H₂O

(1b) (25R)-5 β -cholestane-3 α ,7 α ,12 α ,26-tetraol + 2 reduced adrenodoxin + 2 H⁺ + O₂ = (25R)-

 3α , 7α , 12α -trihydroxy- 5β -cholestan-26-al + **2** oxidized adrenodoxin + **2** H₂O

(1c) (25R)-3 α ,7 α ,12 α -trihydroxy-5 β -cholestan-26-al + 2 reduced adrenodoxin + 2 H⁺ + O₂ = (25R)-

 3α , 7α , 12α -trihydroxy-5 β -cholestan-2 θ -oate + **2** oxidized adrenodoxin + H₂O

Other name(s): 5β -cholestane- 3α , 7α , 12α -triol 26-hydroxylase; 5β -cholestane- 3α , 7α , 12α -triol hydroxylase;

cholestanetriol 26-hydroxylase; sterol 27-hydroxylase; sterol 26-hydroxylase; cholesterol 27-

hydroxylase; CYP27A; CYP27A1; cytochrome P450 27A1'

Systematic name: 5β -cholestane- 3α , 7α , 12α -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: [2695, 3164, 4624, 96, 800, 1698, 3325, 1234, 3326]

[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 + $2 H^+ + O_2$ = calcitetrol + 2 oxidized adrenodoxin + H_2O

(2) calcidiol + 2 reduced adrenodoxin + 2 H^+ + O_2 = secalciferol + 2 oxidized adrenodoxin + H_2O

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 D_3 -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: [2693, 1487, 3639, 3388, 2310, 3681, 3387]

[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 $a + H_2O = \text{red chlorophyll catabolite (spontaneous)}$

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 [3390] and requires reduced ferredoxin, which is generated either by NADPH through the pentose-phosphate pathway or by the action of photosystem I [3545]. 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 [3390, 3389]. Pheophorbide b acts as an inhibitor. In ${}^{18}\text{O}_2$ labelling experiments, only the aldehyde oxygen is labelled, suggesting that the other oxygen

atom may originate from H_2O [1734].

References: [1734, 3390, 692, 3545, 1733, 3389]

[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^+ + O_2 = calcitriol + 2 oxidized adrenodoxin + H_2O

(2) secalciferol + 2 reduced adrenodoxin + 2 H^+ + O_2 = calcitetrol + 2 oxidized adrenodoxin + H_2O

Other name(s): 25-hydroxycholecalciferol 1-hydroxylase; 25-hydroxycholecalciferol 1-monooxygenase; 1-

hydroxylase-25-hydroxyvitamin D₃; 25-hydroxy D3-1α-hydroxylase; 25-hydroxycholecalciferol 1α-

hydroxylase; 25-hydroxyvitamin D₃ 1α-hydroxylase

Systematic name: calcidiol,adrenodoxin:oxygen oxidoreductase (1-hydroxylating)

Comments: A *P*-450 (heme-thiolate) enzyme found in mammals.

References: [1393, 3640, 3682]

[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 1α -hydroxylase

Reaction: testosterone + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 2 H⁺ = 1 α -hydroxytestosterone +

 $H_2O + 2$ oxidized ferredoxin [iron-sulfur] cluster

Other name(s): CYP260A1

Systematic name: testosterone, reduced-ferredoxin: oxygen oxidoreductase (1α-hydroxylating)

Comments: The enzyme, characterized from the bacterium *Sorangium cellulosum*, is a class I cytochrome *P*-

450, and uses ferredoxin as its electron donor [1073]. It was shown to act on several C-19 steroid substrates, including testosterone, androstenedione, testosterone-acetate and 11-oxoandrostenedione

[2081].

References: [1073, 2081]

[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 + $3 O_2$ + $6 H^+$ = biliverdin + Fe²⁺ + CO + $6 H^+$

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 phytochro-

mobilin 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: [2870, 4101, 816]

[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 O_2 = violaxanthin + 4 oxidized

ferredoxin [iron-sulfur] cluster + 2 H₂O (overall reaction)

(1a) zeaxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O_2 = antheraxanthin + 2 oxidized

ferredoxin [iron-sulfur] cluster + H₂O

(1b) antheraxanthin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O_2 = violaxanthin + 2 oxi-

dized 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, violax-

anthin 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: [482, 490, 4268, 1643, 1196, 1195, 2697]

[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 + O_2 + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ = calcidiol + 2 oxidized ferre-

doxin [iron-sulfur] cluster + H₂O

(2) calcidiol + 2 reduced ferredoxin [iron-sulfur] cluster + $2 H^+$ + O_2 = calcitriol + 2 oxidized ferredoxin

[iron-sulfur] cluster + H₂O

Other name(s): CYP105A1; *Streptomyces griseolus* cytochrome P450SU-1 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: [3683, 4097]

[EC 1.14.15.22 created 2016]

Accepted name: chloroacetanilide *N*-alkylformylase

Reaction: butachlor + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 = 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⁺ re-

ductase, for activity.

References: [635]

[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 + H_2O

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 iron(II). Also acts on other carotenoids with a β-end group. In some species

canthaxanthin is the preferred substrate.

References: [4120, 1171, 1172, 406, 2497, 4919, 673]

[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 + O_2 + 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: [1008, 992, 3082, 991]

[EC 1.14.15.25 created 2018]

EC 1.14.15.26

Accepted name: toluene methyl-monooxygenase

Reaction: (1) toluene + O_2 + 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 + H_2O

(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); ntnM (gene names)

Systematic name: methylbenzene,ferredoxin:oxygen oxidoreductase (methyl-hydroxylating)

Comments: The enzyme, characterized from several *Pseudomonas* strains, catalyses the first step in the degra-

dation 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: [4141, 3833, 442, 1884]

[EC 1.14.15.26 created 2018]

EC 1.14.15.27

Accepted name: β-dihydromenaguinone-9 ω-hydroxylase

Reaction: β -dihydromenaquinone-9 + 2 reduced ferredoxin [iron-sulfur] cluster + $O_2 = \omega$ -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: [1703, 3951]

[EC 1.14.15.27 created 2018]

EC 1.14.15.28

Accepted name: cholest-4-en-3-one 26-monooxygenase [(25R)-3-oxocholest-4-en-26-oate forming]

Reaction: cholest-4-en-3-one + 6 reduced [2Fe-2S] ferredoxin + 3 O_2 = (25R)-3-oxocholest-4-en-26-oate + 6

oxidized [2Fe-2S] ferredoxin + 4 H₂O (overall reaction)

(1a) cholest-4-en-3-one + $\bf 2$ reduced [2Fe-2S] ferredoxin + O_2 = (25R)-26-hydroxycholest-4-en-3-one

+ 2 oxidized [2Fe-2S] ferredoxin + H₂O

(1b) (25R)-26-hydroxycholest-4-en-3-one + **2** reduced [2Fe-2S] ferredoxin + O₂ = (25R)-26-

oxocholest-4-en-3-one + 2 oxidized [2Fe-2S] ferredoxin + 2 H₂O

(1c) (25R)-26-oxocholest-4-en-3-one + 2 reduced [2Fe-2S] ferredoxin + O₂ = (25R)-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 [(25R)-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 (25R) conformation. The enzyme also accepts cholesterol as a substrate. cf. EC 1.14.15.29, cholest-4-en-3-one 26-monooxygenase [(25S)-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: [967, 1940]

[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 [(25S)-3-oxocholest-4-en-26-oate forming]

Reaction: cholest-4-en-3-one + 6 reduced ferredoxin [iron-sulfur] cluster + 6 H⁺ + 3 O_2 = (25S)-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⁺ + O_2 = (25S)-26-

hydroxycholest-4-en-3-one + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O

(1b) (25S)-26-hydroxycholest-4-en-3-one + 2 reduced ferredoxin [iron-sulfur] cluster + $2 H^+ + O_2 =$

(25S)-26-oxocholest-4-en-3-one + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O

(1c) (25S)-26-oxocholest-4-en-3-one + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O_2 = (25S)-

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 (am-

biguous)

Systematic name: cholest-4-en-3-one, [reduced ferredoxin]: oxygen oxidoreductase [(25S)-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 [3214]. The products are exclusively in the (25S) 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 9 α -monooxygenase). The enzyme also accepts cholesterol as a substrate. cf. EC 1.14.15.28, cholest-4-

en-3-one 27-monooxygenase.

References: [3577, 2753, 551, 3214]

[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⁺ + $O_2 = 9\alpha$ -

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: [3307, 550, 549]

[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⁺ + O_2 = 2,7-

 $dihydroxy-5-methyl-1-naphthoate + 2\ oxidized\ ferredoxin\ [iron-sulfur]\ cluster + H_2O$

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 bac-

terium Streptomyces carzinostaticus.

References: [1505]

[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 O_2 = pentalen-13-al + 4 oxidized

ferredoxin [iron-sulfur] cluster + 3 H₂O (overall reaction)

(1a) pentalenene + 2 reduced ferredoxin [iron-sulfur] cluster + $2 H^+$ + O_2 = pentalen-13-ol + $2 O_2$ 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: [3410]

[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 $^+$ + O $_2$ = pikromycin + 2 oxidized

ferredoxin [iron-sulfur] cluster + H₂O

(2) narbomycin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H^+ + O_2 = neopikromycin + 2 oxidized

ferredoxin [iron-sulfur] cluster + H₂O

(3) narbomycin + 4 reduced ferredoxin [iron-sulfur] cluster + 4 H^+ + 2 O_2 = novapikromycin + 4

oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O

(4) 10-deoxymethymycin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O_2 = methymycin + 2

oxidized ferredoxin [iron-sulfur] cluster + H₂O

(5) 10-deoxymethymycin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O_2 = 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 bacte-

rial 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: [4710, 3847, 2455]

[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): *tylH*1 (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: [202, 3483]

[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⁺ + O_2 = 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 ery-

thraea. The enzyme is involved in the biosynthesis of the antibiotic erythromycin.

References: [4565, 3814, 788, 2960]

[EC 1.14.15.35 created 2014 as EC 1.14.13.188, transferred 2018 to EC 1.14.15.35]

EC 1.14.15.36

Accepted name: sterol 14α-demethylase (ferredoxin)

Reaction: a 14α -methylsteroid + 6 reduced ferredoxin [iron-sulfur] cluster + 6 H⁺ + 3 O₂ = a Δ^{14} -steroid + for-

mate + 6 oxidized ferredoxin [iron-sulfur] cluster + 4 H₂O (overall reaction)

(1a) a 14α -methylsteroid + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = a 14α -

hydroxymethylsteroid + 2 oxidized ferredoxin [iron-sulfur] cluster + H_2O

(1b) a 14α -hydroxymethylsteroid + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = a 14α -

formylsteroid + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O

(1c) a 14α -formylsteroid + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O₂ = a Δ^{14} -steroid +

formate + 2 oxidized ferredoxin [iron-sulfur] cluster + H₂O

Other name(s): cyp51 (gene name)

Systematic name: sterol,reduced ferredoxin:oxygen oxidoreductase (14-methyl cleaving)

Comments: A cytochrome *P*-450 (heme-thiolate) protein found in several bacterial species. The enzyme, which

is involved in sterol biosynthesis, catalyses a hydroxylation and a reduction of the 14α -methyl group, followed by a second hydroxylation, resulting in the elimination of formate and formation of a 14(15) double bond. The enzyme from *Methylococcus capsulatus* is fused to the ferredoxin by an alanine-

rich linker. cf. EC 1.14.14.154, sterol 14 α -demethylase.

References: [1871, 3507, 889]

[EC 1.14.15.36 created 2019]

EC 1.14.15.37

Accepted name: luteothin monooxygenase

Reaction: luteothin + $2 O_2 + 4$ reduced ferredoxin [iron-sulfur] cluster + $4 H^+$ = aureothin + $3 H_2O + 4$ oxidized

ferredoxin [iron-sulfur] cluster (overall reaction)

(1a) luteothin + O_2 + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ = (7R)-7-hydroxyluteothin +

 $H_2O + 2$ oxidized ferredoxin [iron-sulfur] cluster

(1b) (7R)-7-hydroxyluteothin + O_2 + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ = aureothin + 2

 $H_2O + 2$ oxidized ferredoxin [iron-sulfur] cluster

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

Systematic name: luteothin, ferredoxin: oxygen oxidoreductase (aureothin-forming)

Comments: The enzyme, characterized from the bacterium Streptomyces thioluteus, is a bifunctional cytochrome

P-450 (heme-thiolate) protein that catalyses both the hydroxylation of its substrate and formation of a furan ring, the final step in the biosynthesis of the antibiotic aureothin. In the bacteria *Streptomyces orinoci* and *Streptomyces spectabilis* an orthologous enzyme catalyses a similar reaction that forms

spectinabilin.

References: [1591, 4321]

[EC 1.14.15.37 created 2019]

EC 1.14.15.38

Accepted name: *N*,*N*-dimethyl phenylurea *N*-demethylase

Reaction: an N,N-dimethyl-N'-phenylurea compound + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + O_2 =

an N-methyl-N'-phenylurea compound + formaldehyde + 2 oxidized ferredoxin [iron-sulfur] cluster +

 H_2O

Other name(s): *pdmAB* (gene names)

Systematic name: N,N-dimethyl-N'-phenylurea compound,NAD(P)H:oxygen oxidoreductase (formaldehyde-forming)

Comments: The enzyme, found in members of the *Sphingobium* genus, initiates the degradation of *N*,*N*-dimethyl-

phenylurea herbicides by mono-*N*-demethylation. The catalytic unit contains a Rieske [2Fe-2S] ironsulfur cluster, and catalyses the monooxygenation of a methyl group. The resulting *N*-methoxyl group is unstable and decomposes spontaneously to form formaldehyde. The enzyme associates with additional proteins (a reductase and a [3Fe-4S] type ferredoxin) that are involved in the transfer of elec-

trons from NAD(P)H to the active site.

References: [1434]

[EC 1.14.15.38 created 2020]

EC 1.14.15.39

Accepted name: *epi*-isozizaene 5-monooxygenase

Reaction: (+)-epi-isozizaene + 4 reduced [2Fe-2S] ferredoxin + 4 H⁺ + 2 O₂ = albaflavenone + 4 oxidized [2Fe-

2S] ferredoxin + 3 H₂O (overall reaction)

(1a) (+)-epi-isozizaene + 2 reduced [2Fe-2S] ferredoxin + 2 H⁺ + O₂ = (5S)-albaflavenol + 2 oxidized

[2Fe-2S] ferredoxin + H_2O

(1b) (5S)-albaflavenol + 2 reduced [2Fe-2S] ferredoxin + 2 H⁺ + O_2 = albaflavenone + 2 oxidized

[2Fe-2S] ferredoxin + $2 H_2O$

(2a) (+)-epi-isozizaene + 2 reduced [2Fe-2S] ferredoxin + 2 H⁺ + O₂ = (5R)-albaflavenol + 2 oxidized

[2Fe-2S] ferredoxin + H₂O

(2b) (5R)-albaflavenol + 2 reduced [2Fe-2S] ferredoxin + 2 H⁺ + O_2 = albaflavenone + 2 oxidized

[2Fe-2S] ferredoxin + $2 H_2O$

Other name(s): CYP170A1

Systematic name: (+)-epi-isozizaene,reduced-ferredoxin: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 (5R)-albaflavenol and (5S)-albaflavenol, which can be further oxidized to yield the sesquiterpenoid

antibiotic albaflavenone.

References: [4897]

[EC 1.14.15.39 created 2008 as EC 1.14.13.106, transferred 2021 to EC 1.14.15.39]

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 + a 5,6,7,8-tetrahydropteridine + O_2 = L-tyrosine + a 4a-hydroxy-5,6,7,8-

tetrahydropteridine

Other name(s): phenylalaninase; phenylalanine 4-hydroxylase; phenylalanine hydroxylase

Systematic name: L-phenylalanine,tetrahydropteridine: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-hydroxytetrahydropteridine formed can dehydrate to 6,7-dihydropteridine, both spontaneously and by the action of EC 4.2.1.96, 4a-hydroxytetrahydrobiopterin dehydratase. The 6,7-dihydropteridine must be enzymically reduced back to tetrahydropteridine, by EC 1.5.1.34, 6,7-dihydropteridine reductase, before it slowly rearranges into

the more stable but inactive compound 7,8-dihydropteridine.

References: [1451, 2035, 2829, 4362, 563, 91, 1062]

[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, modified 2019]

EC 1.14.16.2

Accepted name: tyrosine 3-monooxygenase

Reaction: L-tyrosine + a 5,6,7,8-tetrahydropteridine + O_2 = L-dopa + a 4a-hydroxy-5,6,7,8-tetrahydropteridine

Other name(s): L-tyrosine hydroxylase; tyrosine 3-hydroxylase; tyrosine hydroxylase Systematic name: L-tyrosine,tetrahydropteridine:oxygen oxidoreductase (3-hydroxylating)

Comments: The active centre contains mononuclear iron(II). The enzyme is activated by phosphorylation, catal-

ysed by EC 2.7.11.27, [acetyl-CoA carboxylase] kinase. The 4a-hydroxytetrahydropteridine formed can dehydrate to 6,7-dihydropteridine, both spontaneously and by the action of EC 4.2.1.96, 4a-hydroxytetrahydrobiopterin dehydratase. The 6,7-dihydropteridine must be enzymically reduced back to tetrahydropteridine, by EC 1.5.1.34, 6,7-dihydropteridine reductase, before it slowly rearranges into

the more stable but inactive compound 7,8-dihydropteridine.

References: [2780, 1793, 2963, 3323, 1365]

[EC 1.14.16.2 created 1972, modified 2003, modified 2019]

[1.14.16.3 Deleted entry. anthranilate 3-monooxygenase. Withdrawn owing to insufficient evidence.]

[EC 1.14.16.3 created 1972, deleted 2020]

EC 1.14.16.4

Accepted name: tryptophan 5-monooxygenase

Reaction: L-tryptophan + a 5,6,7,8-tetrahydropteridine + $O_2 = 5$ -hydroxy-L-tryptophan + a 4a-hydroxy-5,6,7,8-

tetrahydropteridine

Other name(s): L-tryptophan hydroxylase; indoleacetic acid-5-hydroxylase; tryptophan 5-hydroxylase; tryptophan

hydroxylase

Systematic name: L-tryptophan,tetrahydropteridine: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-hydroxytetrahydropteridine formed can dehydrate to 6,7-dihydropteridine, both spontaneously and by the action of EC 4.2.1.96, 4a-

hydroxytetrahydrobiopterin dehydratase. The 6,7-dihydropteridine must be enzymically reduced back to tetrahydropteridine, by EC 1.5.1.34, 6,7-dihydropteridine reductase, before it slowly rearranges into

the more stable but inactive compound 7,8-dihydropteridine.

References: [1183, 1494, 1789, 1906, 4519]

[EC 1.14.16.4 created 1972, modified 2003, modified 2019]

EC 1.14.16.5

Accepted name: alkylglycerol monooxygenase

Reaction: 1-O-alkyl-sn-glycerol + a 5,6,7,8-tetrahydropteridine + $O_2 = 1$ -O-(1-hydroxyalkyl)-sn-glycerol + a

4a-hydroxy-5,6,7,8-tetrahydropteridine

Other name(s): glyceryl-ether monooxygenase; glyceryl-ether cleaving enzyme; glyceryl ether oxygenase; glyceryl

etherase; O-alkylglycerol monooxygenase

Systematic name: 1-alkyl-sn-glycerol,tetrahydrobiopteridine:oxygen oxidoreductase

Comments: The enzyme cleaves alkylglycerols, but does not cleave alkenylglycerols (plasmalogens). Re-

> quires non-heme iron [4562], reduced glutathione and phospholipids for full activity. The product spontaneously breaks down to form a fatty aldehyde and glycerol. The co-product, 4ahydroxytetrahydropteridine, is rapidly dehydrated to 6,7-dihydropteridine, either spontaneously or

by EC 4.2.1.96, 4a-hydroxytetrahydrobiopterin dehydratase.

References: [1827, 3312, 3948, 3967, 4289, 4164, 4562, 4590]

[EC 1.14.16.5 created 1972 as EC 1.14.99.17, transferred 1976 to EC 1.14.16.5, modified 2010, modified 2020]

EC 1.14.16.6

Accepted name: mandelate 4-monooxygenase

> **Reaction:** (S)-2-hydroxy-2-phenylacetate + a 5,6,7,8-tetrahydropteridine + O_2 = (S)-4-hydroxymandelate + a

> > 4a-hydroxy-5,6,7,8-tetrahydropteridine

Other name(s): L-mandelate 4-hydroxylase; mandelic acid 4-hydroxylase

Systematic name: (S)-2-hydroxy-2-phenylacetate,tetrahydropteridine:oxygen oxidoreductase (4-hydroxylating)

Requires Fe²⁺. The enzyme has been characterized from the bacterium *Pseudomonas putida*. The 4a-**Comments:**

hydroxytetrahydropteridine formed can dehydrate to 6,7-dihydropteridine, both spontaneously and by the action of EC 4.2.1.96, 4a-hydroxytetrahydrobiopterin dehydratase. The 6,7-dihydropteridine must be enzymically reduced back to tetrahydropteridine, by EC 1.5.1.34, 6,7-dihydropteridine reductase,

before it slowly rearranges into the more stable but inactive compound 7,8-dihydropteridine.

References: [326]

[EC 1.14.16.6 created 1984, modified 2020]

EC 1.14.16.7

Accepted name: phenylalanine 3-monooxygenase

> Reaction: L-phenylalanine + a 5.6.7.8-tetrahydropteridine + O_2 = 3-hydroxy-L-phenylalanine + a 4a-hydroxy-

> > 5,6,7,8-tetrahydropteridine

Other name(s): PacX; phenylalanine 3-hydroxylase

L-phenylalanine,tetrahydropteridine:oxygen oxidoreductase (3-hydroxylating) **Systematic name:**

Comments: The enzyme, characterized 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. The 4a-hydroxytetrahydropteridine formed can dehydrate to 6,7dihydropteridine, both spontaneously and by the action of EC 4.2.1.96, 4a-hydroxytetrahydrobiopterin dehydratase. The 6,7-dihydropteridine must be enzymically reduced back to tetrahydropteridine, by EC 1.5.1.34, 6,7-dihydropteridine reductase, before it slowly rearranges into the more stable but inac-

tive compound 7,8-dihydropteridine.

References: [4885]

[EC 1.14.16.7 created 2014, modified 2019]

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 + 2 ascorbate + O_2 = noradrenaline + 2 monodehydroascorbate + O_2

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 -mono-

oxygenase; DβM (gene name)

Systematic name: dopamine, ascorbate: oxygen oxidoreductase (β-hydroxylating)

Comments: A copper protein. The enzyme, found in animals, binds two copper ions with distinct roles during

catalysis. Stimulated by fumarate.

References: [2429, 1184, 3923, 1069]

[EC 1.14.17.1 created 1965 as EC 1.14.2.1, transferred 1972 to EC 1.14.17.1, modified 2020]

[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: [peptide]-glycine + 2 ascorbate + O_2 = [peptide]-(2S)-2-hydroxyglycine + 2 monodehydroascorbate +

 H_2O

Other name(s): peptidylglycine 2-hydroxylase; peptidyl α -amidating enzyme; peptide- α -amide synthetase; peptide

 α -amidating enzyme; peptide α -amide synthase; peptidylglycine α -hydroxylase; peptidylglycine α -amidating monooxygenase; PAM-A; PAM-B; PAM; peptidylglycine,ascorbate:oxygen oxidoreductase

(2-hydroxylating)

Systematic name: [peptide]-glycine,ascorbate:oxygen oxidoreductase (2-hydroxylating)

Comments: A copper protein. The enzyme binds two copper ions with distinct roles during catalysis. Peptidyl-

glycines 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. In mammals, the two activities are part of a bifunctional protein. Involved in the final step of biosynthesis of α -melanotropin

and related biologically active peptides.

References: [418, 1342, 2949, 419, 2948, 2026, 3385, 3384, 689, 619]

[EC 1.14.17.3 created 1989, modified 2019]

EC 1.14.17.4

Accepted name: aminocyclopropanecarboxylate oxidase

Reaction: 1-aminocyclopropane-1-carboxylate + ascorbate + O_2 = ethene + cyanide + dehydroascorbate + CO_2

+ 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 sig-

nalling functions such as stimulation of fruit-ripening.

References: [4893, 4891, 3330, 608, 4279]

[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 + O_2 = dopaquinone + H_2O (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 oxi-

doreductase; 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 [3561]. 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 hydroxy-

lation or monooxygenation of monophenols.

References: [842, 3261, 3349, 3533, 3653, 4019, 3561]

[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 ferrocytochrome b_5 + O₂ + 2 H⁺ = CMP-*N*-glycoloylneuraminate + 2

ferricytochrome $b_5 + H_2O$

Other name(s): CMP-N-acetylneuraminic acid hydroxylase; CMP-Neu5Ac hydroxylase; cytidine monophos-

phoacetylneuraminate monooxygenase; N-acetylneuraminic monooxygenase; cytidine-5'-

monophosphate-N-acetylneuraminic acid hydroxylase

Systematic name: CMP-*N*-acetylneuraminate,ferrocytochrome-*b*₅:oxygen oxidoreductase (*N*-acetyl-hydroxylating)

Comments: This enzyme contains both a Rieske-type [2Fe-2S] cluster and a second iron site. The ferricytochrome

 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: [3835, 2254, 3731, 2046, 3722]

[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 + O_2 = methanol + quinone + H_2O

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: [3855, 234, 2139, 197]

[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 ferrocytochrome b_5 + O_2 + 2 H⁺ = a 1-acyl-2-

[(12R)-12-hydroxyoleoyl]-sn-glycero-3-phosphocholine + **2** ferricytochrome b_5 + H₂O

Other name(s): ricinoleic acid synthase; oleate Δ^{12} -hydroxylase; oleate Δ^{12} -monooxygenase

Systematic name: 1-acyl-2-oleoyl-sn-glycero-3-phosphocholine,ferrocytochrome-b₅:oxygen oxidoreductase (12-

hydroxylating)

Comments: The enzyme, characterized from the plant *Ricinus communis* (castor bean), is involved in produc-

tion 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: [1261, 2882, 3939, 2490, 453]

[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 ferrocytochrome $b_5 + O_2 + 2 H^+ = a (4R) - 4$ -hydroxysphinganine ceramide + 2

ferricytochrome $b_5 + H_2O$

Other name(s): sphinganine C4-monooxygenase; sphingolipid C4-hydroxylase; SUR2 (gene name); SBH1 (gene

name); SBH₂ (gene name); DEGS2 (gene name)

Systematic name: dihydroceramide, ferrocytochrome b₅: oxygen oxidoreductase (C4-hydroxylating)

Comments: The enzyme, which belongs to the familiy of endoplasmic reticular cytochrome b_5 -dependent en-

zymes, is involved in the biosynthesis of sphingolipids in eukaryotes. Some enzymes are bifunctional

and also catalyse EC 1.14.19.17, sphingolipid 4-desaturase [4246].

References: [1461, 1412, 3982, 4246, 2851]

[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 ferrocytochrome $b_5 + O_2 + 2 H^+ = a (2'R) - 2'$ -hydroxyphytoceramide + 2 ferricy-

tochrome $b_5 + H_2O$

Other name(s): FA2H (gene name); SCS7 (gene name)

Systematic name: (4R)-4-hydroxysphinganine ceramide, ferrocytochrome-b₅: 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 (4R)-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: [2828, 986, 64, 1011, 1449]

[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: [2957, 2958, 2959]

[1.14.18.8 Transferred entry. 7α -hydroxycholest-4-en-3-one 12α -hydroxylase. Now included with EC 1.14.14.139, 5β -cholestane- 3α , 7α -diol 12α -hydroxylase]

[EC 1.14.18.8 created 2005 as EC 1.14.13.95, transferred 2015 to EC 1.14.18.8, deleted 2020]

EC 1.14.18.9

Accepted name: 4α-methylsterol monooxygenase

Reaction: 4,4-dimethyl-5 α -cholest-7-en-3 β -ol + **6** ferrocytochrome b_5 + **3** O₂ + **6** H⁺ = 3 β -hydroxy-4 β -methyl-

 5α -cholest-7-ene-4α-carboxylate + **6** ferricytochrome b_5 + **4** H₂O (overall reaction)

(1a) 4,4-dimethyl-5 α -cholest-7-en-3 β -ol + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = 4 α -hydroxymethyl-

 4β -methyl- 5α -cholest-7-en- 3β -ol + **2** ferricytochrome b_5 + H₂O

(1b) 4α -hydroxymethyl- 4β -methyl- 5α -cholest-7-en- 3β -ol + **2** ferrocytochrome b_5 + O₂ + **2** H⁺ = 3β -

hydroxy-4 β -methyl-5 α -cholest-7-ene-4 α -carbaldehyde + 2 ferricytochrome b_5 + 2 H₂O

(1c) 3β-hydroxy-4β-methyl-5α-cholest-7-ene-4α-carbaldehyde + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ =

 3β -hydroxy- 4β -methyl- 5α -cholest-7-ene- 4α -carboxylate + **2** ferricytochrome b_5 + H₂O

Other name(s): methylsterol hydroxylase (ambiguous); 4-methylsterol oxidase (ambiguous); 4,4-dimethyl-5α-

cholest-7-en-3 β -ol,hydrogen-donor:oxygen oxidoreductase (hydroxylating) (ambiguous); methylsterol monooxygenase (ambiguous); ERG25 (gene name); MSMO1 (gene name); 4,4-dimethyl-5 α -cholest-7-en-3 β -ol,ferrocytochrome- b_5 :oxygen oxidoreductase (hydroxylating) (ambiguous)

Systematic name: 4,4-dimethyl- 5α -cholest-7-en- 3β -ol,ferrocytochrome- b_5 :oxygen oxidoreductase (C4 α -methyl-

hydroxylating)

Comments: This enzyme is found in fungi and animals and catalyses a step in the biosynthesis of important sterol

molecules such as ergosterol and cholesterol, respectively. The enzyme acts on the 4α -methyl group. Subsequent decarboxylation by EC 1.1.1.170, 3β -hydroxysteroid- 4α -carboxylate 3-dehydrogenase (decarboxylating), occurs concomitantly with epimerization of the remaining 4β -methyl into the 4α position, thus making it a suitable substrate for a second round of catalysis. *cf.* EC 1.14.13.246, 4β -methylsterol monooxygenase; EC 1.14.18.10, plant 4,4-dimethylsterol C- 4α -methyl-monooxygenase;

and EC 1.14.18.11, plant 4α -monomethylsterol monooxygenase.

References: [2814, 1290, 3831, 420, 1227, 2048]

[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, modified 2019]

EC 1.14.18.10

Accepted name: plant 4,4-dimethylsterol C-4α-methyl-monooxygenase

Reaction: 24-methylidenecycloartanol + **6** ferrocytochrome b_5 + **3** O₂ + **6** H⁺ = 3 β -hydroxy-4 β ,14 α -dimethyl-

9 β ,19-cyclo-5 α -ergost-24(24¹)-en-4 α -carboxylate + **6** ferricytochrome b_5 + **4** H₂O (overall reaction) (1a) 24-methylidenecycloartanol + **2** ferrocytochrome b_5 + O₂ + **2** H⁺ = 4 α -(hydroxymethyl)-4 β ,14 α -

dimethyl-9 β ,19-cyclo-5 α -ergost-24(24¹)-en-3 β -ol + **2** ferricytochrome b_5 + H₂O

(1b) 4α -(hydroxymethyl)- 4β , 14α -dimethyl- 9β ,19-cyclo- 5α -ergost- $24(24^1)$ -en- 3β -ol + **2** ferrocytochrome b_5 + O_2 + **2** H⁺ = 4α -formyl- 4β , 14α -dimethyl- 9β ,19-cyclo- 5α -ergost- $24(24^1)$ -en- 3β -ol +

2 ferricytochrome $b_5 + 2 H_2O$

(1c) 4α -formyl- 4β , 14α -dimethyl- 9β , 19-cyclo- 5α -ergost- $24(24^1)$ -en- 3β -ol + **2** ferrocytochrome b_5 + O_2 + **2** H⁺ = 3β -hydroxy- 4β , 14α -dimethyl- 9β , 19-cyclo- 5α -ergost- $24(24^1)$ -en- 4α -carboxylate + **2** ferrocytochrome

ricytochrome $b_5 + H_2O$

Other name(s): SMO1 (gene name)

Systematic name: 24-methylidenecycloartanol, ferrocytochrome- b_5 : oxygen oxidoreductase (C-4 α -methyl-

hydroxylating)

Comments: This plant enzyme catalyses a step in the biosynthesis of sterols. It acts on the 4α -methyl group of

the 4,4-dimethylated intermediate 24-methylidenecycloartanol and catalyses three successive oxidations, turning it into a carboxyl group. The carboxylate is subsequently removed by EC 1.1.1.418, plant 3 β -hydroxysteroid-4 α -carboxylate 3-dehydrogenase (decarboxylating), which also catalyses the epimerization of the remaining 4 β -methyl into the 4 α position. Unlike the fungal/animal enzyme EC 1.14.18.9, 4 α -methylsterol monooxygenase, this enzyme is not able to remove the methyl group from C-4-monomethylated substrates. That activity is performed in plants by a second enzyme, EC

1.14.18.11, plant 4α -monomethylsterol monooxygenase.

References: [3250, 3428, 828, 829]

[EC 1.14.18.10 created 2019]

EC 1.14.18.11

Accepted name: plant 4α-monomethylsterol monooxygenase

Reaction: 24-methylidenelophenol + **6** ferrocytochrome b_5 + **3** O_2 + **6** H^+ = 3 β -hydroxyergosta-7,24(24¹)-dien-

 4α -carboxylate + **6** ferricytochrome b_5 + **4** H₂O (overall reaction)

(1a) 24-methylidenelophenol + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = 4α -(hydroxymethyl)ergosta-

 $7,24(24^1)$ -dien-3β-ol + **2** ferricytochrome b_5 + H₂O

(1b) 4α -(hydroxymethyl)ergosta-7,24(24¹)-dien-3 β -ol + **2** ferrocytochrome b_5 + O_2 + **2** H⁺ = 4α -

formylergosta-7,24(24¹)-dien-3 β -ol + **2** ferricytochrome b_5 + **2** H₂O

(1c) 4α -formylergosta-7,24(24¹)-dien-3 β -ol + **2** ferrocytochrome b_5 + O_2 + **2** H⁺ = 3 β -hydroxyergosta-

7,24(24¹)-dien-4 α -carboxylate + **2** ferricytochrome b_5 + H₂O

Other name(s): SMO2 (gene name)

Systematic name: 24-ethylidenelophenol,ferrocytochrome- b_5 :oxygen oxidoreductase (C-4 α -methyl-hydroxylating)

Comments: This plant enzyme catalyses a step in the biosynthesis of sterols. It acts on the methyl group of the

 4α -methylated intermediates 24-ethylidenelophenol and 24-methylidenelophenol and catalyses three successive oxidations, turning it into a carboxyl group. The carboxylate is subsequently removed by EC 1.1.1.418, plant 3 β -hydroxysteroid-4 α -carboxylate 3-dehydrogenase (decarboxylating). Unlike the fungal/animal enzyme EC 1.14.18.9, 4 α -methylsterol monooxygenase, this enzyme is not able to act on 4,4-dimethylated substrates. That activity, which occurs earlier in the pathway, is performed in plants by a second enzyme, EC 1.14.18.10, plant 4,4-dimethylsterol C-4 α -methyl-monooxygenase.

References: [3250, 3428, 828, 829]

[EC 1.14.18.11 created 2019]

EC 1.14.18.12

Accepted name: 2-hydroxy fatty acid dioxygenase

Reaction: a (2*R*)-2-hydroxy C_n -fatty acid + O_2 = a C_{n-1} -fatty acid + O_2

Other name(s): MPO1 (gene name)

Systematic name: 2-hydroxyfatty acid:oxygen oxidoreductase (CO₂,H₂O-forming)

Comments: Requires iron(II). The enzyme, characterized from yeast, is involved in phytosphingosine metabolism.

The reaction is mediated by iron(IV) peroxide and results in the release of a water molecule and a carbon dioxide molecule, shortening the substrate by a single carbon atom and forming an odd-numbered fatty acid. Both oxygen atoms of the original carboxylate group are released - one as the leaving water molecule, the other as one of the oxygens of the carbon dioxide molecule. The two oxygen atoms in the newly-formed carboxylate originate from the 2-hydroxy group and from molecular oxygen, respectively. The other oxygen atom of the molecular oxygen is incorporated into the leaving CO_2 molecule. The enzyme from the yeast $Saccharomyces\ cerevisiae$ is active at least toward C_{14} to C_{26}

2-hydroxyfatty acids, but not against C₈ 2-hydroxyfatty acid.

References: [2220, 3791]

[EC 1.14.18.12 created 2020]

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: stearoyl-CoA 9-desaturase

Reaction: stearoyl-CoA + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = oleoyl-CoA + 2 ferricytochrome b_5 + 2 H₂O **Other name(s):** Δ^9 -desaturase; acyl-CoA desaturase; fatty acid desaturase; stearoyl-CoA, hydrogen-donor:oxygen

oxidoreductase

Systematic name: stearoyl-CoA,ferrocytochrome-b₅: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: [1228, 3197, 3198, 4069]

[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: stearoyl-[acyl-carrier-protein] 9-desaturase

Reaction: stearoyl-[acyl-carrier protein] + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 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: stearoyl-[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] [521, 547].

References: [1894, 2955, 3820, 521, 547]

[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: acvl-CoA 6-desaturase

Reaction: (1) linoleoyl-CoA + 2 ferrocytochrome b_5 + O_2 + 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

 $+ 2 H_2O$

Other name(s): Δ^6 -desaturase; Δ^6 -fatty acyl-CoA desaturase; Δ^6 -acyl CoA desaturase; fatty acid Δ^6 -desaturase;

fatty acid 6-desaturase; linoleate desaturase; linoleic desaturase; linoleic acid desaturase; linoleoyl CoA desaturase; linoleoyl-coenzyme A desaturase; long-chain fatty acid Δ^6 -desaturase; linoleoyl-CoA,hydrogen-donor:oxygen oxidoreductase; linoleoyl-CoA desaturase; FADS2 (gene name)

Systematic name: acyl-CoA, ferrocytochrome b₅; 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 carboxylend of the fatty acid. The human enzyme has a broad substrate range. It also acts on palmitoyl-CoA, generating sapienoyl-CoA [1292], and on (9Z,12Z,15Z,18Z,21Z)-tetracosa-9,12,15,18,21-pentaenoyl-CoA, converting it to (6Z,9Z,12Z,15Z,18Z,21Z)-tetracosa-6,9,12,15,18,21-hexaenoyl-CoA as part of a pathway that produces docosahexaenoate [3990]. 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: [3161, 665, 3990, 1292, 942]

[EC 1.14.19.3 created 1986 as EC 1.14.99.25, transferred 2000 to EC 1.14.19.3, modified 2015]

Accepted name: acyl-lipid (11-3)-desaturase

Reaction: (1) an (11Z,14Z)-icosa-11,14-dienoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O_2 + 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 + O_2 + 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; Δ^8 fatty acid desaturase; Δ^8 -desaturase; Δ^8 -fatty-acid desaturase; efd1 (gene

name); D8Des (gene name); phytosphinganine,hydrogen donor:oxygen Δ^8 -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 [4503] and the microalga Rebecca salina

[4917], introduces a cis double bond at the 8-position in 20-carbon fatty acids that are incorporated into a glycerolipid and have an existing Δ^{11} 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: [4503, 4917]

[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 + O_2 + 2 H⁺ = an (11Z)-enoyl-CoA + 2 ferricytochrome b_5 + 2

H₂O

Other name(s): Δ^{11} desaturase; fatty acid Δ^{11} -desaturase; TpDESN; Cro-PG; Δ^{11} fatty acid desaturase; Z/E11-

desaturase; Δ^{11} -palmitoyl-CoA desaturase; acyl-CoA,hydrogen donor:oxygen Δ^{11} -oxidoreductase;

 Δ^{11} -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) [4309], that from the leafroller moth *Choristoneura rosaceana* desaturates myristoyl-CoA (14:0) [1522], while that from the moth *Spodoptera littoralis* accepts both substrates [2673]. The enzyme contains three histidine boxes that are conserved in all desaturases [3547]. It is membrane-bound, and contains a cytochrome b_5 -like do-

main at the N-terminus that serves as the electron donor for the active site of the desaturase.

References: [2673, 3547, 3027, 4309, 1522]

[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 + O_2 + 2 H⁺ = linoleoyl-CoA + 2 ferricytochrome b_5 + 2

 H_2O

(2) palmitoleoyl-CoA + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = (9Z,12Z)-hexadeca-9,12-dienoyl-CoA +

2 ferricytochrome $b_5 + 2 H_2O$

Other name(s): oleoyl-CoA 12-desaturase; Δ^{12} fatty acid desaturase; $\Delta^{12}(\omega^6)$ -desaturase; oleoyl-CoA Δ^{12} desaturase;

 Δ^{12} desaturase; Δ^{12} -desaturase; Δ^{12} -fatty-acid desaturase; acyl-CoA,hydrogen donor:oxygen Δ^{12} -

oxidoreductase

Systematic name: acyl-CoA, ferrocytochrome b₅:oxygen oxidoreductase (12,13 cis-dehydrogenating)

Comments: This microsomal enzyme introduces a cis double bond at position 12 of fatty-acyl-CoAs that con-

tain a *cis* double bond at position 9. When acting on $19:1\Delta^{10}$ 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 [3306].

References: [391, 2534, 4298, 3306]

[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 + O_2 + 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: [4920]

[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 + O_2 + 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* catal-

yses the initial step in the biosynthesis of rebeccamycin [4786]. 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: [947, 4786, 339, 1603]

[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** ferrocytochrome b_5 + O_2 + **2** H⁺ = (Z)-icos-5-enoyl-CoA + **2** ferricytochrome b_5

+ 2 H₂O

Other name(s): acyl-CoA Δ^5 -desaturase (ambiguous)

Systematic name: icosanoyl-CoA, ferrocytochrome 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: [522]

[EC 1.14.19.10 created 2015]

Accepted name: acyl-[acyl-carrier-protein] 4-desaturase

Reaction: palmitoyl-[acyl-carrier protein] + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 2 H⁺ = (4Z)-

hexadec-4-enoyl-[acyl-carrier protein] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O

Other name(s): Δ^4 -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: [525, 523, 4613]

[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 ferrocytochrome $b_5 + O_2 + 2 H^+$ = pinolenoyl-[glycerolipid] + 2 ferri-

cytochrome $b_5 + 2 H_2O$

(2) α -linolenoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = coniferonoyl-[glycerolipid] + 2

ferricytochrome $b_5 + 2 H_2O$

Other name(s): acyl-lipid ω-13 desaturase; acyl-lipid 7-desaturase (ambiguous)

Systematic name: acyl-[glycerolipid], ferrocytochrome b_5 :oxygen oxidoreductase [$\omega(9-4), \omega(9-5)$ 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 C_{18} or C_{20} 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 $20:2\Delta(11,14)$ and $20:3\Delta(11,14,17)$ 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: [1981]

[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 + $O_2 = (9Z,12Z,15Z)$ -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 plant *Sorghum bicolor*, is involved in the biosynthesis of sor-

goleone, 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: [3229]

[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 + O_2 = an (8E,10E,12Z)-octadeca-8,10,12-trienoyl-

[glycerolipid] + acceptor + 2 H₂O

Systematic name: linoleoyl-lipid,reduced acceptor:oxygen 8,11-allylic oxidase (8*E*,10*E*-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: [3406, 524]

[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 + $O_2 = (10E, 12Z)$ -hexadeca-10,12-dienoyl-CoA +

acceptor + $2 H_2O$

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: [2909]

[EC 1.14.19.15 created 2015]

EC 1.14.19.16

Accepted name: linoleoyl-lipid Δ^{12} conjugase (11*E*,13*Z*-forming)

Reaction: a linoleoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = a (9Z,11E,13Z)-octadeca-9,11,13-

trienoyl-[glycerolipid] + 2 ferricytochrome b_5 + 2 H_2O

Other name(s): Fac (gene name)

Systematic name: linoleoyl-lipid, ferrocytochrome-b₅: oxygen 11,14 allylic oxidase (11E,13Z-forming)

Comments: The enzyme, characterized from the plants *Punica granatum* (pomegranate) and *Trichosanthes kir*-

ilowii (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 (11*E*,13*E*-forming).

References: [1732, 1856]

[EC 1.14.19.16 created 2015]

EC 1.14.19.17

Accepted name: sphingolipid 4-desaturase

Reaction: a dihydroceramide + 2 ferrocytochrome $b_5 + O_2 + 2 H^+ = a (4E)$ -sphing-4-enine ceramide + 2 ferri-

cytochrome $b_5 + 2 H_2O$

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 [4036]. The preferred substrate is dihydroceramide, but the enzyme is also active with dihydroglucosylceramide [2792]. Unlike EC 1.14.19.29, sphingolipid 8-desaturase, this enzyme does not contain an integral cytochrome b_5 domain [4246] and requires an external cytochrome b_5 [576]. The product serves as an important signalling molecules in

mammals and is required for spermatide differentiation [2789].

References: [4036, 2792, 576, 4246, 2789]

[EC 1.14.19.17 created 2015]

Accepted name: sphingolipid 8-(*E*)-desaturase

Reaction: a (4E)-sphing-4-enine ceramide + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = a (4E,8E)-sphing-4,8-dienine

ceramide + 2 ferricytochrome b_5 + 2 H_2O

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 dehydrogenat-

ing)

Comments: The enzyme, characterized from the yeasts *Kluyveromyces lactis* and *Candida albicans* [4175] and

from the diatom *Thalassiosira pseudonana* [4310], 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 [3216]. 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: [4175, 4310, 3216]

[EC 1.14.19.18 created 2015]

EC 1.14.19.19

Accepted name: sphingolipid 10-desaturase

Reaction: a (4E,8E)-sphinga-4,8-dienine ceramide + 2 ferrocytochrome b_5 + O_2 + 2 H^+ = a (4E,8E,10E)-

sphinga-4,8,10-trienine ceramide + 2 ferricytochrome b_5 + 2 H₂O

Other name(s): desA (gene name)

Systematic name: a (4E,8E)-sphinga-4,8-dienine ceramide,ferrocytochrome 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: [2788]

[EC 1.14.19.19 created 2015]

EC 1.14.19.20

Accepted name: Δ^7 -sterol 5(6)-desaturase

Reaction: a Δ^7 -sterol + **2** ferrocytochrome b_5 + O_2 + **2** H⁺ = a $\Delta^{5,7}$ -sterol + **2** ferricytochrome b_5 + **2** H₂O **Other name(s):** lathosterol oxidase; Δ^7 -sterol Δ^5 -dehydrogenase; Δ^7 -sterol 5-desaturase; Δ^7 -sterol-C5(6)-desaturase;

5-DES; SC5DL (gene name); ERG3 (gene name)

Systematic name: Δ^7 -sterol, ferrocytochrome b_5 : oxygen oxidoreductase 5,6-dehydrogenating

Comments: This enzyme, found in eukaryotic organisms, catalyses the introduction of a double bond between the

 C_5 and C_6 carbons of the B ring of Δ^7 -sterols, to yield the corresponding $\Delta^{5,7}$ -sterols. The enzymes from yeast, plants and vertebrates act on avenasterol, episterol, and lathosterol, respectively. The en-

zyme is located at the endoplasmic reticulum and is membrane bound.

References: [876, 1708, 138, 4218, 3080, 4217, 3343]

[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 + O_2 + NAD(P)H + H⁺ = cholesta-5,7-dien-3 β -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 the biosythesis 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: [4819, 4659, 2972, 228]

[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 ferrocytochrome $b_5 + O_2 + 2 H^+ = a$ linoleoyl-[glycerolipid] + 2 ferricy-

tochrome $b_5 + 2 H_2O$

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,ferrocytochrome-b₅: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 phos-

phatidylcholine. cf. EC 1.14.19.23, acyl-lipid ω-6 desaturase (ferredoxin).

References: [3393, 3925, 4082, 3937, 2050, 2819]

[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 + O_2 + 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 (ambigu-

ous); oleoyl-CoA desaturase (ambiguous); oleoylphosphatidylcholine desaturase (ambiguous); phos-

phatidylcholine 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 [1675]. *cf.* EC 1.14.19.34, acyl-lipid (9+3)-(*E*)-desaturase.

References: [3727, 3728, 1675, 1079, 3726]

[EC 1.14.19.23 created 2015]

EC 1.14.19.24

Accepted name: acyl-CoA 11-(*E*)-desaturase

Reaction: an acyl-CoA + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = an (11*E*)-enoyl-CoA + 2 ferricytochrome b_5 + 2

 H_2O

Systematic name: acyl-CoA, ferrocytochrome b₅: 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: [1151, 2673, 3027, 3327]

[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 $b_5 + O_2 + 2 H^+ = \text{an } \alpha$ -linoleoyl-[glycerolipid] + 2

ferricytochrome $b_5 + 2 H_2O$

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 [3646]. cf. EC 1.14.19.35, sn-2 acyl-lipid ω-3 desaturase (ferredoxin).

References: [464, 136, 3646]

[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 + O_2 + 2 H⁺ = (6Z)-

 $hexadec-6-enoyl-[acyl-carrier\ protein] + \textbf{2}\ oxidized\ ferredoxin\ [iron-sulfur]\ cluster + \textbf{2}\ H_2O$

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 posi-

tion of the double bond is determined by its distance from the carboxyl end of the fatty acid.

References: [519, 521]

[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 + O_2 + 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: [655]

[EC 1.14.19.27 created 2015]

Accepted name: sn-1 stearoyl-lipid 9-desaturase

Reaction: a 1-stearoyl-2-acyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 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: [4482, 1644, 3642]

[EC 1.14.19.28 created 2015]

EC 1.14.19.29

Accepted name: sphingolipid 8-(E/Z)-desaturase

Reaction: (1) a (4R)-4-hydroxysphinganine ceramide + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = a (4R,8E)-4-

hydroxysphing-8-enine ceramide + $\mathbf{2}$ ferricytochrome b_5 + $\mathbf{2}$ H₂O

(2) a (4R)-4-hydroxysphinganine ceramide + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = a (4R,8Z)-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: (4R)-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 Δ^8 -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 [3983]. 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: [3983, 3979, 3981, 264, 3612, 634]

[EC 1.14.19.29 created 2015]

EC 1.14.19.30

Accepted name: acyl-lipid (8-3)-desaturase

Reaction: (1) an (8Z,11Z,14Z)-icosa-8,11,14-trienoyl-[glycerolipid] + 2 ferrocytochrome $b_5 + O_2 + 2 H^+ = a$

(5Z,8Z,11Z,14Z)-icosatetra-5,8,11,14-tetraenoyl-[glycerolipid] + **2** ferricytochrome b_5 + **2** H₂O (2) an (8Z,11Z,14Z,17Z)-icosa-8,11,14,17-tetraenoyl-[glycerolipid] + **2** ferrocytochrome b_5 + O₂ + **2** H⁺ = a (5Z,8Z,11Z,14Z,17Z)-icosa-5,8,11,14,17-pentaenoyl-[glycerolipid] + **2** ferricytochrome b_5 + **2**

H₂O

Other name(s): acyl-lipid 5-desaturase; Δ^5 -fatty-acid desaturase; DES5 (gene name); D5des (gene name); FADS1

Systematic name: Δ^8 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 Δ^8 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: [2787, 1971, 4917]

[EC 1.14.19.30 created 2015]

Accepted name: acyl-lipid (7-3)-desaturase

Reaction: (1) a (7Z,10Z,13Z,16Z,19Z)-docosa-7,10,13,16,19-pentaenoyl-[glycerolipid] + **2** ferrocytochrome

 $b_5 + O_2 + 2 H^+ = a (4Z,7Z,10Z,13Z,16Z,19Z) - docosa - 4,7,10,13,16,19 - hexaenoyl - [glycerolipid] + 2$

ferricytochrome $b_5 + 2 H_2O$

(2) a (7Z,10Z,13Z,16Z)-docosa-7,10,13,16-tetra
enoyl-[glycerolipid] + $\bf 2$ ferrocytochrome
 b_5 + O_2 + $\bf 2$

 $H^+ = a (4Z,7Z,10Z,13Z,16Z) - docosa-4,7,10,13,16$ -pentaenoyl-[glycerolipid] + 2 ferricytochrome b_5 +

2 H₂O

Other name(s): D4Des (gene name); des1 (gene name); $Cr\Delta^4FAD$ (gene name); acyl-lipid 4-desaturase

Systematic name: Δ^7 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 polyun-saturated fatty acids that contain a Δ^7 double bond. The enzyme from the fresh water alga *Chlamy-domonas reinhardtii* acts on the 16 carbon fatty acid (7Z,10Z,13Z)-hexadeca-7,10,13-trienoate [4862].

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: [3405, 4308, 2785, 4917, 4862]

[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 ferrocytochrome b_5 + O₂ + 2 H⁺ = (14*E*)-hexadec-14-enoyl-CoA + 2 ferricy-

tochrome $b_5 + 2 H_2O$

(2) palmitoyl-CoA + 2 ferrocytochrome b_5 + O₂ + 2 H⁺ = (14Z)-hexadec-14-enoyl-CoA + 2 ferricy-

tochrome $b_5 + 2 H_2O$

Systematic name: palmitoyl-CoA, ferrocytochrome 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: [3552, 4709, 3638]

[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 lineleoyl-[glycerolipid] + 2 ferrocytochrome $b_5 + O_2 + 2 H^+ = \text{an } \alpha$ -eleostearoyl-[glycerolipid]

+ 2 ferricytochrome b_5 + 2 H_2O

(2) a γ -linolenoyl-[glycerolipid] + 2 ferrocytochrome $b_5 + O_2 + 2 H^+ = \text{an } \alpha$ -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, ferrocytochrome- b_5 : oxygen 11,14 allylic oxidase (11E,13E-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: [518, 996]

[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 ferrocytochrome $b_5 + O_2 + 2 H^+ = a (9Z,12E)$ -octadeca-9,12-dienoyl-

[glycerolipid] + 2 ferricytochrome b_5 + 2 H₂O

(2) a palmitoleoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = a (9Z,12E)-hexadeca-9,12-

dienoyl-[glycerolipid] + $\mathbf{2}$ ferricytochrome b_5 + $\mathbf{2}$ H₂O

Other name(s): acyl-lipid 12-(*E*)-desaturase; DsFAD2-1; FADX

Systematic name: Δ^9 acyl-lipid, ferrocytochrome 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: [996, 520]

[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 +

 $O_2 + 2 H^+ = a (7Z,10Z,13Z)$ -hexadeca-7,10,13-trienoyl-[glycerolipid] + 2 oxidized ferredoxin [iron-

sulfur] cluster + $2 H_2O$

(2) a linoleoyl-[glycerolipid] + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 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

urase (ferredoxin).

References: [1783, 2742, 4433]

[EC 1.14.19.35 created 2015]

EC 1.14.19.36

Accepted name: sn-1 acyl-lipid $\omega-3$ 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] + $\mathbf{2}$ reduced ferredoxin [iron-sulfur] cluster + O_2 + $\mathbf{2}$ H⁺ = a

 $1-\alpha$ -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: [3641]

[EC 1.14.19.36 created 2015]

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 + $2 H_2O$

(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 car-

bon 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: [3688]

[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 + O_2 + 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 + O_2 + 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: [3980]

[EC 1.14.19.38 created 2015]

EC 1.14.19.39

Accepted name: acyl-lipid Δ^{12} -acetylenase

Reaction: $linoleoyl-[glycerolipid] + 2 ferrocytochrome <math>b_5 + O_2 + 2 H^+ = crepenynyl-[glycerolipid] + 2 ferricy-$

tochrome $b_5 + 2 H_2O$

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: [206, 2388, 3003]

[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 + O_2 + 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 pro-

duction 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: [4926]

[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⁺

 $+ 2 H_2O$

Other name(s): ERG5 (gene name); CYP710A (gene name)

Systematic name: ergosta-5,7,24(28)-trien-3β-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 brassicast-

erol, respectively.

References: [2061, 3922, 2890]

[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 + O_2 + 2 H⁺ = a 1-

acyl-2-[(7Z)-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 po-

sition of glycerolipids. The enzyme from the plant Arabidopsis thaliana is specific for palmitate in

monogalactosyldiacylglycerol.

References: [2294, 1610]

[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 + O_2 + 2 H⁺ = a 1-

acyl-2-[(3E)-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

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 [1191].

References: [1191, 1270]

[EC 1.14.19.43 created 2015]

EC 1.14.19.44

Accepted name: acyl-CoA (8-3)-desaturase

Reaction: (1) (8Z,11Z,14Z)-icosa-8,11,14-trienoyl-CoA + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = arachidonoyl-

CoA + 2 ferricytochrome $b_5 + 2$ H_2O

(2) (8Z,11Z,14Z,17Z)-icosa-8,11,14,17-tetraenoyl-CoA + **2** ferrocytochrome b_5 + O_2 + **2** H⁺ =

(5Z,8Z,11Z,14Z,17Z)-icosa-5,8,11,14,17-pentaenoyl-CoA + **2** ferricytochrome 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 po-

sition 8. The enzymes from algae, mosses, mammals and the protozoan *Leishmania major* catalyse the desaturation of dihomo- γ -linoleate [(8Z,11Z,14Z)-icosa-8,11,14-trienoate] and (8Z,11Z,14Z,17Z)-icosa-8,11,14,17-tetraenoate to generate arachidonate and (5Z,8Z,11Z,14Z,17Z)-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: [664, 2418, 4331, 4223]

[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 + O_2 + 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: [4481, 1644, 85]

[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 + O_2 + 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: [1644, 3471, 2299]

[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 ferrocytochrome b_5 + O_2 + 2 H⁺ = a stearidonoyl-

[glycerolipid] + 2 ferricytochrome b_5 + 2 H_2O

(2) a linoleoyl-[glycerolipid] + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = a γ -linoleoyl-[glycerolipid] + 2

ferricytochrome $b_5 + 2 H_2O$

Other name(s): DES6 (gene name); acyl-lipid 6-desaturase; acyl-lipid Δ^6 -desaturase; Δ^6 -desaturase (ambiguous) Systematic name: Δ^9 acyl-[glycerolipid],ferrocytochrome b_5 :oxygen oxidoreductase (6,7-cis-dehydrogenating)

Comments: The enzyme, characterized from the moss *Physcomitrella patens* and the plant *Borago officinalis* (bor-

age), 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: [3689, 1329]

[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 *Aquincola 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: [3700, 3760]

[EC 1.14.19.48 created 2016]

EC 1.14.19.49

Accepted name: tetracycline 7-halogenase

Reaction: tetracycline + FADH₂ + chloride + O_2 + H^+ = 7-chlorotetracycline + FAD + $\mathbf{2}$ 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: [813, 4924]

[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] + $O_2 = (4aR, 10bS)$ -

noroxomaritidine + [oxidized NADPH—hemoprotein reductase] + 2 H₂O

(2) 4'-O-methylnorbelladine + [reduced NADPH—hemoprotein reductase] + O_2 = (4aS,10bR)-

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 (daf-

fodil), 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: [2088]

[EC 1.14.19.50 created 2016]

EC 1.14.19.51

Accepted name: (S)-corytuberine synthase

Reaction: (S)-reticuline + [reduced NADPH—hemoprotein reductase] + $O_2 = (S)$ -corytuberine + [oxidized

NADPH—hemoprotein reductase] + $2 \text{ H}_2\text{O}$.

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 qua-

ternary benzylisoquinoline alkaloid magnoflorine in the plant *Coptis japonica*. It is specific for (S)-

reticuline.

References: [1799]

[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] +

 $O_2 = (R)$ -dihydrocamalexate + hydrogen cyanide + [oxidized NADPH—hemoprotein reductase] + 2

 H_2O

(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 *Ara-*

bidopsis 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: [3749, 403]

[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 + $2 H_2O$

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: [1053, 2258]

[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] + $O_2 = 1,2$ -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:** [1669, 4641, 1094]

[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 O_2 + 2 H^+ = 2,4-dibromophenol + 2 NADP⁺ +

 $CO_2 + 4 H_2O$ (overall reaction)

 $(1a) \ 4-hydroxybenzoate + NADPH + bromide + O_2 + H^+ = 3-bromo-4-hydroxybenzoate + NADP^+ + 1-2-bromo-4-hydroxybenzoate + 1-2-b$

 $\mathbf{2} H_2O$

(1b) 3-bromo-4-hydroxybenzoate + NADPH + bromide + O_2 + H^+ = 2,4-dibromophenol + NADP+ +

 $CO_2 + 2 H_2O$

(2) 3,4-dihydroxybenzoate + 2 NADPH + 2 bromide + 2 O_2 + 2 H^+ = 3,5-dibromobenzene-1,2-diol +

 $2 \text{ NADP}^+ + \text{CO}_2 + 4 \text{ H}_2\text{O}$ (overall reaction)

(2a) 3,4-dihydroxybenzoate + NADPH + bromide + O_2 + H^+ = 3-bromo-4,5-dihydroxybenzoate +

 $NADP^+ + 2 H_2O$

(2b) 3-bromo-4,5-dihydroxybenzoate + NADPH + bromide + O_2 + H^+ = 3,5-dibromobenzene-1,2-diol

 $+ \text{ NADP}^+ + \text{CO}_2 + 2 \text{ H}_2\text{O}$

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: [33, 34]

[EC 1.14.19.55 created 2018]

EC 1.14.19.56

Accepted name: 1*H*-pyrrole-2-carbonyl-[peptidyl-carrier protein] chlorinase

Reaction: 1H-pyrrole-2-carbonyl-[PltL peptidyl-carrier protein] + **2** FADH₂ + **2** chloride + **2** O₂ = 4,5-dichloro-

1*H*-pyrrole-2-carbonyl-[PltL peptidyl-carrier protein] + 2 FAD + 4 H₂O (overall reaction)

(1a) ^{1}H -pyrrole-2-carbonyl-[PltL peptidyl-carrier protein] + FADH₂ + chloride + O₂ = 5-chloro-1 ^{1}H -

pyrrole-2-carbonyl-[PltL peptidyl-carrier protein] + FAD + 2 H₂O

(1b) 5-chloro-1H-pyrrole-2-carbonyl-[PltL peptidyl-carrier protein] + FADH₂ + chloride + O₂ = 4,5-

dichloro-1*H*-pyrrole-2-carbonyl-[PltL peptidyl-carrier protein] + FAD + H₂O

Other name(s): pltA (gene name)

Systematic name: 1*H*-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: [3112, 953, 3231]

[EC 1.14.19.56 created 2018]

EC 1.14.19.57

Accepted name: 1*H*-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-1*H*-pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + 3 FAD + 6 H₂O (overall reaction) (1a) 1*H*-pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + FADH₂ + bromide + O₂ = 5-bromo-1*H*-

pyrrole-2-carbonyl-[Bmp1 peptidyl-carrier protein] + FAD + 2 H₂O

(1b) 5-bromo-1*H*-pyrrole-2-carbonyl- $\lceil Bmp1 \rceil$ peptidyl-carrier protein + FADH₂ + bromide + O₂ = 4,5-

dibromo-1*H*-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 + $2H_2O$

Other name(s): bmp2 (gene name)

Systematic name: 1*H*-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: [33]

[EC 1.14.19.57 created 2018]

EC 1.14.19.58

Accepted name: tryptophan 5-halogenase

Reaction: L-tryptophan + FADH₂ + chloride + O_2 + 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* cataly-

ses 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: [4865, 4925]

[EC 1.14.19.58 created 2018]

EC 1.14.19.59

Accepted name: tryptophan 6-halogenase

Reaction: (1) L-tryptophan + FADH₂ + chloride + O_2 + H^+ = 6-chloro-L-tryptophan + FAD + 2 H₂O

(2) D-tryptophan + FADH₂ + chloride + O_2 + H^+ = 6-chloro-D-tryptophan + FAD + 2 H_2O

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: [4869, 2805, 3844]

[EC 1.14.19.59 created 2018]

Accepted name: 7-chloro-L-tryptophan 6-halogenase

Reaction: 7-chloro-L-tryptophan + FADH₂ + chloride + O_2 + 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: [1603]

[EC 1.14.19.60 created 2018]

EC 1.14.19.61

Accepted name: dihydrorhizobitoxine desaturase

Reaction: dihydrorhizobitoxine + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 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: [4781, 3162]

[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 monoterpenoid in-

dole alkaloids and ipecac alkaloids.

References: [4737, 4736, 1823]

[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] + O_2 = 5-hydroxypseudobaptigenin + [oxi-

dized 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 incorpo-

rate oxygen into the product. Catalyses a step in the biosynthesis of (–)-maackiain, the main ptero-

carpan phytoalexin in chickpea (Cicer arietinum).

References: [3617]

[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] + O_2 = (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 incorpo-

rate 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: [245]

[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] + O_2 = (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: [245, 621]

[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 alka-

loid 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 guattagaumer-

ine.

References: [3995]

[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] + O_2 = 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-

oupling)

Comments: A cytochrome *P*-450 (heme-thiolate) protein found in plants. Forms the morphinan alkaloid salutari-

dine by intramolecular phenol oxidation of reticuline without the incorporation of oxygen into the

product.

References: [1300]

[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] + O_2 = (S)-canadine + [ox-

idized 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 reac-

tion 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: [3597, 1800, 820]

[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⁺ + $O_2 = 3.3'$ -biflaviolin + 2 oxidized

ferredoxin [iron-sulfur] cluster + 2 H₂O

(2) 2 flaviolin + 2 reduced ferredoxin [iron-sulfur] cluster + 2 H⁺ + $O_2 = 3.8'$ -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 [4894, 4896]. The products are highly conjugated pigments that protect the bacterium from the

deleterious effects of UV irradiation [4894].

References: [4894, 4895, 4896]

[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: $\operatorname{cyclo}(L\text{-tyrosyl}-L\text{-tyrosyl}) + 2 \operatorname{reduced} \operatorname{ferredoxin} [\operatorname{iron-sulfur}] \operatorname{cluster} + 2 \operatorname{H}^+ + \operatorname{O}_2 = \operatorname{mycocyclosin} +$

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: [278]

[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] + O_2 = 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: [2019]

[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 hexan*-

drum 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: [2657]

[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] + $O_2 = (S)$ -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 re-

action 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: [1798, 621]

[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] + O_2 = (+)-piperitol + [oxidized

NADPH-hemoprotein reductase] + $2 H_2O$

(2) (+)-piperitol + [reduced NADPH-hemoprotein reductase] + O_2 = (+)-sesamin + [oxidized NADPH-hemoprotein reductase]

hemoprotein reductase] + $2 H_2O$

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. radia-

tum (black sesame).

References: [3185]

[EC 1.14.19.74 created 2018]

Accepted name: very-long-chain acyl-lipid ω-9 desaturase

Reaction: (1) 1-hexacosanoyl-2-acyl-[phosphoglycerolipid] + 2 ferrocytochrome $b_5 + O_2 + 2 H^+ = 1$ -[(17Z)-

hexacos-17-enoyl]-2-acyl-[phosphoglycerolipid] + 2 ferricytochrome b_5 + 2 H₂O

(2) 1-tetracosanoyl-2-acyl-[phosphoglycerolipid] + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = 1-[(15Z)-

tetracos-15-enoyl]-2-acyl-[phosphoglycerolipid] + $\mathbf{2}$ ferricytochrome b_5 + $\mathbf{2}$ H₂O

Other name(s): ADS2 (gene name)

Systematic name: very-long-chain acyl-[glycerolipid], ferrocytochrome b_5 : oxygen oxidoreductase (ω^9, ω^8 -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 cu-

ticular and epicuticular waxes, and in suberin.

References: [1218, 3938]

[EC 1.14.19.75 created 2018]

EC 1.14.19.76

Accepted name: flavone synthase II

Reaction: a flavanone + [reduced NADPH—hemoprotein reductase] + O_2 = 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: [2661, 1131, 2330]

[EC 1.14.19.76 created 2018]

EC 1.14.19.77

Accepted name: plasmanylethanolamine desaturase

Reaction: a plasmanylethanolamine + 2 ferrocytochrome b_5 + O_2 + 2 H⁺ = a plasmenylethanolamine + 2 ferri-

cytochrome $b_5 + 2 H_2O$

Other name(s): TMEM189 (gene name); 2-acyl-1-alkyl-sn-glycero-3-phosphoethanolamine desaturase; alkylacyl-

glycerophosphoethanolamine desaturase; alkylacylglycero-phosphorylethanolamine dehydrogenase; alkyl-acylglycerophosphorylethanolamine dehydrogenase; 1-*O*-alkyl-2-acyl-*sn*-glycero-3-phosphorylethanolamine desaturase; 1-*O*-alkyl 2-acyl-*sn*-glycero-3-phosphorylethanolamine desat-

urase

Systematic name: plasmanylethanolamine, ferrocytochrome b₅: oxygen oxidoreductase (plasmenylethanolamine-

forming)

Comments: The enzyme catalyses the introduction of a double bond at position 1 of the alkyl group attached by

an ether bond at the *sn*-1 position of plasmanylethanolamine, generating a vinyl ether-containing plasmenylethanolamine. The enzyme is found in animals and some bacteria, but not in plants, fungi, or

most aerobic bacteria.

References: [4041, 3226, 3227, 4690, 1259]

[EC 1.14.19.77 created 1976 as EC 1.14.99.19, transferred 2020 to EC 1.14.19.77]

EC 1.14.19.78

Accepted name: decanoyl-[acyl-carrier protein] acetylenase

Reaction: decanoyl-[acyl-carrier protein] + 4 reduced ferredoxin [iron-sulfur] cluster + 2 O_2 + 4 H^+ = dec-9-

ynoyl-[acyl-carrier protein] + 4 oxidized ferredoxin [iron-sulfur] cluster + 4 H₂O (overall reaction)

(1a) decanoyl-[acyl-carrier protein] + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 2 H⁺ = dec-9-

enoyl-[acyl-carrier protein] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O

(1b) dec-9-enoyl-[acyl-carrier protein] + 2 reduced ferredoxin [iron-sulfur] cluster + O_2 + 2 H^+ = dec-

9-ynoyl-[acyl-carrier protein] + 2 oxidized ferredoxin [iron-sulfur] cluster + 2 H₂O

Other name(s): ttuB (gene name) (ambiguous)

Systematic name: decanoyl-[acyl-carrier protein], reduced ferredoxin: oxygen oxidoreductase (9,10-dehydrogenating)

Comments: The enzyme, characterized from the bacterium Teredinibacter turnerae, is specific for decanoyl-[acyl-

carrier protein]. Activity is maximal when decanoate is loaded onto a dedicated acyl-carrier protein

(TtuC), which is encoded by a gene in the same operon.

References: [4927]

[EC 1.14.19.78 created 2021]

EC 1.14.19.79

Accepted name: 3β,22α-dihydroxysteroid 3-dehydrogenase

Reaction: (1) (22S)-22-hydroxycampesterol + [reduced NADPH-hemoprotein reductase] + O_2 = (22S)-22-

hydroxycampest-4-en-3-one + [oxidized NADPH-hemoprotein reductase] + 2 H₂O

(2) 6-deoxoteasterone + [reduced NADPH-hemoprotein reductase] + O_2 = 3-dehydro-6-

deoxoteasterone + [oxidized NADPH-hemoprotein reductase] + 2 H₂O

Other name(s): CYP90A1 (gene name)

Systematic name: 3β,22α-dihydroxysteroid,[reduced NADPH-hemoprotein reductase]:oxygen 3-oxidoreductase

Comments: This cytochrome *P*-450 (heme-thiolate) enzyme, characterized from the plant *Arabidopsis thaliana*,

catalyses C-3 dehydrogenation of all 3β-hydroxy brassinosteroid synthesis intermediates with 22-

hydroxylated or 2^2 , 2^3 -dihydroxylated side chains.

References: [3141]

[EC 1.14.19.79 created 2022]

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 + O_2 = deacetoxycephalosporin C + succinate + CO_2 + H_2O

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: [546, 2383, 4787, 4390, 957]

[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: (5R)-carbapenem-3-carboxylate synthase

Reaction: (3S,5S)-carbapenam-3-carboxylate + 2-oxoglutarate + $O_2 = (5R)$ -carbapen-2-em-3-carboxylate + suc-

cinate + CO_2 + H_2O

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

Systematic name: (3S,5S)-carbapenam-3-carboxylate,2-oxoglutarate:oxygen oxidoreductase (dehydrating)

Comments: Requires Fe^{2+} . The enzyme is involved in the biosynthesis of the carbapenem β -lactam antibiotic

(5R)-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: [702, 4005, 3927]

[EC 1.14.20.3 created 2013]

EC 1.14.20.4

Accepted name: anthocyanidin synthase

Reaction: a (2R,3S,4S)-leucoanthocyanidin + 2-oxoglutarate + O_2 = an anthocyanidin + succinate + CO_2 + 2

H₂O (overall reaction)

(1a) a (2R,3S,4S)-leucoanthocyanidin + 2-oxoglutarate + O_2 = a (4S)- 2,3-dehydroflavan-3,4-diol +

succinate + CO_2 + H_2O

(1b) a (4S)- 2,3-dehydroflavan-3,4-diol = an anthocyanidin + H_2O

Other name(s): leucocyanidin oxygenase; leucocyanidin,2-oxoglutarate:oxygen oxidoreductase; ANS (gene name)

Systematic name: (2R,3S,4S)-leucoanthocyanidin,2-oxoglutarate:oxygen oxidoreductase

Comments: The enzyme requires iron(II) and ascorbate. It is involved in the pathway by which many flowering

plants make anthocyanin flower pigments (glycosylated anthocyandins). 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) [4352, 4639].

References: [3630, 4352, 4639, 4350, 4582]

[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 + O_2 = a flavone + succinate + CO_2 + H_2O

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 ac-

tivity.

References: [2663, 2559, 2662]

[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 + O_2 = a flavonol + succinate + CO_2 + H_2O

Other name(s): FLS (gene name)

Systematic name: dihydroflavonol,2-oxoglutarate:oxygen oxidoreductase

Comments: In addition to the desaturation of (2R,3R)-dihydroflavonols to flavonols, the enzyme from Citrus un-

shiu (satsuma mandarin) also has a non-specific activity that trans-hydroxylates the flavanones (2S)-naringenin and the unnatural (2R)-naringenin at C-3 to kaempferol and (2R,3R)-dihydrokaempferol,

respectively [2560]. Requires Fe²⁺.

References: [4583, 2560, 2662, 4351]

[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 + O_2 = succinate + CO_2 + guanidine + (S)-1-pyrroline-5-carboxylate +

H₂O (overall reaction)

(1a) L-arginine + 2-oxoglutarate + O_2 = succinate + CO_2 + 5-hydroxy-L-arginine (1b) 5-hydroxy-L-arginine = guanidine + (S)-1-pyrroline-5-carboxylate + H_2O

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 etheneforming reaction for each cycle of the succinate-forming reaction, so that the stoichiometry of the

products ethene and succinate is 2:1.

References: [2954, 1222, 1221, 2672]

[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 + O_2 = (-)-deoxypodophyllotoxin + succinate + CO_2 + H_2O

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: [2365]

 $[EC\ 1.14.20.8\ created\ 2016\ as\ EC\ 1.14.11.50,\ transferred\ 2018\ to\ EC\ 1.14.20.8]$

EC 1.14.20.9

Accepted name: L-tyrosine isonitrile desaturase

Reaction: (2S)-3-(4-hydroxyphenyl)-2-isocyanopropanoate + 2-oxoglutarate + O_2 = (2E)-3-(4-hydroxyphenyl)-

2-isocyanoprop-2-enoate + succinate + CO_2 + H_2O

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

Systematic name: (2S)-3-(4-hydroxyphenyl)-2-isocyanopropanoate,2-oxoglutarate:oxygen oxidoreductase

Comments: The enzyme is a member of the Fe^{2+} , 2-oxoglutarate-dependent oxygenases and requires Fe^{2+} . 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: [698, 963, 4922]

[EC 1.14.20.9 created 2018]

EC 1.14.20.10

Accepted name: L-tyrosine isonitrile desaturase/decarboxylase

Reaction: (2S)-3-(4-hydroxyphenyl)-2-isocyanopropanoate + 2-oxoglutarate + O_2 = 4-[(E)-2-

isocyanoethenyl]phenol + succinate + 2 CO_2 + H_2O

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

Systematic name: (2S)-3-(4-hydroxyphenyl)-2-isocyanopropanoate,2-oxoglutarate:oxygen oxidoreductase (decarboxy-

lating)

Comments: The enzyme, characterized from the bacterium Xenorhabdus nematophila, is involved in rhabdus-

> cin 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 decar-

boxylation of the substrate.

[770, 4922] **References:**

[EC 1.14.20.10 created 2018]

EC 1.14.20.11

Accepted name: 3-[(Z)-2-isocyanoethenyl]-1H-indole synthase

> (2S)-3-(1H-indol-3-yl)-2-isocyanopropanoate + 2-oxoglutarate + $O_2 = 3$ -[(Z)-2-isocyanoethenyl]-1H-**Reaction:**

> > indole + succinate + 2 CO_2 + H_2O

Other name(s): ambI3 (gene name); famH3 (gene name); L-tryptophan isonitrile desaturase/decarboxylase (3-[(Z)-2-

isocyanoethenyl]-1*H*-indole-forming)

Systematic name: (2S)-3-(1H-indol-3-yl)-2-isocyanopropanoate,2-oxoglutarate:oxygen oxidoreductase (decarboxylat-

ing, 3-[(Z)-2-isocyanoethenyl]-1H-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-oxoglutaratedependent monoxygenation 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, 3-[(E)-2-isocyanoethenyl]-1H-indole

synthase.

[1659, 601] **References:**

[EC 1.14.20.11 created 2018]

EC 1.14.20.12

3-[(E)-2-isocyanoethenyl]-1H-indole synthaseAccepted name:

> **Reaction:** (2S)-3-(1H-indol-3-yl)-2-isocyanopropanoate + 2-oxoglutarate + O_2 = 3-[(E)-2-isocyanoethenyl]-1H-

> > indole + succinate + 2 CO_2 + H_2O

Other name(s): isnB (gene name); L-tryptophan isonitrile desaturase/decarboxylase (3-[(E)-2-isocyanoethenyl]-1H-

indole-forming)

(2S)-3-(1H-indol-3-yl)-2-isocyanopropanoate,2-oxoglutarate:oxygen oxidoreductase (decarboxylat-**Systematic name:**

ing, 3-[(E)-2-isocyanoethenyl]-1H-indole-forming)

The enzyme has been characterized from an unidentified soil bacterium. It catalyses an Fe²⁺, 2-**Comments:**

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, 3-[(Z)-2-

isocyanoethenyl]-1*H*-indole synthase.

[421, 601] **References:**

[EC 1.14.20.12 created 2018]

EC 1.14.20.13

Accepted name: 6β-hydroxyhyoscyamine epoxidase

(6S)-6β-hydroxyhyoscyamine + 2-oxoglutarate + O_2 = scopolamine + succinate + CO_2 + H_2O **Reaction:** Other name(s):

hydroxyhyoscyamine dioxygenase; (6S)-6-hydroxyhyoscyamine,2-oxoglutarate oxidoreductase

(epoxide-forming)

Systematic name: (6S)-6β-hydroxyhyoscyamine,2-oxoglutarate:oxygen oxidoreductase (epoxide-forming)

Requires Fe²⁺ and ascorbate. **Comments:**

References: [1550]

[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 + O_2 + chloride = hapalindole G + succinate + CO_2 + H_2O

(2)12-epi-fischerindole U + 2-oxoglutarate + O₂ + chloride = 12-epi-fischerindole G + succinate + CO₂

 $+ H_2O$

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 reac-

tion that requires oxygen, chloride ions, iron(II) and 2-oxoglutarate.

References: [1657, 4923, 1658]

[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 + O_2 + Cl^- = a 4-chloro-L-threonyl-[L-

threonyl-carrier protein] + succinate + CO_2 + H_2O

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: [4388]

[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 + $2 O_2$ = prostaglandin H_2 + acceptor + H_2O

 $\textbf{Other name}(\textbf{s})\textbf{:} \quad \text{prostaglandin synthase; prostaglandin G/H synthase; PG synthetase; prostaglandin metabolic prost$

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: [896, 3139]

[EC 1.14.99.1 created 1972, modified 1990]

EC 1.14.99.2

Accepted name: kynurenine 7,8-hydroxylase

Reaction: kynurenate + reduced acceptor + O_2 = 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: [4210]

[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 + O_2 = testosterone acetate + acceptor + H_2O

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 radicicola* (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: [3429]

[EC 1.14.99.4 created 1972, modified 1999]

[1.14.99.5 Transferred entry. stearoyl-CoA desaturase. Now EC 1.14.19.1, stearoyl-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 17α-monooxygenase, now classified as EC 1.14.14.19, steroid 17α-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 6β-monooxygenase

Reaction: estradiol-17 β + reduced acceptor + O₂ = 6β -hydroxyestradiol-17 β + acceptor + H₂O

Other name(s): estradiol 6β -hydroxylase

Systematic name: estradiol-17β,hydrogen-donor:oxygen oxidoreductase (6β-hydroxylating)

References: [1479, 2915]

 $[EC\ 1.14.99.11\ created\ 1965\ as\ EC\ 1.14.1.10,\ transferred\ 1972\ to\ EC\ 1.14.99.11]$

EC 1.14.99.12

Accepted name: androst-4-ene-3,17-dione monooxygenase

Reaction: androstenedione + reduced acceptor + O_2 = testololactone + acceptor + H_2O

Other name(s): androstene-3,17-dione hydroxylase; androst-4-ene-3,17-dione 17-oxidoreductase; androst-4-ene-3,17-dione

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 radicicola* (EC 1.14.13.54,

ketosteroid monooxygenase) catalyses both this reaction and that catalysed by EC 1.14.99.4, proges-

terone monooxygenase.

References: [3369]

[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 11α-monooxygenase

Reaction: progesterone + reduced acceptor + $O_2 = 11\alpha$ -hydroxyprogesterone + acceptor + H_2O

Other name(s): progesterone 11α -hydroxylase

Systematic name: progesterone, hydrogen-donor: oxygen oxidoreductase (11α-hydroxylating)

References: [3851]

[EC 1.14.99.14 created 1972]

EC 1.14.99.15

Accepted name: 4-methoxybenzoate monooxygenase (*O*-demethylating)

Reaction: 4-methoxybenzoate + reduced acceptor + O_2 = 4-hydroxybenzoate + formaldehyde + acceptor + H_2O **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: [305, 3251, 4357]

[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]

[1.14.99.19 Transferred entry. plasmanylethanolamine desaturase. Now classified as EC 1.14.19.77, plasmanylethanolamine

desaturase]

[EC 1.14.99.19 created 1976, deleted 2020]

EC 1.14.99.20

Accepted name: phylloquinone monooxygenase (2,3-epoxidizing)

Reaction: phylloquinone + reduced acceptor + $O_2 = 2.3$ -epoxyphylloquinone + acceptor + H_2O

Other name(s): phylloquinone epoxidase; vitamin K 2,3-epoxidase; vitamin K epoxidase; vitamin K₁ epoxidase

Systematic name: phylloquinone,hydrogen-donor:oxygen oxidoreductase (2,3-epoxidizing)

References: [4638]

[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 +

 $H_2O + hv$

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: [3875, 3877]

[EC 1.14.99.21 created 1976, modified 1982]

Accepted name: ecdysone 20-monooxygenase

Reaction: ecdysone + reduced acceptor + O_2 = 20-hydroxyecdysone + acceptor + H_2O

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: [1935, 3071, 3944]

[EC 1.14.99.22 created 1978]

EC 1.14.99.23

Accepted name: 3-hydroxybenzoate 2-monooxygenase

Reaction: 3-hydroxybenzoate + reduced acceptor + O_2 = 2,3-dihydroxybenzoate + acceptor + H_2O

Other name(s): 3-hydroxybenzoate 2-hydroxylase; 3-HBA-2-hydroxylase

Systematic name: 3-hydroxybenzoate,hydrogen-donor:oxygen oxidoreductase (2-hydroxylating)

References: [836]

[EC 1.14.99.23 created 1984]

EC 1.14.99.24

Accepted name: steroid 9α-monooxygenase

Reaction: pregna-4,9(11)-diene-3,20-dione + reduced acceptor + $O_2 = 9.11\alpha$ -epoxypregn-4-ene-3,20-dione +

acceptor + H₂O

Other name(s): steroid 9α -hydroxylase

Systematic name: steroid,hydrogen-donor:oxygen oxidoreductase (9-epoxidizing)

Comments: An enzyme system involving a flavoprotein (FMN) and two iron-sulfur proteins.

References: [4067]

[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 + O_2 = 2,5-dihydroxypyridine + acceptor + H_2O

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: [3828]

[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]

Accepted name: deoxyhypusine monooxygenase

Reaction: [eIF5A]-deoxyhypusine + reduced acceptor + O_2 = [eIF5A]-hypusine + acceptor + H_2O

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 ini-

tiation 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 fun-

gus Botrytis cinerea is induced by the substrate analogue, 6-prenylnaringenin.

References: [4195]

[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 + O_2 = 5-hydroxythiophene-2-carbonyl-CoA + accep-

 $tor + H_2O$

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: [203]

[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]

[1.14.99.37 Transferred entry. taxadiene 5α-hydroxylase. Now EC 1.14.14.176, taxadiene 5α-hydroxylase]

[EC 1.14.99.37 created 2002, deleted 2020]

EC 1.14.99.38

Accepted name: cholesterol 25-monooxygenase

Reaction: cholesterol + reduced acceptor + O_2 = 25-hydroxycholesterol + acceptor + H_2O

Other name(s): cholesterol 25-hydroxylase (ambiguous)

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 [2563]. 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 [1153, 3607]. In cell cultures, this enzyme down-regulates cholesterol synthesis and the processing of sterol regulatory element binding proteins (SREBPs). cf. EC 1.17.99.10, choles-

terol C-25 hydroxylase.

References: [2563, 632, 2561, 1153, 3607]

[EC 1.14.99.38 created 2005, modified 2020]

EC 1.14.99.39

ammonia monooxygenase Accepted name:

> Reaction: NH_3 + a reduced acceptor + O_2 = NH_2OH + an acceptor + H_2O

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 [1055], iron [4853] and possibly zinc [1325]. The enzyme requires two electrons, which are

derived indirectly from the quinone pool via a membrane-bound donor.

References: [1055, 1779, 298, 1699, 4853, 2860, 4610, 137, 1325]

[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 syn-

thase]

[EC 1.14.99.40 created 2010, deleted 2014]

Transferred entry. all-trans-8'-apo-β-carotenal 15,15'-oxygenase. Now EC 1.13.11.75, all-trans-8'-apo-β-[1.14.99.41 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

> 4,4'-diapolycopene + 4 reduced acceptor + 4 O₂ = 4,4'-diapolycopenedial + 4 acceptor + 6 H₂O Reaction:

Other name(s): crtP (ambiguous)

4,4'-diapolycopene,AH₂:oxygen oxidoreductase (4,4'-hydroxylating) **Systematic name:**

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 dihydrox-

ymethyl group, followed by the spontaneous loss of water to give an aldehyde group.

References: [2802, 4215]

[EC 1.14.99.44 created 2011]

[1.14.99.45] Transferred entry. carotene \(\epsilon\)-monooxygenase. Now EC 1.14.14.158, carotene \(\epsilon\)-monooxygenase]

[EC 1.14.99.45 created 2011, deleted 2018]

EC 1.14.99.46

Accepted name: pyrimidine oxygenase

Reaction: (1) uracil + FMNH₂ + O₂ + NADH = (Z)-3-ureidoacrylate + H₂O + FMN + NAD⁺ + H⁺ (overall

reaction)

(1a) $FMNH_2 + O_2 = FMN-N^5$ -peroxide

(1b) uracil + FMN- N^5 -peroxide = (Z)-3-ureidoacrylate + FMN- N^5 -oxide

(1c) FMN- N^5 -oxide + NADH = FMN + H₂O + NAD⁺ + H⁺ (spontaneous)

(2) thymine + FMNH₂ + O₂ + NADH = (Z)-2-methylureidoacrylate + H_2O + FMN + NAD^+ + H^+

(overall reaction)

(2a) $FMNH_2 + O_2 = FMN-N^5$ -peroxide

(2b) thymine + FMN- N^5 -peroxide = (Z)-2-methylureidoacrylate + FMN- N^5 -oxide

(2c) FMN- N^5 -oxide + NADH = FMN + H₂O + NAD⁺ + H⁺ (spontaneous)

Other name(s): rutA (gene name)

Systematic name: uracil,FMNH₂:oxygen oxidoreductase (uracil hydroxylating, ring-opening)

Comments: The enzyme participates in the Rut pyrimidine catabolic pathway. The flavin- N^5 -oxide that is formed

by the enzyme reacts spontaneously with NADH to give oxidized flavin, releasing a water molecule.

References: [2918, 2101, 20, 19, 2723]

[EC 1.14.99.46 created 2012, modified 2019]

EC 1.14.99.47

Accepted name: (+)-larreatricin hydroxylase

Reaction: (+)-larreatricin + reduced acceptor + $O_2 = (+)-3'$ -hydroxylarreatricin + acceptor + H_2O

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: [666]

[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 O_2 = β -staphylobilin + Fe^{2+} + formaldehyde + 5 acceptor + 4

H₂O

(2) protoheme + 5 reduced acceptor + 4 $O_2 = \delta$ -staphylobilin + Fe^{2+} + formaldehyde + 5 acceptor + 4

Η2Ο

Other name(s): haem oxygenase (ambiguous); heme oxygenase (decyclizing) (ambiguous); heme oxidase (ambiguous)

ous); 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: [3500, 2700, 4061]

[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 hercynylcysteine S-oxide synthase

Reaction: hereynine + γ -L-glutamyl-L-cysteine + O₂ = γ -L-glutamyl-S-(hereyn-2-yl)-L-cysteine S-oxide + H₂O

Other name(s): EgtB

Systematic name: hercynine,γ-L-glutamyl-L-cysteine:oxygen oxidoreductase [γ-L-glutamyl-S-(hercyn-2-yl)-L-cysteine

S-oxide-forming]

Comments: Requires Fe²⁺ for activity. The enzyme, found in bacteria, is specific for both hercynine and γ -L-

glutamyl-L-cysteine. It is part of the biosynthesis pathway of ergothioneine.

References: [3777, 3337]

[EC 1.14.99.50 created 2015]

[1.14.99.51 Transferred entry. hercynylcysteine S-oxide synthase, now listed as EC 1.21.3.10, hercynylcysteine S-oxide synthase.]

[EC 1.14.99.51 created 2015, deleted 2021]

EC 1.14.99.52

Accepted name: L-cysteinyl-L-histidinylsulfoxide synthase

Reaction: L-histidine + L-cysteine + $O_2 = S$ -(L-histidin-5-yl)-L-cysteine S-oxide + H_2O

Other name(s): OvoA

Systematic name: L-histidine,L-cysteine:oxygen [S-(L-histidin-5-yl)-L-cysteine S-oxide-forming]

Comments: Requires Fe^{2+} 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

hercynylcysteine sulfoxide synthase, albeit with low activity [3960].

References: [428, 3961, 2680, 3960]

[EC 1.14.99.52 created 2015]

EC 1.14.99.53

Accepted name: lytic chitin monooxygenase

Reaction: $[(1 \rightarrow 4)-N-acetyl-\beta-D-glucosaminyl](m+n) + reduced acceptor + O₂ = <math>[(1 \rightarrow 4)-N-acetyl-\beta-D-acetyl-3-acetyl-$

glucosaminyl](m-1)-(1 \rightarrow 4)-2-(acetylamino)-2-deoxy-D-glucono-1,5-lactone + [(1 \rightarrow 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-

dehdyrogenating)

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* ascor-

bate can serve as reducing agent. The enzyme contains copper at the active site.

References: [4385, 4384, 1437, 4874]

[EC 1.14.99.53 created 2017]

EC 1.14.99.54

Accepted name: lytic cellulose monooxygenase (C1-hydroxylating)

Reaction: $[(1 \rightarrow 4) - \beta - D - glucosyl]_{n+m} + reduced acceptor + O_2 = [(1 \rightarrow 4) - \beta - D - glucosyl]_{m-1} - (1 \rightarrow 4) - D - glucono-glucosyl]_{m-1}$

1,5-lactone + $[(1\rightarrow 4)-\beta$ -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) [3313]. Ascorbate

can serve as the electron donor in vitro.

References: [3313, 268, 2460, 323, 1194, 3253, 752]

[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 + H_2O

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: [4479, 1437, 2403]

[EC 1.14.99.55 created 2017]

EC 1.14.99.56

Accepted name: lytic cellulose monooxygenase (C4-dehydrogenating)

Reaction: $[(1 \rightarrow 4) - \beta - D - glucosyl]_{n+m} + reduced acceptor + O_2 = 4 - dehydro-\beta-D-glucosyl-[(1 \rightarrow 4) - \beta-D-glucosyl-gluc$

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: [268, 2460, 1148, 392, 3253]

[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 O_2 = mycobilin a + Fe²⁺ + 3 acceptor + 3 H_2O

(2) protoheme + 3 reduced acceptor + 3 O_2 = mycobilin b + Fe^{2+} + 3 acceptor + 3 H_2O

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: [653, 3008, 1388]

[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 O_2 = biliverdin-IX- δ + CO + Fe²⁺ + 3 acceptor + 3 H_2O

(2) protoheme + 3 reduced acceptor + 3 O_2 = biliverdin-IX- β + CO + Fe²⁺ + 3 acceptor + 3 H_2O

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: [3457, 527, 1181]

[EC 1.14.99.58 created 2017]

EC 1.14.99.59

Accepted name: tryptamine 4-monooxygenase

Reaction: tryptamine + reduced acceptor + O_2 = 4-hydroxytryptamine + acceptor + H_2O

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: [1179]

[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 + $O_2 = 3$ -

demethylubiquinol + acceptor + H_2O

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: [2644, 4389, 2320, 4022, 4323]

[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 + O_2 = cyclooctat-9-ene-5,7-diol + acceptor + H_2O

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 biosyn-

thesis of cyclooctatin.

References: [2107, 1369]

[EC 1.14.99.61 created 2018]

Accepted name: cyclooctatin synthase

Reaction: cyclooctat-9-ene-5,7-diol + reduced acceptor + O_2 = cyclooctatin + acceptor + H_2O

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: [2107, 1369]

[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 O_2 = echinenone + 2 acceptor + 3 H_2O

(2) echinenone + 2 reduced acceptor + 2 O_2 = canthaxanthin + 2 acceptor + 3 H_2O

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 bifuntional and also catalyses the activity of EC 1.14.15.24, β -carotene 3-hydroxylase.

References: [2542, 435, 4017, 3150, 4216, 2015]

[EC 1.14.99.63 created 2018]

EC 1.14.99.64

Accepted name: zeaxanthin 4-ketolase

Reaction: (1) zeaxanthin + 2 reduced acceptor + 2 O_2 = adonixanthin + 2 acceptor + 3 H_2O

(2) adonixanthin + 2 reduced acceptor + 2 $O_2 = (3S,3'S)$ -astaxanthin + 2 acceptor + 3 H_2O

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 en-

zyme is able to also act on zeaxanthin.

References: [4910, 1754]

[EC 1.14.99.64 created 2018]

EC 1.14.99.65

Accepted name: 4-amino-L-phenylalanyl-[CmlP-peptidyl-carrier-protein] 3-hydroxylase

Reaction: 4-amino-L-phenylalanyl-[CmlP-peptidyl-carrier-protein] + reduced acceptor + O_2 = 2-(4-

 $amin ophenyl) \hbox{-L-seryl-[CmlP-peptidyl-carrier-protein]} + acceptor + H_2O$

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

Systematic name: 4-amino-L-phenylalanyl-[CmlP-peptidyl-carrier-protein], acceptor: oxygen 3-oxidoreductase

Comments: The enzyme, characterized from the bacterium Streptomyces venezuelae, participates in the biosynthe-

sis of the antibiotic chloramphenicol. It carries an oxygen-bridged dinuclear iron cluster. The native electron donor remains unknown, and the enzyme was assayed *in vitro* using sodium dithionite. The enzyme only acts on its substrate when it is loaded onto the peptidyl-carrier domain of the CmlP non-

ribosomal peptide synthase.

References: [2628]

[EC 1.14.99.65 created 2019]

Accepted name: [histone H3]- N^6 , N^6 -dimethyl-L-lysine⁴ FAD-dependent demethylase

Reaction: a [histone H3]- N^6 , N^6 -dimethyl-L-lysine⁴ + 2 acceptor + 2 H₂O = a [histone H3]-L-lysine⁴ + 2

formaldehyde + 2 reduced acceptor (overall reaction)

(1a) a [histone H3]- N^6 , N^6 -dimethyl-L-lysine⁴ + acceptor + H₂O = a [histone H3]- N^6 -methyl-L-lysine⁴

+ formaldehyde + reduced acceptor

(1b) a [histone H3]- N^6 -methyl-L-lysine⁴ + acceptor + H₂O = a [histone H3]-L-lysine⁴ + formaldehyde

+ reduced acceptor

Other name(s): KDM1 (gene name); LSD1 (gene name); lysine-specific histone demethylase 1 Systematic name: [histone H3]- N^6 , N^6 -dimethyl-L-lysine⁴: acceptor oxidoreductase (demethylating)

Comments: The enzyme specifically removes methyl groups from mono- and dimethylated lysine⁴ of histone 3.

During the reaction the substrate is oxidized by the FAD cofactor of the enzyme to generate the corresponding imine, which is subsequently hydrolysed in the form of formaldehyde. The enzyme is similar to flavin amine oxidases, and differs from all other known histone lysine demethylases, which are iron(II)- and 2-oxoglutarate-dependent dioxygenases. The physiological electron acceptor is not known with certainty. *In vitro* the enzyme can use oxygen, which is reduced to hydrogen peroxide, but generation of hydrogen peroxide in the chromatin environment is unlikely as it will result in ox-

idative damage of DNA.

References: [1144, 1143]

[EC 1.14.99.66 created 2019]

EC 1.14.99.67

Accepted name: α -N-dichloroacetyl-p-aminophenylserinol N-oxygenase

Reaction: α-N-dichloroacetyl-p-aminophenylserinol + reduced acceptor + 2 O₂ = chloramphenicol + acceptor +

 $2 H_2O$

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

Systematic name: α -N-dichloroacetyl-p-aminophenylserinol,acceptor:oxygen oxidoreductase (N-hydroxylating)

Comments: The enzyme, isolated from the bacterium *Streptomyces venezuelae*, is involved in the biosynthesis of

the antibiotic chloramphenicol. It contains a carboxylate-bridged binuclear non-heme iron cluster. The components of the native electron chain have not been identified, although the immediate donor is likely to be an iron-sulfur protein. The reaction mechanism involves formation of an extremely stable peroxo intermediate that catalyses three individual two-electron oxidations via a hydroxylamine and a nitroso intermediates without releasing the intermediates. *cf.* EC 1.14.99.68, 4-aminobenzoate

N-oxygenase.

References: [2550, 2629, 2215]

[EC 1.14.99.67 created 2020]

EC 1.14.99.68

Accepted name: 4-aminobenzoate *N*-oxygenase

Reaction: 4-aminobenzoate + reduced acceptor + $2 O_2 = 4$ -nitrobenzoate + acceptor + $2 H_2 O$

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

Systematic name: 4-aminobenzoate, acceptor: oxygen oxidoreductase (N-hydroxylating)

Comments: The enzyme, characterized from the bacterium *Streptomyces thioluteus*, catalyses an early step in the

biosynthesis of the antibiotic aureothin. It contains a carboxylate-bridged binuclear non-heme iron cluster. The native electron donor has not been identified, but is likely an iron-sulfur protein. The reaction mechanism involves formation of an extremely stable peroxo intermediate that catalyses three two-electron oxidations via a hydroxylamine and dihydroxylamine intermediates. *cf.* EC 1.14.99.67,

N-[1-(4-aminophenyl)-1,3-dihydroxypropan-2-yl]-2,2-dichloroacetamide N-oxygenase.

References: [1589, 2385, 4935, 675, 2230, 2452]

[EC 1.14.99.68 created 2020]

Accepted name: tRNA 2-(methylsulfanyl)- N^6 -isopentenyladenosine³⁷ hydroxylase

Reaction: 2-(methylsulfanyl)- N^6 -prenyladenosine³⁷ in tRNA + reduced acceptor + $O_2 = N^6$ -[(2E)-4-hydroxy-3-

methylbut-2-en-1-yl]-2-(methylsulfanyl)adenosine³⁷ in tRNA + acceptor + H₂O

Other name(s): miaE (gene name); tRNA 2-methylthio- N^6 -isopentenyl adenosine(37) hydroxylase; tRNA 2-

(methylsulfanyl)-N⁶-dimethylallyladenosine³⁷ hydroxylase

Systematic name: $tRNA 2-(methylsulfanyl)-N^6$ -prenyladenosine³⁷, donor:oxygen 4-oxidoreductase (trans-

hydroxylating)

Comments: The enzyme, found only within a small subset of facultative anaerobic bacteria, belongs to the non-

heme diiron family. The enzyme from Salmonella typhimurium was shown to catalyse a stereoselec-

tive (E)-hydroxylation at the terminal C^4 -position of the prenyl group.

References: [3294, 3295, 734]

[EC 1.14.99.69 created 2020]

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⁺ = O_2 + H_2O_2

Other name(s): superoxidase dismutase; copper-zinc superoxide dismutase; Cu-Zn superoxide dismutase; ferrisu-

peroxide 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 man-

ganese or iron.

References: [2053, 3686, 4417]

[EC 1.15.1.1 created 1972]

EC 1.15.1.2

Accepted name: superoxide reductase

Reaction: superoxide + reduced rubredoxin + $2 H^+$ = H_2O_2 + oxidized rubredoxin

Other name(s): neelaredoxin; desulfoferrodoxin
Systematic name: rubredoxin:superoxide oxidoreductase
Comments: The enzyme contains non-heme iron.

References: [1901, 4785, 2535, 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: $Hg + NADP^+ + H^+ = Hg^{2+} + NADPH$

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:** [1154, 1155]

[EC 1.16.1.1 created 1984]

EC 1.16.1.2

Accepted name: diferric-transferrin reductase

Reaction: transferrin[Fe(II)]₂ + NAD⁺ + H⁺ = transferrin[Fe(III)]₂ + NADH

Other name(s): diferric transferrin reductase; NADH diferric transferrin reductase; transferrin reductase

Systematic name: transferrin[Fe(II)]₂:NAD⁺ oxidoreductase

References: [2547]

[EC 1.16.1.2 created 1989]

[1.16.1.3 Deleted entry. aquacobalamin reductase. This entry has been deleted since no specific enzyme catalysing this activity has been identified and it has been shown that aquacobalamin is efficiently reduced by free dihydroflavins and by non-specific reduced flavoproteins.]

[EC 1.16.1.3 created 1972 as EC 1.6.99.8, transferred 2002 to EC 1.16.1.3, modified 2020, deleted 2020]

[1.16.1.4 Deleted entry. cob(II)alamin reductase. This entry has been deleted since no specific enzyme catalysing this activity has been identified and it has been shown that cob(II)alamin is efficiently reduced by free dihydroflavins and by non-specific reduced flavoproteins]

[EC 1.16.1.4 created 1972 as EC 1.6.99.9, transferred 2002 to EC 1.16.1.4, deleted 2021]

[1.16.1.5 Deleted entry. aquacobalamin reductase (NADPH). This entry has been deleted since the enzyme the entry was based on was later shown to be EC 1.2.1.51, pyruvate dehydrogenase (NADP $^+$). On the other hand, it has been shown that non-enzymatic reduction of cob(III)alamin to cob(II)alamin occurs efficiently in the presence of free dihydroflavins or non-specific reduced flavoproteins.]

[EC 1.16.1.5 created 1989 as EC 1.6.99.11, transferred 2002 to EC 1.16.1.5, modified 2020, deleted 2020]

EC 1.16.1.6

Accepted name: cyanocobalamin reductase

Reaction: 2 cob(II) alamin-[cyanocobalamin reductase] + $2 \text{ hydrogen cyanide} + \text{NADP}^+ = 2$

cyanocob(III)alamin + 2 [cyanocobalamin reductase] + NADPH + H⁺

Other name(s): MMACHC (gene name); CblC; cyanocobalamin reductase (NADPH, cyanide-eliminating);

cyanocobalamin reductase (NADPH, CN-eliminating); NADPH:cyanocob(III)alamin oxidoreductase (cyanide-eliminating); cob(I)alamin, cyanide:NADP⁺ oxidoreductase; cyanocobalamin reductase

(cyanide-eliminating)

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 correspond-

ing glutathione thioether (cf. EC 2.5.1.151, alkylcobalamin dealkylase).

References: [4551, 2095, 2249, 2612]

[EC 1.16.1.6 created 1989 as EC 1.6.99.12, transferred 2002 to EC 1.16.1.6, modified 2018, modified 2021]

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 reduc-

tase; 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: [147, 468, 469, 487, 3654, 2737]

[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(III)alamin + 2 S-adenosyl-L-homocysteine + NADP⁺ = 2 [me-

thionine synthase]-cob(II)alamin + NADPH + H⁺ + 2 S-adenosyl-L-methionine

Other name(s): methionine synthase cob(II)alamin reductase (methylating); methionine synthase reductase; [me-

thionine synthase]-cobalamin methyltransferase (cob(II)alamin reducing); [methionine synthase]-

methylcob(I)alamin,S-adenosylhomocysteine:NADP+ oxidoreductase

Systematic name: [methionine synthase]-methylcob(III)alamin,S-adenosyl-L-homocysteine:NADP⁺ oxidoreductase

Comments: In humans, the enzyme is a flavoprotein containing FAD and FMN. The substrate of the enzyme is the inactivated cobalt(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: [2375, 3177, 3178]

[EC 1.16.1.8 created 1999 as EC 2.1.1.135, transferred 2003 to EC 1.16.1.8, modified 2020]

EC 1.16.1.9

Accepted name: ferric-chelate reductase (NADPH)

Reaction: 2 Fe(II)-siderophore + NADP $^+$ + H $^+$ = 2 Fe(III)-siderophore + NADPH

Other name(s): ferric chelate reductase (ambiguous); iron chelate reductase (ambiguous); NADPH:Fe³⁺-EDTA re-

ductase; NADPH-dependent ferric reductase; yqjH (gene name); $Fe(II):NADP^+$ oxidoreductase

 $\textbf{Systematic name:} \quad Fe(II)\text{-siderophore:} NADP^+ \ oxidoreduct as expression of the property of the prope$

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 [2796]. *cf.* EC 1.16.1.7, ferric-chelate reductase (NADH) and EC 1.16.1.10, ferric-chelate

reductase [NAD(P)H].

References: [204, 4533, 2796]

[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 Fe(II)-siderophore + NAD(P)⁺ + H⁺ = 2 Fe(III)-siderophore + 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: [4387, 660]

[EC 1.16.1.10 created 2014]

EC 1.16.3 With oxygen as acceptor

EC 1.16.3.1

Accepted name: ferroxidase

Reaction: $4 \text{ Fe}(\text{II}) + 4 \text{ H}^+ + \text{O}_2 = 4 \text{ Fe}(\text{III}) + 2 \text{ H}_2\text{O}$

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 hu-

mans 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: [3193, 3194, 2499, 4174, 629]

[EC 1.16.3.1 created 1972, modified 2011]

EC 1.16.3.2

Accepted name: bacterial non-heme ferritin

Reaction: $4 \text{ Fe(II)} + O_2 + 6 \text{ H}_2\text{O} = 4 \text{ [FeO(OH)]} + 8 \text{ H}^+ \text{ (overall reaction)}$

(1a) 2 Fe(II) + O_2 + 4 H₂O = 2 [FeO(OH)] + 4 H⁺ + H₂O₂

(1b) 2 Fe(II) + H_2O_2 + 2 H_2O = 2 [FeO(OH)] + 4 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 subse-

quent reaction.

References: [1762, 4033, 405]

[EC 1.16.3.2 created 2014]

EC 1.16.3.3

Accepted name: manganese oxidase

Reaction: $4 \text{ Mn}^{2+} + 2 \text{ O}_2 + 4 \text{ H}_2\text{O} = 4 \text{ Mn}^{\text{IV}}\text{O}_2 + 8 \text{ H}^+ \text{ (overall reaction)}$

(1a) $\mathbf{4} \, \mathrm{Mn^{2+}} + \mathrm{O_2} + \mathbf{4} \, \mathrm{H^+} = \mathbf{4} \, \mathrm{Mn^{3+}} + \mathbf{2} \, \mathrm{H_2O}$ (1b) $\mathbf{4} \, \mathrm{Mn^{3+}} + \mathrm{O_2} + \mathbf{6} \, \mathrm{H_2O} = \mathbf{4} \, \mathrm{Mn^{IV}O_2} + \mathbf{12} \, \mathrm{H^+}$

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: [740, 1162, 3518, 1310, 4085]

[EC 1.16.3.3 created 2017]

EC 1.16.3.4

Accepted name: cuproxidase

Reaction: $4 \text{ Cu}^+ + 4 \text{ H}^+ + \text{O}_2 = 4 \text{ Cu}^{2+} + 2 \text{ H}_2\text{O}$

Other name(s): cueO (gene name); cuprous oxidase; Cu(I) oxidase; copper efflux oxidase

Systematic name: copper(I):oxygen oxidoreductase

Comments: The enzyme, characterized from the bacterium *Escherichia coli*, is involved in copper tolerance under

aerobic conditions. The enzyme contains a substrate binding (type 1) copper site and a trinuclear copper center (consisting of type 2 and type 3 copper sites) in which oxygen binding and reduction takes place. It also contains a methionine rich region that can bind additional copper ions. *In vitro*, if the substrate binding site is occupied by copper(II), the enzyme can function as a laccase-type quinol oxidase (EC 1.10.3.2). However, *in vivo* this site is occupied by a copper(I) ion and the enzyme functions

as a cuprous oxidase.

References: [2091, 1384, 3217, 3537, 3538, 3911, 1260, 929, 3912, 742]

[EC 1.16.3.4 created 2021]

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

[1.16.8.1 Deleted entry. cob(II)yrinic acid a,c-diamide reductase. This activity is now known to be catalyzed by EC 2.5.1.17, corrinoid adenosyltransferase]

[EC 1.16.8.1 created 2004, deleted 2019]

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 (ambiguous)

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 7.1.1.9).

References: [348, 118, 4778, 4777, 4165, 573, 3411]

[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 1.16.99 With unknown physiological acceptors

EC 1.16.99.1

Accepted name: [Co(II) methylated amine-specific corrinoid protein] reductase

(1) ATP + a [Co(II) methylamine-specific corrinoid protein] + reduced acceptor + $H_2O = ADP +$ **Reaction:**

phosphate + a [Co(I) methylamine-specific corrinoid protein] + acceptor

(2) ATP + a [Co(II) dimethylamine-specific corrinoid protein] + reduced acceptor + $H_2O = ADP +$

phosphate + a [Co(I) dimethylamine-specific corrinoid protein] + acceptor

(3) ATP + a [Co(II) trimethylamine-specific corrinoid protein] + reduced acceptor + $H_2O = ADP +$

phosphate + a [Co(I) trimethylamine-specific corrinoid protein] + acceptor

Systematic name:

acceptor:[cobalt(II) methylated amines-specific corrinoid protein] oxidoreductase (ATP-hydrolysing) Methyltrophic corrinoid proteins must have the cobalt atom in the active cobalt(I) state to become **Comments:**

methylated. Because the cobalt(I)/cobalt(II) transformation has a very low redox potential the corrinoid cofactor is subject to adventitious oxidation to the cobalt(II) state, which renders the proteins inactive. This enzyme, characterized from the methanogenic archaeon Methanosarcina barkeri, reduces cobalt(II) back to cobalt(I), restoring activity. The enzyme acts on the corrinoid proteins involved in methanogenesis from methylamine, dimethylamine, and trimethylamine, namely MtmC, MtbC, and MttC, respectively. While in vitro the enzyme can use Ti(III)-citrate as the electron donor, the in vivo donor is not known. The enzyme from Methanosarcina barkeri contains a C-terminal [4Fe-4S]

ferredoxin-like domain.

References: [1104, 989]

[EC 1.16.99.1 created 2021]

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. Subsubclasses 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

CDP-4-dehydro-6-deoxyglucose reductase Accepted name:

> CDP-4-dehydro-3,6-dideoxy-D-glucose + $NAD(P)^+$ + H_2O = CDP-4-dehydro-6-deoxy-D-glucose + Reaction:

> > $NAD(P)H + H^{+}$

Other name(s): CDP-4-keto-6-deoxyglucose reductase; cytidine diphospho-4-keto-6-deoxy-D-glucose reductase; cyti-

dine 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: [3234, 3590, 2515]

[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: (2R,3S)-catechin + NADP⁺ + H₂O = 2,3-trans-3,4-cis-leucocyanidin + NADPH + H⁺

Other name(s): leucocyanidin reductase

Systematic name: (2R,3S)-catechin:NADP⁺ 4-oxidoreductase

 $\textbf{Comments:} \quad \text{The enzyme catalyses the synthesis of catechin, catechin-} 4\beta\text{-ol (leucocyanidin) and the related flavan-}$

3-ols afzelechin and gallocatechin, 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: [4212, 4211]

[EC 1.17.1.3 created 2003]

EC 1.17.1.4

Accepted name: xanthine dehydrogenase

Reaction: xanthine + NAD⁺ + H_2O = 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 [4167]. 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: [238, 741, 3249, 3436, 3945, 1797, 1048, 3634, 3246, 1786, 1054, 4335, 1654, 4167, 3081]

[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 + H_2O + $NADP^+$ = 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 nicoti-

nate analogues to varying degrees, including pyrazine-2-carboxylate, pyrazine 2,3-dicarboxylate, trigonelline and 6-methylnicotinate. The enzyme from *Clostridium barkeri* also possesses a catalyt-

ically essential, labile selenium that can be removed by reaction with cyanide.

References: [1690, 1335, 1334, 916, 915, 2965]

[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 7α -dehydroxylase. Now EC 1.17.99.5, bile-acid 7α -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: The substrate of the enzyme was initially thought to be (S)-2,3-dihydrodipicolinate [1090], and the

enzyme was classified accordingly as EC 1.3.1.26, dihydrodipicolinate reductase. Later studies of the enzyme from the bacterium *Escherichia coli* have suggested that the actual substrate of the enzyme is (2*S*,4*S*)-4-hydroxy-2,3,4,5-tetrahydrodipicolinate, and that its activity includes a dehydration step [890], and thus the enzyme has been reclassified as 4-hydroxy-tetrahydrodipicolinate reductase. However, the identity of the substrate is still controversial, as more recently it has been suggested that it

may be (S)-2,3-dihydrodipicolinate after all [2000].

References: [1090, 890, 2000]

[EC 1.17.1.8 created 1976 as EC 1.3.1.26, transferred 2013 to EC 1.17.1.8, modified 2020]

EC 1.17.1.9

Accepted name: formate dehydrogenase

Reaction: formate + NAD^+ = CO_2 + NADH

Other name(s): formate-NAD⁺ oxidoreductase; FDH I; FDH II; N-FDH; formic hydrogen-lyase; formate hydro-

genlyase; hydrogenlyase; NAD^+ -linked formate dehydrogenase; NAD^+ -dependent formate dehydrogenase; 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 pro-

teobacterium *Methylosinus trichosporium* contains iron-sulfur centres, flavin and a molybdenum centre [1941]. Together with EC 1.12.1.2 hydrogen dehydrogenase, forms a system previously known as

formate hydrogenlyase.

References: [841, 3412, 1941]

[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⁺ = CO_2 + 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 ex-

tremely sensitive to oxygen.

References: [98, 4740]

[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 CO_2 + 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: [4529]

[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 + $H_2O = 6$ -hydroxynicotinate + a ferrocytochrome + $2H^+$

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

[1915].

References: [1915, 4769]

[EC 1.17.2.1 created 2010]

EC 1.17.2.2

Accepted name: lupanine 17-hydroxylase (cytochrome *c*)

Reaction: lupanine + 2 ferricytochrome $c + H_2O = 17$ -hydroxylupanine + 2 ferrocytochrome $c + 2 H^+$

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: [1718, 1717]

[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 = CO_2 + 2 ferrocytochrome c-553 + H⁺

Systematic name: formate:ferricytochrome-*c*-553 oxidoreductase

Comments: The enzyme has been characterized from the bacterium *Desulfovibrio vulgaris*. *In vitro*, yeast cy-

tochrome c, ferricyanide and phenazine methosulfate can act as acceptors.

References: [4719, 4720]

[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: [4801]

[EC 1.17.3.1 created 1983]

EC 1.17.3.2

Accepted name: xanthine oxidase

Reaction: xanthine $+ H_2O + O_2 = urate + H_2O_2$

Other name(s): hypoxanthine oxidase; hypoxanthine:oxygen oxidoreductase; Schardinger enzyme; xanthine oxidore-

ductase; 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: RH + H_2O + 2 O_2 = ROH + 2 O_2 · + 2 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]. [161, 238, 429, 741, 1797, 1048, 3634, 562, 1022, 3081]

[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

References:

Accepted name: 6-hydroxynicotinate dehydrogenase

Reaction: 6-hydroxynicotinate + $H_2O + O_2 = 2,6$ -dihydroxynicotinate + H_2O_2

Other name(s): 6-hydroxynicotinic acid hydroxylase; 6-hydroxynicotinic acid dehydrogenase; 6-hydroxynicotinate

 $hydroxylase; 6\hbox{-}hydroxynicotinate} : O_2 \ oxidoreductase$

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 re-

quired for growth on nicotinic acid.

References: [2964, 2965]

[EC 1.17.3.3 created 2004]

EC 1.17.3.4

Accepted name: juglone 3-hydroxylase

Reaction: 2 juglone + O_2 = 2 3,5-dihydroxy-1,4-naphthoquinone (overall reaction)

(1a) 2 juglone + 2 $H_2O = 2$ naphthalene-1,2,4,8-tetrol

(1b) 2 naphthalene-1,2,4,8-tetrol + O_2 = 2 3,5-dihydroxy-1,4-naphthoquinone + 2 H_2O

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: [3504]

[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'-deoxyribonucleoside 5'-diphosphate + thioredoxin disulfide + H_2O = ribonucleoside 5'-

diphosphate + 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 deoxyri-

bonucleoside 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: [2357, 2358, 2873, 2356, 2335, 4078, 2414, 2368, 3404]

[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 + H_2O = 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: [350, 1377, 4077, 145, 2370, 2478]

[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 + $H_2O = 2,3$ -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 phylloquinol 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 phylloquinone (vitamin K_1) and menaquinone (vitamin K_2). Inhibited

strongly by (S)-warfarin and ferulenol.

References: [4609, 2387, 2917, 2457, 4490, 3988, 3752]

[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 reduc-

tase (warfarin-sensitive)].

References: [2917]

[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 + H_2O + 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 [3508]. A second enzyme, EC 3.1.2.25, phenylacetyl-CoA hydrolase, converts the phenylglyoxylyl-CoA formed into phenylglyoxylate.

References: [3508, 3737]

[EC 1.17.5.1 created 2004]

EC 1.17.5.2

Accepted name: caffeine dehydrogenase

Reaction: caffeine + ubiquinone + $H_2O = 1,3,7$ -trimethylurate + ubiquinol

Systematic name: caffeine:ubiquinone oxidoreductase

Comments: This enzyme, characterized from the soil bacterium *Pseudomonas* sp. CBB1, catalyses the incorpora-

tion 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: [4832]

[EC 1.17.5.2 created 2010]

EC 1.17.5.3

Accepted name: formate dehydrogenase-N

Reaction: formate + a quinone = CO_2 + 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 un-

der anaerobic conditions [1950].

References: [1052, 1951, 1950]

[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 + $H_2O + 2$ 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] clus-

ter [3152]. 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

[3152].

References: [3152, 3784, 3783, 3782]

[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 $a + H_2O + 2$ oxidized ferredoxin = 7^1 -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 chloro-

phyllide *a*.

References: [2760]

[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 $+ H_2O + \text{oxidized flavodoxin} = 2-C$ -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 [4871]. Plants and cyanobacteria have a similar enzyme that utilizes ferredoxin rather than flavodoxin (*cf.* EC 1.17.7.1).

References: [1596, 4871, 3391]

[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) 3-methylbut-3-en-1-yl diphosphate + **2** oxidized ferredoxin [iron-sulfur] cluster + $H_2O = (E)$ -4-

hydroxy-3-methylbut-2-en-1-yl diphosphate + $\mathbf{2}$ reduced ferredoxin [iron-sulfur] cluster + $\mathbf{2}$ H⁺ (2) prenyl diphosphate + $\mathbf{2}$ 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; isopentenyl-diphosphate:ferredoxin oxi-

doreductase

Systematic name: 3-methylbut-3-en-1-yl-diphosphate:ferredoxin oxidoreductase

Comments: An iron-sulfur protein that contains either a [3Fe-4S] [1389] or a [4Fe-4S] [4657] cluster. This en-

zyme 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 3-methylbut-3-en-1-yl diphosphate and prenyl diphosphate.

References: [3555, 1664, 609, 3556, 4657, 1389]

[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 + H_2O = hydroxysqualene + FAD H_2

Other name(s): hpnE (gene name)

Systematic name: squalene:FAD oxidoreductase (hydroxylating)

Comments: This enzyme, isolated from the bacteria *Rhodopseudomonas palustris* and *Zymomonas mobilis*, partic-

ipates, 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: [3228]

[EC 1.17.8.1 created 2016]

EC 1.17.9 With a copper protein as acceptor

EC 1.17.9.1

Accepted name: 4-methylphenol dehydrogenase (hydroxylating)

Reaction: 4-methylphenol + 4 oxidized azurin + $H_2O = 4$ -hydroxybenzaldehyde + 4 reduced azurin + $H_2O = 4$ -hydroxybenzaldehyde + 4 reduced azurin + $H_2O = 4$ -hydroxybenzaldehyde + 5 reduced azurin + $H_2O = 4$ -hydroxybenzaldehyde + 5 reduced azurin + $H_2O = 4$ -hydroxybenzaldehyde + 6 reduced azurin + $H_2O = 4$ -hydroxybenzaldehyde + 7 reduced azurin + $H_2O = 4$ -hydroxybenzaldehyde + 7 reduced azurin + $H_2O = 4$ -hydroxybenzaldehyde + 7 reduced azurin + $H_2O = 4$ -hydroxybenzaldehyde + 7 reduced azurin + $H_2O = 4$ -hydroxybenzaldehyde + $H_2O = 4$

(overall reaction)

(1a) 4-methylphenol + $\bf 2$ oxidized azurin + $\bf H_2O$ = 4-hydroxybenzyl alcohol + $\bf 2$ reduced azurin + $\bf 2$ H⁺ (1b) 4-hydroxybenzyl alcohol + $\bf 2$ oxidized azurin = 4-hydroxybenzaldehyde + $\bf 2$ reduced azurin + $\bf 2$

 H^{+}

Other name(s): pchCF (gene names); p-cresol-(acceptor) oxidoreductase (hydroxylating); p-cresol methylhydroxy-

lase; 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: [1719, 2750, 1716, 401, 3481, 3298, 1922]

[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 1.17.9.2

Accepted name: (+)-pinoresinol hydroxylase

Reaction: (+)-pinoresinol + 2 oxidized azurin + $H_2O = (+)$ -6-hydroxypinoresinol + 2 reduced azurin + 2 reduced a

Other name(s): pinoresinol α -hydroxylase; pinAB (gene names)

Systematic name: (+)-pinoresinol:azurin oxidoreductase

Comments: Contains FAD. This enzyme, characterized from the bacterium *Pseudomonas* sp. SG-MS2, catalyses

the incorporation of an oxygen atom originating from a water molecule into position C-6 of the lignan (+)-pinoresinol. The enzyme consists of a flavoprotein subunit and a c-type cytochrome subunit. Electrons that originate in the substrate are transferred via the FAD cofactor and the cytochrome subunit to

the blue-copper protein azurin.

References: [3848]

[EC 1.17.9.2 created 2020]

EC 1.17.98 With other, known, physiological acceptors

[1.17.98.1 Deleted entry. bile-acid 7\alpha-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 $c + H_2O = a$ bacteriochlorophyllide e + 2.5'

deoxyadenosine + 2 L-methionine (overall reaction)

(1a) S-adenosyl-L-methionine + a bacteriochlorophyllide c + H_2O = a 7-

(hydroxymethyl)bacteriochlorophyllide c + 5'-deoxyadenosine + L-methionine

(1b) S-adenosyl-L-methionine + a 7-(hydroxymethyl)bacteriochlorophyllide $c + H_2O = a$ 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 $\it c$ to form a geminal diol intermediate that

spontaneously dehydrates to produce the formyl group of bacteriochlorophyllide e.

References: [1526, 4281]

[EC 1.17.98.2 created 2016, modified 2017]

EC 1.17.98.3

Accepted name: formate dehydrogenase (coenzyme F_{420})

Reaction: formate + oxidized coenzyme $F_{420} = CO_2$ + reduced coenzyme F_{420}

Other name(s): coenzyme F_{420} reducing formate dehydrogenase; coenzyme F_{420} -dependent formate dehydrogenase

Systematic name: formate:coenzyme-F₄₂₀ oxidoreductase

Comments: The enzyme, characterized from methanogenic archaea, is involved in formate-dependent H₂ produc-

tion. It contains noncovalently bound FAD [3703].

References: [3703, 3704, 2568]

[EC 1.17.98.3 created 2014 as EC 1.2.99.9, transferred 2017 to EC 1.17.98.3]

EC 1.17.98.4

Accepted name: formate dehydrogenase (hydrogenase)

Reaction: formate + an [oxidized hydrogenase] = CO_2 + a [reduced hydrogenase]

Other name(s): FDHH; FDH-H; FDH-O; formate dehydrogenase H; formate dehydrogenase O

Systematic name: formate:[oxidized hydrogenase] 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 [164]. The enzyme contains an [4Fe-4S] cluster, a selenocysteine residue and a molybdopterin cofac-

tor [164].

References: [164, 1333, 2079]

[EC 1.17.98.4 created 2010 as EC 1.1.99.33, transferred 2018 to EC 1.17.99.7, transferred 2020 to 1.17.98.4.]

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 + H_2O + 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 ferroce-

nium can act as electron acceptor. Contains molybdopterin, [4Fe-4S] clusters and heme b.

References: [2167, 1931]

[EC 1.17.99.2 created 2001]

EC 1.17.99.3

Accepted name: 3α , 7α , 12α -trihydroxy-5 β -cholestanoyl-CoA 24-hydroxylase

Reaction: (25R)- 3α , 7α , 12α -trihydroxy- 5β -cholestan-26-oyl-CoA + H₂O + acceptor = (24R,25R)-

 3α , 7α , 12α , 24-tetrahydroxy- 5β -cholestan-26-oyl-CoA + reduced acceptor

Other name(s): trihydroxycoprostanoyl-CoA oxidase; THC-CoA oxidase; THCA-CoA oxidase; 3α , 7α , 12α -

trihydroxy-5 β -cholestanoyl-CoA oxidase; 3α , 7α , 12α -trihydroxy-5 β -cholestan-26-oate 24-

hydroxylase

Systematic name: $(25R)-3\alpha$, 7α , 12α -trihydroxy-5 β -cholestan-26-oyl-CoA: acceptor 24-oxidoreductase (24R-

hydroxylating)

Comments: Requires ATP. The reaction in mammals possibly involves dehydrogenation to give a 24(25)-double

bond followed by hydration [1455]. 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 (25R)-3 α ,7 α ,12 α -trihydroxy-5 β -cholestan-26-oate and not via hydration of a 24(25) double bond [3277]. 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 [1455].

References: [1455, 3711, 911, 912, 3277, 3607]

[EC 1.17.99.3 created 2005]

EC 1.17.99.4

Accepted name: uracil/thymine dehydrogenase

Reaction: (1) $uracil + H_2O + acceptor = barbiturate + reduced acceptor$

(2) thymine $+ H_2O + acceptor = 5$ -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 [3968].

References: [1572, 4534, 4535, 2349, 3968]

[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\alpha-dehydroxylase. Now classified as EC 1.17.98.1, bile-acid 7\alpha-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 + H_2O = 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. Two types of enzymes are known to catalyse this activity. QueG enzymes are cobalamin-dependent, while QueH en-

zymes contain a [4Fe-4S] metallocluster along with an adjacent coordinated iron metal.

References: [2807, 4856, 2453]

[EC 1.17.99.6 created 2014]

[1.17.99.7 Transferred entry. formate dehydrogenase (acceptor). Now classified as EC 1.17.98.4, formate dehydrogenase (hydrogenase).]

[EC 1.17.99.7 created 2010 as EC 1.1.99.33, transferred 2017 to EC 1.17.99.7, deleted 2020]

EC 1.17.99.8

Accepted name: limonene dehydrogenase

Reaction: (1) (S)-limonene + H_2O + acceptor = (-)-perillyl alcohol + reduced acceptor

(2) (R)-limonene + H_2O + acceptor = (+)-perillyl alcohol + reduced acceptor

Other name(s): *ctmAB* (gene names)

Systematic name: limonene:acceptor oxidoreductase (7-hydroxylating)

Comments: Contains FAD. The enzyme, characterized from the bacterium *Castellaniella defragrans* 65Phen,

hydroxylates the R- and S-enantiomers at a similar rate. The in vivo electron acceptor may be a het-

erodimeric electron transfer flavoprotein (ETF).

References: [3297, 3392]

[EC 1.17.99.8 created 2020]

EC 1.17.99.9

Accepted name: heme *a* synthase

Reaction: ferroheme $o + H_2O + 2$ acceptor = ferroheme a + 2 reduced acceptor (overall reaction)

(1a) ferroheme $o + H_2O + acceptor = ferroheme i + reduced acceptor$

(1b) ferroheme $i + H_2O +$ acceptor = hydroxyferroheme i + reduced acceptor

(1c) hydroxyferroheme i = ferroheme a + H₂O (spontaneous)

Other name(s): COX15 (gene name); ctaA (gene name)

Systematic name: ferroheme *o*:acceptor C-8¹-oxidoreductase (heme *a*-forming)

Comments: Contains a heme b cofactor. The enzyme catalyses the conversion of heme o to heme a by two successions.

sive hydroxylations of the methyl group at C-8, using water as the oxygen source. The first hydroxylation forms heme i, the second hydroxylation results in an unstable dihydroxymethyl group, which spontaneously dehydrates, resulting in the formyl group of heme a [461, 1602]. The electrons produced by the reaction are transferred to a heme b cofactor [3091]. However, the electron acceptor that is used to restore the heme b cofactor to its oxidized state is still not known (both a thioredoxin-like

protein and menaquinol have been proposed).

References: [226, 461, 462, 1602, 1601, 3091]

[EC 1.17.99.9 created 2020]

Accepted name: steroid C-25 hydroxylase

Reaction: cholest-4-en-3-one + acceptor + $H_2O = 25$ -hydroxycholest-4-en-3-one + reduced acceptor

Other name(s): s25dA1 (gene name); s25dA1B3 (gene name); s25dA1C3 (gene name); cholesterol C-25 dehydroge-

nase; steroid C-25 dehydrogenase

Systematic name: cholest-4-en-3-one:acceptor oxidoreductase (25-hydroxylating)

Comments: The enzyme, characterized from the bacterium Sterolibacterium denitrificans, participates in the

anaerobic degradation of cholesterol. The enzyme can accept several substrates including vitamin D₃. The enzyme contains a bis(guanylyl molybdopterin) cofactor, five [Fe-S] clusters, and one heme *b. cf*. EC 1.14.99.38, cholesterol 25-monooxygenase, an oxygen-requiring eukaryotic enzyme that catalyses

a similar transformation.

References: [886, 3600, 3601, 1874]

[EC 1.17.99.10 created 2020]

EC 1.17.99.11

Accepted name: $3-oxo-\Delta^1$ -steroid hydratase/dehydrogenase

Reaction: a 3-oxo- Δ^1 -steroid + H₂O + acceptor = a steroid 1,3-dione + reduced acceptor (overall reaction)

(1a) a 3-oxo- Δ^1 -steroid + H₂O = a 1-hydroxy-3-oxo-steroid

(1b) a 1-hydroxy-3-oxo-steroid + acceptor = a steroid 1,3-dione + reduced acceptor

Other name(s): *atcABC* (gene names)

Systematic name: 3-oxo- Δ^1 -steroid:acceptor 1-oxidoreductase

Comments: A molybdenum enzyme. The enzyme, characterized from the bacterium Steroidobacter denitrifi-

cans, is involved in the anaetrobic degradation of steroids. It is specific to 3-oxo- Δ^1 -steroids such as

androsta-1-ene-3,17-dione and Δ^1 -dihydrotestosterone and does not act on 3-oxo- Δ^4 -steroids.

References: [4763]

[EC 1.17.99.11 created 2020]

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 oxidoreduc-

tase; 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: [3301, 4364, 4365, 3305]

[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] ferre-

doxins, but in other bacteria it can also reduce bacterial [4Fe-4S] ferredoxins and flavodoxin.

References: [3881, 2162, 1998, 2878]

[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: [1961, 1477, 3441, 3833]

[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 ade-

nine; 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, in-

cluding benzyl viologen, menadione and 2,6-dichloroindophenol, but rubredoxin is the most efficient.

Ferredoxin is not utilized.

References: [3304, 2574]

[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-

monooxygenase).

References: [3568, 2193, 3302, 3811, 3808, 3809, 3941]

[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: [3180, 688, 4105, 1519, 1518, 1517, 4931]

[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: ADH-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 [4914]. The enzyme from *Pseudomonas* NCIB 9816 is specific for the ferredoxin associated with naphthalene dioxygenase; it

contains FAD and a [2Fe-2S] cluster.

References: [4914, 1477]

[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 [2470]. 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: [4944, 2470, 817, 592]

[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-depedent 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 [2380, 3915].

References: [1003, 2813, 4276, 917, 918, 998, 2380, 2381, 3915]

[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] Transferred entry, 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: [2751, 2374, 4510, 396, 397, 3924]

[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 + N_2 + 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 succesive 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: [4943, 1004, 863]

[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 $^+$ + H $_2$ O = 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: [747, 4478]

[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 + H_2O + 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 molybdoprotein 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: [4420, 3660, 423, 2484]

[EC 1.20.2.1 created 2011]

EC 1.20.4 With disulfide as acceptor

EC 1.20.4.1

Accepted name: arsenate reductase (glutathione/glutaredoxin)

Reaction: arsenate + glutathione + glutaredoxin = arsenite + a glutaredoxin-glutathione disulfide + H_2O **Other name(s):** ArsC (ambiguous); arsenate:glutaredoxin oxidoreductase; arsenate reductase (glutaredoxin)

Systematic name: arsenate:glutathione/glutaredoxin oxidoreductase

Comments: The enzyme is part of a system for detoxifying arsenate. The substrate binds to a catalytic cysteine

residue, forming a covalent thiolate—As(V) intermediate. A tertiary intermediate is then formed between the arsenic, the enzyme's cysteine, and a glutathione cysteine. This intermediate is reduced by glutaredoxin, which forms a dithiol with the glutathione, leading to the dissociation of arsenite. Thus reduction of As(V) is mediated by three cysteine residues: one in ArsC, one in glutathione, and one in glutaredoxin. Although the arsenite formed is more toxic than arsenate, it can be extruded from some bacteria by EC 7.3.2.7, 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: [1336, 1337, 1702, 2256, 2666, 3422, 3671, 3849, 2919, 2778]

[EC 1.20.4.1 created 2000 as EC 1.97.1.5, transferred 2001 to EC 1.20.4.1, modified 2015, modified 2019, modified 2020]

EC 1.20.4.2

Accepted name: methylarsonate reductase

Reaction: methylarsonate + 2 glutathione = methylarsonite + glutathione disulfide + H_2O

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: [4855]

[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-mycothiol + mycoredoxin = arsenite + mycothiol-mycoredoxin disulfide

Other name(s): Mrx1; MrxI

Systematic name: arseno-mycothiol:mycoredoxin oxidoreductase

Comments: Reduction of arsenate is part of a defense mechanism of the cell against toxic arsenate. The substrate

arseno-mycothiol is formed by EC 2.8.4.2 (arsenate:mycothiol transferase). A second mycothiol recy-

cles mycoredoxin and forms mycothione.

References: [3190]

[EC 1.20.4.3 created 2010]

EC 1.20.4.4

Accepted name: arsenate reductase (thioredoxin)

Reaction: arsenate + thioredoxin = arsenite + thioredoxin disulfide + H_2O

Other name(s): ArsC (ambiguous)

Systematic name: arsenate:thioredoxin oxidoreductase

Comments: The enzyme, characterized in bacteria of the Firmicutes phylum, is specific for thioredoxin [1910].

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 7.3.2.7, 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 [4864].

References: [1910, 2776, 4864, 2777]

[EC 1.20.4.4 created 2015, modified 2019]

EC 1.20.9 With a copper protein as acceptor

EC 1.20.9.1

Accepted name: arsenate reductase (azurin)

Reaction: arsenite + $H_2O + 2$ 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 cofac-

tors 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 O_2 as acceptors.

References: [93, 1039]

[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), re-

duced glutaredoxin cannot serve as a reductant.

References: [2256, 3422]

[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 With NAD+ or NADP+ as acceptor

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: [3574, 1348, 1182, 4266]

[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: [3564]

[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-[(5S)-5-amino-5-carboxypentanoyl]-L-cysteinyl-D-valine + O₂ = isopenicillin N + 2 H₂O

Other name(s): isopenicillin N synthetase

Systematic name: N-[(5S)-5-amino-5-carboxypentanoyl]-L-cysteinyl-D-valine:oxygen oxidoreductase (cyclizing)

Comments: Forms part of the penicillin biosynthesis pathway (for pathway, click here).

References: [1763, 3532]

[EC 1.21.3.1 created 2002]

EC 1.21.3.2

Accepted name: columbamine oxidase

Reaction: 2 columbamine + O_2 = 2 berberine + 2 H_2O

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: [3595]

[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 + O_2 = (S)-scoulerine + H_2O_2

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

[2311]. 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: [4014, 922, 2311]

[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 + $O_2 = 2$ (+)-bisdechlorogeodin + 2 H_2O

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. In-

volved in the biosynthesis of mould metabolites related to the antibiotic griseofulvin.

References: [3105]

[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 + $O_2 = 2$ (-)-bisdechlorogeodin + 2 H_2O

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. In-

volved in the biosynthesis of mould metabolites related to the antibiotic griseofulvin.

References: [3105]

[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 $4'-O-\beta$ -D-glucoside + O_2 = aureusidin $6-O-\beta$ -D-glucoside + O_2

(2) 2',3,4,4',6'-pentahydroxychalcone $4'-O-\beta$ -D-glucoside + $\frac{1}{2}$ O₂ = aureusidin $6-O-\beta$ -D-glucoside +

 H_2O

(3) 2',3,4,4',6'-pentahydroxychalcone $4'-O-\beta$ -D-glucoside + O_2 = bracteatin $6-O-\beta$ -D-glucoside + O_2 = bracteatin O_2 -D-glucoside + O_3 -D-glucoside + O

Other name(s): AmAS1

Systematic name: 2',4,4',6'-tetrahydroxychalcone $4'-O-\beta$ -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 [3001] and catalyses two separate chemical transformations, i.e. 3-hydroxylation and oxidative cyclization (2',-dehydrogenation). H_2O_2 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 [3184].

References: [3001, 3000, 3672, 3184]

[EC 1.21.3.6 created 2003, modified 2012]

EC 1.21.3.7

Accepted name: tetrahydrocannabinolic acid synthase

Reaction: cannabigerolate + $O_2 = \Delta^9$ -tetrahydrocannabinolate + H_2O_2 **Other name(s):** THCA synthase; Δ^1 -tetrahydrocannabinolic acid synthase

Systematic name: cannabigerolate:oxygen oxidoreductase (cyclizing, Δ^9 -tetrahydrocannabinolate-forming)

Comments: A flavoprotein (FAD). The cofactor is covalently bound. Part of the cannabinoids biosynthetic path-

way in the plant *Cannabis sativa*. The enzyme can also convert cannabinerolate (the (Z)-isomer of cannabigerolate) to Δ^9 -THCA with lower efficiency. Whereas the product was originally called Δ^1 -tetrahydrocannabinolate, the recommended name according to systematic peripheral numbering is

 Δ^9 -tetrahydrocannabinolate.

References: [4220, 3917, 3893, 3894]

[EC 1.21.3.7 created 2012]

EC 1.21.3.8

Accepted name: cannabidiolic acid synthase

Reaction: cannabigerolate + O_2 = cannabidiolate + H_2O_2

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: [4219, 4221]

[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 1.21.3.10

Accepted name: hercynylcysteine *S*-oxide synthase

Reaction: hereynine + L-cysteine + $O_2 = S$ -(hereyn-2-yl)-L-cysteine S-oxide + H_2O

Other name(s): Egt1; Egt-1

Systematic name: hercynine,L-cysteine:oxygen [S-(hercyn-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 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 hercynylselenocys-

teine, which can be converted to selenoneine.

References: [3337]

[EC 1.21.3.10 created 2015 as 1.14.99.51, transferred 2022 to EC 1.21.3.10]

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: [3998, 1683, 1966, 266, 1134]

[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 + NH_3 + thioredoxin disulfide + H_2O = 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: [4487, 266]

[EC 1.21.4.2 created 2003]

EC 1.21.4.3

Accepted name: sarcosine reductase

Reaction: acetyl phosphate + methylamine + thioredoxin disulfide + $H_2O = N$ -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: [4487, 1730]

[EC 1.21.4.3 created 2003]

EC 1.21.4.4

Accepted name: betaine reductase

Reaction: acetyl phosphate + trimethylamine + thioredoxin disulfide + H_2O = 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: [4487, 266]

[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 glu-

tathione

(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 chlorophenolicum, 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: [4715, 2741]

[EC 1.21.4.5 created 2018]

EC 1.21.98 With other, known, physiological acceptors

EC 1.21.98.1

Accepted name: cyclic dehypoxanthinyl futalosine synthase

Reaction: dehypoxanthine futalosine + S-adenosyl-L-methionine = cyclic dehypoxanthinyl futalosine + S-

deoxyadenosine + L-methionine

Other name(s): MqnC; dehypoxanthinyl futalosine cyclase

Systematic name: dehypoxanthine futalosine: S-adenosyl-L-methionine oxidoreductase (cyclizing)

Comments: This enzyme is a member of the 'AdoMet radical' (radical SAM) family. The enzyme, found in sev-

eral bacterial species, is part of the futalosine pathway for menaquinone biosynthesis.

References: [1671, 727]

[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-iminopropanoate + H₂O₂ = dichlorochromopyrrolate + NH₃ + 2 H₂O

Other name(s): RebD; chromopyrrolic acid synthase; chromopyrrolate synthase

Systematic name: 3-(7-chloroindol-3-yl)-2-iminopropanoate ammonia-lyase (dichlorochromopyrrolate-forming)

Comments: This enzyme catalyses a step in the biosynthesis of rebeccamycin, an indolocarbazole alkaloid pro-

duced 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 [3087]. Contains one molecule of heme *b* per monomer, as well as non-heme iron that is not part of an iron-sulfur center [1743]. *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

[3989].

References: [3087, 1743, 3989]

[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 + $H_2O = 3.8$ -

divinyl protochlorophyllide a + 35'-deoxyadenosine + 3 L-methionine (overall reaction)

(1a) magnesium-protoporphyrin IX 13-monomethyl ester + S-adenosyl-L-methionine + $H_2O = 13^1$ -hydroxy-magnesium-protoporphyrin IX 13-monomethyl ester + S-deoxyadenosine + L-methionine (1b) 13^1 -hydroxy-magnesium-protoporphyrin IX 13-monomethyl ester + S-adenosyl-L-methionine = 13^1 -oxo-magnesium-protoporphyrin IX 13-monomethyl ester + S-adenosyl-L-methionine (1c) 13^1 -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 bac-

teria, 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: [4775, 1374, 3212, 389]

[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: [4566, 2360, 224]

[EC 1.21.98.4 created 2018]

EC 1.21.98.5

Accepted name: tetraether lipid synthase

Reaction: (1) 2 a 2,3-bis-O-phytanyl-sn-glycero-phospholipid + 4 S-adenosyl-L-methionine + 2 reduced

acceptor = a glycerol dibiphytanyl glycerol tetraether phospholipid + 4 L-methionine + 4 5'-

deoxyadenosine + 2 acceptor

(2) a 2,3-bis-*O*-phytanyl-*sn*-glycero-phospholipid + **2** *S*-adenosyl-L-methionine + reduced acceptor = a

macrocyclic archaeol phospholipid + 2 L-methionine + 2 5'-deoxyadenosine + acceptor

Other name(s): GDGT/MA synthase; GDGT/MAS; tetraether synthase; Tes; Mj0619 (locus name)

Systematic name: a 2,3-bis-O-phytanyl-sn-glycero-phospholipid:S-adenosyl-L-methionine,acceptor oxidoreductase (cy-

clyzing)

Comments: This archaeal enzyme catalyses a C-C bond formation during the biosynthesis of tetraether lipids.

The bond is formed between the termini of two lipid tails from two glycerophospholipids to generate the macrocycle glycerol dibiphytanyl glycerol tetraether (GDGT). The enzyme does not distinguish whether the two lipids are connected in antiparallel or parallel geometry, resulting in formation of two forms of the product, which are known as caldarchaeol and isocaldarchaeol, respectively. The enzyme can also form macrocyclic archaeol phospholipids by joining the two lipid tails of a single substrate molecule. Even though the reaction shown here describes phospholipid substrates, the enzyme can also act on glycolipids or lipids that contains mixed types of polar head groups. The enzyme is a radical SAM enzyme that contains 3 [4Fe-4S] clusters and one mononuclear rubredoxin-like iron ion, each found in a separate domain. The enzyme uses the 5'-deoxyadenosyl radical to initiate the reaction, which involves the formation of an intermediate bond between the substrate carbon and a sulfur of one of the [4Fe-4S] clusters. Two radicals are needed per C-C bond formed. The source of the re-

quired additional electrons is not known.

References: [4870, 2528]

[EC 1.21.98.5 created 2022]

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) oxidore-

ductase (cyclizing)

Systematic name: β-cyclopiazonate:acceptor oxidoreductase (cyclizing)

Comments: A flavoprotein (FAD). Cytochrome c and various dyes can act as acceptor. Cyclopiazonate is a micro-

bial toxin.

References: [1018, 3693]

[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 dehypoxanthinyl futalosine synthase. Now classified as EC 1.21.98.1, cyclic dehypoxanthinyl futalosine 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: [677, 2232]

[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: [677, 1371, 3930, 2232]

[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 re-

sponsible 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. Methyl viologen can act as electron donor

in vitro.

References: [1696, 1345, 3048, 3758, 3757]

 $[EC\ 1.21.99.5\ created\ 2001\ as\ EC\ 1.97.1.8,\ transferred\ 2017\ to\ EC\ 1.21.99.5]$

EC 1.22 Acting on halogen in donors

EC 1.22.1 With NAD+ or NADP+ as acceptor

[1.22.1.1 Transferred entry. iodotyrosine deiodinase. Now EC 1.21.1.1, iodotyrosine 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* [687, 920], *Thuja plicata* (western red cedar) [1211], *Linum perenne* (perennial flax) [1623] and *Linum corymbulosum* [249]. The 4-*pro-R* hydro-

gen of NADH is transferred to the 7-pro-R position of lariciresinol [687].

References: [687, 920, 1211, 2817, 1623, 249]

[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* [687, 920], *Thuja plicata* (western red cedar) [1211], *Linum perenne* (perennial

flax) [1623] and Linum corymbulosum [249].

References: [687, 920, 1211, 2817, 1623, 249]

[EC 1.23.1.2 created 2013]

EC 1.23.1.3

Accepted name: (–)-pinoresinol reductase

Reaction: (-)-laricinesinol + 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) [1211], *Linum perenne* (perennial

flax) [1623] and Arabidopsis thaliana (thale cress) [2997].

References: [1211, 1623, 2997]

[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) [1211] and Linum corymbulosum [1623].

References: [1211, 1623]

[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 + H_2O (1b) antheraxanthin + L-ascorbate = zeaxanthin + L-dehydroascorbate + H_2O

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 vi-

olaxanthin) 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: [4739, 3544, 490, 2315, 2362, 1370, 2361]

[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 + H_2O + chlorite

Other name(s): chlorate reductase C

Systematic name: chlorite:acceptor oxidoreductase

Comments: Flavins or benzylviologen can act as acceptor.

References: [170]

[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 transhy-

 $droxylase; 1,2,3,5\text{-}tetra hydroxybenzene-pyrogallol\ hydroxyltransferase\ (transhydroxylase);\ pyrogallol\ hydroxyltransferase\ (transhydroxyltransferase\ (transhydroxyltransferase\ (transhydroxyltransferase\ (transhydroxyltransferase\ (transhydroxyltransferas$

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 phlorogluci-

nol, 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: [474]

[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]-glycin-

2-yl radical

Other name(s): PFL activase; PFL-glycine: S-adenosyl-L-methionine H transferase (flavodoxin-oxidizing, S-adenosyl-

ing); pyruvate formate-lyase activating enzyme; pyruvate formate-lyase 1 activating enzyme

 $\textbf{Systematic name:} \quad [formate \ \textit{C}-acetyltransferase] - glycine \ dihydroflavodoxin: \textit{S}-adenosyl-L-methionine oxidoreductase}$

(S-adenosyl-L-methionine cleaving)

Comments: An iron-sulfur protein. A single glycine residue in EC 2.3.1.54, formate *C*-acetyltransferase, is oxi-

dized to the corresponding radical by transfer of H from its CH_2 to AdoMet with concomitant cleavage of the latter. The reaction requires Fe^{2+} . 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: [1176, 4486, 1178]

[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 + H_2O + acceptor = selenate + reduced acceptor

Systematic name: selenite:reduced acceptor oxidoreductase

Comments: The periplasmic enzyme from *Thauera selenatis* is a complex comprising three heterologous subunits

 $(\alpha, \beta \text{ and } \gamma)$ 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: [3746, 2597, 2255, 4048]

[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 + hv = 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: [4168, 4416, 659, 88]

[EC 1.97.1.12 created 2011]

EC 1.98 Enzymes using H₂ as reductant (deleted subclass)

EC 1.98.1 Enzymes using H₂ as reductant (deleted subclass)

[1.98.1.1 Transferred entry. hydrogenase. 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 11α -hydroxylase]	
	[EC 1.99.1.6 created 1961, deleted 1965]	
[1.99.1.7	Transferred entry. Now EC 1.14.15.4, steroid 11β-monooxygenase]	
	[EC 1.99.1.7 created 1961, deleted 1965]	
[1.99.1.8	Deleted entry. steroid 6β-hydroxylase]	
	[EC 1.99.1.8 created 1961, deleted 1965]	
[1.99.1.9	Transferred entry. Now EC 1.14.99.9, steroid 17\alpha-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 5.4.99.7 (lar	Deleted entry. squalene cyclohydroxylase, covered by EC 1.14.99.7 (squalene monooxygenase) and by EC nosterol 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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