The Enzyme List Class 5 — Isomerases

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

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EC 5.1 Racemases and epimerases

This subclass contains enzymes that catalyse either racemization or epimerization of a centre of chirality. Sub-subclasses are based on the substrate: amino acids and derivatives (EC 5.1.1), hydroxy acids and derivatives (EC 5.1.2), carbohydrates and derivatives (EC 5.1.3), or other compounds (EC 5.1.99).

EC 5.1.1 Acting on amino acids and derivatives

EC 5.1.1.1

Accepted name: alanine racemase

Reaction: L-alanine = D-alanine

Other name(s): L alanine racemase

Other name(s): L-alanine racemase

Systematic name: alanine racemase

Comments: A pyridoxal-phosphate protein.

References: [176, 323, 324]

[EC 5.1.1.1 created 1961]

EC 5.1.1.2

Accepted name: methionine racemase

Reaction: L-methionine = D-methionine

Systematic name: methionine racemase

Comments: A pyridoxal-phosphate protein.

References: [131]

[EC 5.1.1.2 created 1961]

EC 5.1.1.3

Accepted name: glutamate racemase

Reaction: L-glutamate = D-glutamate

Systematic name: glutamate racemase

Comments: A pyridoxal-phosphate protein.

References: [94]

[EC 5.1.1.3 created 1961]

EC 5.1.1.4

Accepted name: proline racemase

Reaction: L-proline = D-proline

Systematic name: proline racemase

References: [269]

[EC 5.1.1.4 created 1961]

EC 5.1.1.5

Accepted name: lysine racemase

Reaction: L-lysine = D-lysine **Systematic name:** lysine racemase

References: [118]

[EC 5.1.1.5 created 1961]

EC 5.1.1.6

Accepted name: threonine racemase

Reaction: L-threonine = D-threonine

Systematic name: threonine racemase

Comments: Inverts both chiral centres.

References: [9]

[EC 5.1.1.6 created 1961, modified 1981]

EC 5.1.1.7

Accepted name: diaminopimelate epimerase

Reaction: LL-2,6-diaminoheptanedioate = meso-diaminoheptanedioate

Systematic name: LL-2,6-diaminoheptanedioate 2-epimerase

References: [14]

[EC 5.1.1.7 created 1961]

EC 5.1.1.8

Accepted name: 4-hydroxyproline epimerase

Reaction: *trans*-4-hydroxy-L-proline = *cis*-4-hydroxy-D-proline

Other name(s): hydroxyproline epimerase; hydroxyproline 2-epimerase; L-hydroxyproline epimerase

Systematic name: 4-hydroxyproline 2-epimerase

Comments: Also interconverts *trans-*4-hydroxy-D-proline and *cis-*4-hydroxy-L-proline.

References: [2]

[EC 5.1.1.8 created 1965, modified 1983]

EC 5.1.1.9

Accepted name: arginine racemase
Reaction: L-arginine = D-arginine
Systematic name: arginine racemase

Comments: A pyridoxal-phosphate protein.

References: [335]

[EC 5.1.1.9 created 1972]

EC 5.1.1.10

Accepted name: amino-acid racemase

Reaction: an L-amino acid = a D-amino acid

Other name(s): L-amino acid racemase Systematic name: amino-acid racemase

Comments: A pyridoxal-phosphate protein.

References: [265]

[EC 5.1.1.10 created 1972]

EC 5.1.1.11

Accepted name: phenylalanine racemase (ATP-hydrolysing)

Reaction: ATP + L-phenylalanine + $H_2O = AMP + diphosphate + D-phenylalanine$

Other name(s): phenylalanine racemase; phenylalanine racemase (adenosine triphosphate-hydrolysing); gramicidin S

synthetase I

Systematic name: phenylalanine racemase (ATP-hydrolysing)

References: [329]

[EC 5.1.1.11 created 1972]

EC 5.1.1.12

Accepted name: ornithine racemase **Reaction:** L-ornithine = D-ornithine

Systematic name: ornithine racemase

References: [47]

[EC 5.1.1.12 created 1972 as EC 5.4.3.1, transferred 1976 to EC 5.1.1.12]

EC 5.1.1.13

Accepted name: aspartate racemase
Reaction: L-aspartate = D-aspartate
Other name(s): D-aspartate racemase; McyF

Systematic name: aspartate racemase

Comments: Also acts, at half the rate, on L-alanine.

References: [160, 332, 168, 259, 331]

[EC 5.1.1.13 created 1976]

EC 5.1.1.14

Accepted name: nocardicin-A epimerase
Reaction: isonocardicin A = nocardicin A
Other name(s): isonocardicin A epimerase
Systematic name: nocardicin-A epimerase

Comments: The (9'S) configuration of isonocardicin A is converted into the (9'R) configuration.

References: [313]

[EC 5.1.1.14 created 1992]

EC 5.1.1.15

Accepted name: 2-aminohexano-6-lactam racemase

Reaction: L-2-aminohexano-6-lactam = D-2-aminohexano-6-lactam

Other name(s): α-amino-ε-caprolactam racemase
Systematic name: 2-aminohexano-6-lactam racemase

Comments: Contains pyridoxal 5'-phosphate. Also racemises 2-aminopentano-5-lactam (α-amino-δ-valerolactam)

and 2-amino-4-thiahexano-6-lactam (where S replaces CH2 of C-4). It does not catalyse the racemisa-

tion of α -amino acids but has some transaminase activity with them.

References: [4, 5]

[EC 5.1.1.15 created 1999]

EC 5.1.1.16

Accepted name: protein-serine epimerase

Reaction: [protein]-L-serine = [protein]-D-serine

Other name(s): protein-serine racemase

Systematic name: [protein]-serine epimerase

Comments: The enzyme specifically interconverts the configuration of Ser-46 of the peptide ω-agatoxin-KT,

found in the venom of the funnel web spider, Agelenopsis aperta, but not that of the other serine

residue, Ser-28.

References: [256]

[EC 5.1.1.16 created 1999]

EC 5.1.1.17

Accepted name: isopenicillin-N epimerase Reaction: isopenicillin N = penicillin N

Systematic name: penicillin-N 5-amino-5-carboxypentanoyl-epimerase

Comments: This enzyme contains pyridoxal phosphate. Epimerization at C-5 of the 5-amino-5-carboxypentanoyl

group to form penicillin N is required to make a substrate for EC 1.14.20.1, deactoxycephalosporin-C synthase, to produce cephalosporins. Forms part of the penicillin biosynthesis pathway (for pathway,

click here).

References: [299, 159, 43, 333]

[EC 5.1.1.17 created 2002]

EC 5.1.1.18

Accepted name: serine racemase **Reaction:** L-serine = D-serine

Other name(s): SRR

Systematic name: serine racemase

Comments: A pyridoxal-phosphate protein that is highly selective for L-serine as substrate. D-Serine is found in

type-II astrocytes in mammalian brain, where it appears to be an endogenous ligand of the glycine site of *N*-methyl-D-aspartate (NMDA) receptors [321, 322]. The reaction can also occur in the reverse

direction but does so more slowly at physiological serine concentrations [82].

References: [321, 322, 196, 82]

[EC 5.1.1.18 created 2007]

EC 5.1.2 Acting on hydroxy acids and derivatives

EC 5.1.2.1

Accepted name: lactate racemase **Reaction:** (S)-lactate = (R)-lactate

Other name(s): lacticoracemase; hydroxyacid racemase; lactic acid racemase

Systematic name: lactate racemase **References:** [120, 145]

[EC 5.1.2.1 created 1961]

EC 5.1.2.2

Accepted name: mandelate racemase

Reaction: (S)-mandelate = (R)-mandelate

Systematic name: mandelate racemase

References: [101]

[EC 5.1.2.2 created 1961]

EC 5.1.2.3

Accepted name: 3-hydroxybutyryl-CoA epimerase

Reaction: (S)-3-hydroxybutanoyl-CoA = (R)-3-hydroxybutanoyl-CoA

Other name(s): 3-hydroxybutyryl coenzyme A epimerase; 3-hydroxyacyl-CoA epimerase

Systematic name: 3-hydroxybutanoyl-CoA 3-epimerase

References: [272, 307]

[EC 5.1.2.3 created 1961]

EC 5.1.2.4

Accepted name: acetoin racemase

Reaction: (S)-acetoin = (R)-acetoin **Other name(s):** acetylmethylcarbinol racemase

Systematic name: acetoin racemase

References: [284]

[EC 5.1.2.4 created 1972]

EC 5.1.2.5

Accepted name: tartrate epimerase

Reaction: (R,R)-tartrate = meso-tartrate

Other name(s): tartaric racemase Systematic name: tartrate epimerase

References: [232]

[EC 5.1.2.5 created 1972]

EC 5.1.2.6

Accepted name: isocitrate epimerase

Reaction: (1R,2S)-1-hydroxypropane-1,2,3-tricarboxylate = (1S,2S)-1-hydroxypropane-1,2,3-tricarboxylate

Systematic name: (1*R*,2*S*)-1-hydroxypropane-1,2,3-tricarboxylate 1-epimerase

Comments: (1R,2S)-1-hydroxypropane-1,2,3-tricarboxylate is the commonly occurring isomer of isocitrate.

References: [116]

[EC 5.1.2.6 created 1984]

EC 5.1.3 Acting on carbohydrates and derivatives

EC 5.1.3.1

Accepted name: ribulose-phosphate 3-epimerase

Reaction: D-ribulose 5-phosphate = D-xylulose 5-phosphate

Other name(s): phosphoribulose epimerase; erythrose-4-phosphate isomerase; phosphoketopentose 3-epimerase; xy-

lulose phosphate 3-epimerase; phosphoketopentose epimerase; ribulose 5-phosphate 3-epimerase; D-ribulose phosphate-3-epimerase; D-ribulose 5-phosphate epimerase; D-ribulose-5-P 3-epimerase;

D-xylulose-5-phosphate 3-epimerase; pentose-5-phosphate 3-epimerase

Systematic name: D-ribulose-5-phosphate 3-epimerase

Comments: The enzyme also converts D-erythrose 4-phosphate into D-erythrulose 4-phosphate and D-threose 4-

phosphate.

References: [16, 64, 121, 276, 286]

[EC 5.1.3.1 created 1961, modified 1989]

EC 5.1.3.2

Accepted name: UDP-glucose 4-epimerase UDP-glucose = UDP-galactose

Other name(s): UDP-galactose 4-epimerase; uridine diphosphoglucose epimerase; galactowaldenase; UDPG-4-

epimerase; uridine diphosphate galactose 4-epimerase; uridine diphospho-galactose-4-epimerase; UDP-glucose epimerase; UDP-galactose 4-epimerase; 4-epimerase; UDPG-4-epimerase; uridine diphosphoglucose 4-epimerase; uridine diphosphate glucose 4-epimerase; UDP-D-galactose 4-epimerase; uridine diphosphate glucose 4-epime

epimerase

Systematic name: UDP-glucose 4-epimerase

Comments: Requires NAD⁺. Also acts on UDP-2-deoxyglucose.

References: [164, 186, 314]

[EC 5.1.3.2 created 1961]

EC 5.1.3.3

Accepted name: aldose 1-epimerase

Reaction: α -D-glucose = β -D-glucose

Other name(s): mutarotase; aldose mutarotase; galactose mutarotase; galactose 1-epimerase; D-galactose 1-epimerase

Systematic name: aldose 1-epimerase

Comments: Also acts on L-arabinose, D-xylose, D-galactose, maltose and lactose. This enzyme catalyses the first

step in galactose metabolism by converting β -D-glucose into α -D-glucose, which is the substrate for

EC 2.7.1.6, galactokinase [24, 289].

References: [27, 28, 140, 166, 24, 289, 288]

[EC 5.1.3.3 created 1961]

EC 5.1.3.4

Accepted name: L-ribulose-5-phosphate 4-epimerase

Reaction: L-ribulose 5-phosphate = D-xylulose 5-phosphate

Other name(s): phosphoribulose isomerase; ribulose phosphate 4-epimerase; L-ribulose-phosphate 4-epimerase; L-

ribulose 5-phosphate 4-epimerase; AraD; L-Ru5P

Systematic name: L-ribulose-5-phosphate 4-epimerase Comments: Requires a divalent cation for activity.

References: [42, 62, 162, 320, 12, 161, 245]

[EC 5.1.3.4 created 1965, modified 2005]

EC 5.1.3.5

Accepted name: UDP-arabinose 4-epimerase

Reaction: UDP-L-arabinose = UDP-D-xylose

Other name(s): uridine diphosphoarabinose epimerase; UDP arabinose epimerase; uridine 5'-diphosphate-D-xylose

4-epimerase; UDP-D-xylose 4-epimerase

Systematic name: UDP-L-arabinose 4-epimerase

References: [74]

[EC 5.1.3.5 created 1965]

EC 5.1.3.6

Accepted name: UDP-glucuronate 4-epimerase

Reaction: UDP-glucuronate = UDP-D-galacturonate

Other name(s): uridine diphospho-D-galacturonic acid; UDP glucuronic epimerase; uridine diphosphoglucuronic

epimerase; UDP-galacturonate 4-epimerase; uridine diphosphoglucuronate epimerase; UDP-D-

galacturonic acid 4-epimerase

Systematic name: UDP-glucuronate 4-epimerase

References: [74]

[EC 5.1.3.6 created 1965]

EC 5.1.3.7

Accepted name: UDP-*N*-acetylglucosamine 4-epimerase

Reaction: UDP-*N*-acetyl-D-glucosamine = UDP-*N*-acetyl-D-galactosamine

Other name(s): UDP acetylglucosamine epimerase; uridine diphosphoacetylglucosamine epimerase; uridine diphos-

phate *N*-acetylglucosamine-4-epimerase; uridine 5'-diphospho-*N*-acetylglucosamine-4-epimerase

Systematic name: UDP-*N*-acetyl-D-glucosamine 4-epimerase

References: [93, 153]

[EC 5.1.3.7 created 1965]

EC 5.1.3.8

Accepted name: *N*-acylglucosamine 2-epimerase

Reaction: N-acyl-D-glucosamine = N-acyl-D-mannosamine

Other name(s): acylglucosamine 2-epimerase; *N*-acetylglucosamine 2-epimerase

Systematic name: *N*-acyl-D-glucosamine 2-epimerase **Comments:** Requires catalytic amounts of ATP.

References: [92]

[EC 5.1.3.8 created 1972]

EC 5.1.3.9

Accepted name: *N*-acylglucosamine-6-phosphate 2-epimerase

Reaction: N-acyl-D-glucosamine 6-phosphate = N-acyl-D-mannosamine 6-phosphate

Other name(s): acylglucosamine-6-phosphate 2-epimerase; acylglucosamine phosphate 2-epimerase

Systematic name: *N*-acyl-D-glucosamine-6-phosphate 2-epimerase

References: [91]

[EC 5.1.3.9 created 1972]

EC 5.1.3.10

Accepted name: CDP-paratose 2-epimerase

Reaction: CDP-3,6-dideoxy-D-glucose = CDP-3,6-dideoxy-D-mannose

Other name(s): CDP-paratose epimerase; cytidine diphosphoabequose epimerase; cytidine diphosphodideoxyglucose

epimerase; cytidine diphosphoparatose epimerase; cytidine diphosphate paratose-2-epimerase; CDP-

abequose epimerase (incorrect); CDP-D-abequose 2-epimerase (incorrect)

Systematic name: CDP-3,6-dideoxy-D-glucose 2-epimerase

Comments: Requires NAD⁺. CDP-paratose (CDP-3,6-dideoxy-D-glucose), is more systematically called CDP-

α-3,6-dideoxy-D-ribo-hexose. CDP-tyvelose (CDP-3,6-dideoxy-D-mannose) is systematically called

CDP-3,6-dideoxy-D-arabino-hexose.

References: [185, 167]

[EC 5.1.3.10 created 1972, modified 2005]

EC 5.1.3.11

Accepted name: cellobiose epimerase

Reaction: cellobiose = D-glucosyl-D-mannose

Systematic name: cellobiose 2-epimerase

References: [296]

[EC 5.1.3.11 created 1972]

EC 5.1.3.12

Accepted name: UDP-glucuronate 5'-epimerase

Reaction: UDP-glucuronate = UDP-L-iduronate

Other name(s): uridine diphosphoglucuronate 5'-epimerase; UDP-glucuronic acid 5'-epimerase; C-5-uronosyl

epimerase

Systematic name: UDP-glucuronate 5'-epimerase

Comments: Requires NAD⁺.

References: [125]

[EC 5.1.3.12 created 1972]

EC 5.1.3.13

Systematic name:

Accepted name: dTDP-4-dehydrorhamnose 3,5-epimerase

Reaction: dTDP-4-dehydro-6-deoxy-D-glucose = dTDP-4-dehydro-6-deoxy-L-mannose

Other name(s): dTDP-L-rhamnose synthetase; dTDP-L-rhamnose synthetase; thymidine diphospho-4-ketorhamnose

3,5-epimerase; TDP-4-ketorhamnose 3,5-epimerase; dTDP-4-dehydro-6-deoxy-D-glucose 3,5-

epimerase; TDP-4-keto-L-rhamnose-3,5-epimerase dTDP-4-dehydro-6-deoxy-D-glucose 3,5-epimerase

Comments: The enzyme occurs in a complex with EC 1.1.1.133 dTDP-4-dehydrorhamnose reductase.

References: [88, 189]

[EC 5.1.3.13 created 1972]

EC 5.1.3.14

Accepted name: UDP-*N*-acetylglucosamine 2-epimerase

Reaction: UDP-*N*-acetyl-D-glucosamine = UDP-*N*-acetyl-D-mannosamine

Other name(s): UDP-N-acetylglucosamine 2'-epimerase; uridine diphosphoacetylglucosamine 2'-epimerase; uridine all diphosphoacetylglucosamine 2'-epimerase; uridin

dine diphospho-N-acetylglucosamine 2'-epimerase; uridine diphosphate-N-acetylglucosamine-2'-

epimerase

Systematic name: UDP-*N*-acetyl-D-glucosamine 2-epimerase

Comments: The enzyme hydrolyses the product to UDP and *N*-acetyl-D-mannosamine.

References: [142]

[EC 5.1.3.14 created 1976]

EC 5.1.3.15

Accepted name: glucose-6-phosphate 1-epimerase

Reaction: α -D-glucose 6-phosphate = β -D-glucose 6-phosphate

Systematic name: D-glucose-6-phosphate 1-epimerase

References: [326]

[EC 5.1.3.15 created 1976]

EC 5.1.3.16

Accepted name: UDP-glucosamine 4-epimerase

Reaction: UDP-glucosamine = UDP-galactosamine

Systematic name: UDP-glucosamine 4-epimerase

References: [173, 260]

[EC 5.1.3.16 created 1984]

EC 5.1.3.17

Accepted name: heparosan-N-sulfate-glucuronate 5-epimerase

Reaction: heparosan-*N*-sulfate D-glucuronate = heparosan-*N*-sulfate L-iduronate

Other name(s): heparosan epimerase; heparosan-*N*-sulfate-D-glucuronosyl 5-epimerase; C-5 uronosyl epimerase;

polyglucuronate epimerase; D-glucuronyl C-5 epimerase; poly[(1,4)-β-D-glucuronosyl-(1,4)-N-sulfo-

α-D-glucosaminyl] glucurono-5-epimerase

Systematic name: poly[$(1\rightarrow 4)$ - β -D-glucuronosyl- $(1\rightarrow 4)$ -N-sulfo- α -D-glucosaminyl] glucurono-5-epimerase

Comments: Acts on D-glucuronosyl residues adjacent to sulfated D-glucosamine units in the heparin precursor.

Not identical with EC 5.1.3.19 chondroitin-glucuronate 5-epimerase.

References: [126]

[EC 5.1.3.17 created 1984]

EC 5.1.3.18

Accepted name: GDP-mannose 3,5-epimerase **Reaction:** GDP-mannose = GDP-L-galactose

Other name(s): GDP-D-mannose:GDP-L-galactose epimerase; guanosine 5'-diphosphate D-mannose:guanosine 5'-

diphosphate L-galactose epimerase

Systematic name: GDP-mannose 3,5-epimerase

References: [19, 110]

[EC 5.1.3.18 created 1986]

EC 5.1.3.19

Accepted name: chondroitin-glucuronate 5-epimerase

Reaction: chondroitin D-glucuronate = dermatan L-iduronate

Other name(s): polyglucuronate 5-epimerase; dermatan-sulfate 5-epimerase; urunosyl C-5 epimerase; chondroitin

D-glucuronosyl 5-epimerase

Systematic name: chondroitin-D-glucuronate 5-epimerase

Comments: Not identical with EC 5.1.3.17 heparosan-*N*-sulfate-glucuronate 5-epimerase.

References: [174]

[EC 5.1.3.19 created 1986]

EC 5.1.3.20

Accepted name: ADP-glyceromanno-heptose 6-epimerase

Reaction: ADP-D-glycero-D-manno-heptose = ADP-L-glycero-D-manno-heptose

Systematic name: ADP-L-*glycero*-D-*manno*-heptose 6-epimerase

Comments: Requires NAD⁺.

References: [65, 229]

[EC 5.1.3.20 created 1999]

EC 5.1.3.21

Accepted name: maltose epimerase Reaction: α -maltose = β -maltose Systematic name: maltose 1-epimerase

Comments: The enzyme catalyses the interconversion of α and β anomers of maltose more effectively than those

of disaccharides such as lactose and cellobiose.

References: [258]

[EC 5.1.3.21 created 2002]

EC 5.1.3.22

Accepted name: L-ribulose-5-phosphate 3-epimerase

Reaction: L-ribulose 5-phosphate = L-xylulose 5-phosphate **Other name(s):** L-xylulose 5-phosphate 3-epimerase; UlaE; SgaU

Systematic name: L-ribulose-5-phosphate 3-epimerase

Comments: Along with EC 4.1.1.85, 3-dehydro-L-gulonate-6-phosphate decarboxylase, this enzyme is involved in

a pathway for the utilization of L-ascorbate by Escherichia coli.

References: [334]

[EC 5.1.3.22 created 2005]

EC 5.1.3.23

Accepted name: UDP-2,3-diacetamido-2,3-dideoxyglucuronic acid 2-epimerase

Reaction: UDP-2,3-diacetamido-2,3-dideoxy- α -D-glucuronate = UDP-2,3-diacetamido-2,3-dideoxy- α -D-glucuronate

mannuronate

Other name(s): UDP-GlcNAc3NAcA 2-epimerase; UDP-α-D-GlcNAc3NAcA 2-epimerase; 2,3-diacetamido-2,3-

dideoxy-α-D-glucuronic acid 2-epimerase; WbpI; WlbD

Systematic name: 2,3-diacetamido-2,3-dideoxy-α-D-glucuronate 2-epimerase

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 the B-band lipopolysaccharide of *Pseudomonas aeroginosa* serotype O5 and of the band-A trisaccharide of *Bordetella pertussis*, both important respiratory pathogens [311]. The enzyme is highly specific as UDP- α -D-GlcNAc, UDP- α -D-GlcNAcA (UDP-2-acetamido-2-deoxy- α -D-glucuronic acid) and UDP- α -D-GlcNAc3NAc (UDP-2,3-diacetamido-2,3-dideoxy- α -D-glucose) cannot act as substrates [311].

References: [311, 310, 135]

[EC 5.1.3.23 created 2007]

EC 5.1.99 Acting on other compounds

EC 5.1.99.1

Accepted name: methylmalonyl-CoA epimerase

Reaction: (R)-methylmalonyl-CoA = (S)-methylmalonyl-CoA

Other name(s): methylmalonyl-CoA racemase; methylmalonyl coenzyme A racemase; DL-methylmalonyl-CoA race-

mase; 2-methyl-3-oxopropanoyl-CoA 2-epimerase [incorrect]

Systematic name: methylmalonyl-CoA 2-epimerase

References: [187, 218]

[EC 5.1.99.1 created 1965, modified 1981]

EC 5.1.99.2

Accepted name: 16-hydroxysteroid epimerase

Reaction: 16α -hydroxysteroid = 16β -hydroxysteroid

Systematic name: 16-hydroxysteroid 16-epimerase

References: [56]

[EC 5.1.99.2 created 1972]

EC 5.1.99.3

Accepted name: allantoin racemase

Reaction: (S)(+)-allantoin = (R)(-)-allantoin

Systematic name: allantoin racemase

References: [302]

[EC 5.1.99.3 created 1976]

EC 5.1.99.4

Accepted name: α-methylacyl-CoA racemase

Reaction: (2S)-2-methylacyl-CoA = (2R)-2-methylacyl-CoA

Systematic name: 2-methylacyl-CoA 2-epimerase

Comments: α-methyl-branched acyl-CoA derivatives with chain lengths of more than C10 are substrates. Also

active towards some aromatic compounds (e.g. ibuprofen) and bile acid intermediates, such as

trihydroxycoprostanoyl-CoA. Not active towards free acids

References: [248]

[EC 5.1.99.4 created 1999]

EC 5.1.99.5

Accepted name: hydantoin racemase

Reaction: D-5-monosubstituted hydantoin = L-5-monosubstituted hydantoin

Other name(s): 5'-monosubstituted-hydantoin racemase; HyuA; HyuE

Systematic name: D-5-monosubstituted-hydantoin racemase

Comments: This enzyme, along with *N*-carbamoylase (EC 3.5.1.77 and EC 3.5.1.87) and hydantoinase, forms

part of the reaction cascade known as the "hydantoinase process", which allows the total conversion of D,L-5-monosubstituted hydantoins into optically pure D- or L-amino acids [8]. The enzyme from *Pseudomonas* sp. (HyuE) has a preference for hydantoins with aliphatic substituents, e.g. D- and L-5-(2-methylthioethyl)hydantoin, whereas that from *Arthrobacter aurescens* shows highest activity with arylalkyl substituents, especially 5-benzylhydantoin, at the 5-position [312]. In the enzyme from *Sinorhizobium meliloti*, Cys⁷⁶ is responsible for recognition and proton retrieval of D-isomers, while

Cys¹⁸¹ is responsible for L-isomer recognition and racemization [180].

References: [308, 312, 182, 181, 279, 180, 8]

[EC 5.1.99.5 created 2008]

EC 5.2 cis-trans-Isomerases

This subclass contains a single sub-subclass for enzymes that rearrange the geometry at double bonds (*cis-trans* isomerases; EC 5.2.1).

EC 5.2.1 cis-trans Isomerases (only sub-subclass identified to date)

EC 5.2.1.1

Accepted name: maleate isomerase **Reaction:** maleate = fumarate

Systematic name: maleate *cis-trans*-isomerase

References: [25]

[EC 5.2.1.1 created 1961]

EC 5.2.1.2

Accepted name: maleylacetoacetate isomerase

Reaction: 4-maleylacetoacetate = 4-fumarylacetoacetate

Other name(s): maleylacetoacetic isomerase; maleylacetone isomerase; maleylacetone cis-trans-isomerase

Systematic name: 4-maleylacetoacetate *cis-trans*-isomerase

Comments: Also acts on maleylpyruvate.

References: [68, 158, 252]

[EC 5.2.1.2 created 1961]

EC 5.2.1.3

Accepted name: retinal isomerase

Reaction: all-trans-retinal = 11-cis-retinal
Other name(s): retinene isomerase; retinoid isomerase
Systematic name: all-trans-retinal 11-cis-trans-isomerase

Comments: Light shifts the reaction towards the *cis*-isomer.

References: [119, 255]

[EC 5.2.1.3 created 1961, modified 1976]

EC 5.2.1.4

Accepted name: maleylpyruvate isomerase

Reaction: 3-maleylpyruvate = 3-fumarylpyruvate **Systematic name:** 3-maleylpyruvate *cis-trans*-isomerase

References: [158]

[EC 5.2.1.4 created 1965]

EC 5.2.1.5

Accepted name: linoleate isomerase

Reaction: 9-cis,12-cis-octadecadienoate = 9-cis,11-trans-octadecadienoate

Other name(s): linoleic acid isomerase

Systematic name: linoleate Δ^{12} -*cis*- Δ^{11} -*trans*-isomerase

References: [141]

[EC 5.2.1.5 created 1972]

EC 5.2.1.6

Accepted name: furylfuramide isomerase

Reaction: (E)-2-(2-furyl)-3-(5-nitro-2-furyl)acrylamide = (Z)-2-(2-furyl)-3-(5-nitro-2-furyl)acrylamide

Systematic name: 2-(2-furyl)-3-(5-nitro-2-furyl)acrylamide *cis-trans*-isomerase

Comments: Requires NADH.

References: [291]

[EC 5.2.1.6 created 1978]

EC 5.2.1.7

Accepted name: retinol isomerase

Reaction: *all-trans*-retinol = 11-*cis*-retinol **Other name(s):** *all-trans*-retinol isomerase

Systematic name: *all-trans*-retinol 11-*cis-trans*-isomerase

Comments: Converts *all-trans*-retinol to 11-cis-retinol in the dark, thus reversing the effect of EC 5.2.1.3 retinal

isomerase.

References: [29, 38]

[EC 5.2.1.7 created 1989]

EC 5.2.1.8

Accepted name: peptidylprolyl isomerase

Reaction: peptidylproline (ω =180) = peptidylproline (ω =0)

Other name(s): PPIase; cyclophilin [misleading, see comments]; peptide bond isomerase; peptidyl-prolyl *cis-trans*

isomerase

Systematic name: peptidylproline *cis-trans*-isomerase

Comments: The first type of this enzyme found [79] proved to be the protein cyclophilin, which binds the im-

munosuppressant cyclosporin A. Other distinct families of the enzyme exist, one being FK-506 binding proteins (FKBP) and another that includes parvulin from *Escherichia coli*. The three families are structurally unrelated and can be distinguished by being inhibited by cyclosporin A, FK-506 and 5-

hydroxy-1,4-naphthoquinone, respectively.

References: [79, 80, 81, 280, 112, 78, 106, 71]

[EC 5.2.1.8 created 1989, modified 2002]

EC 5.2.1.9

Accepted name: farnesol 2-isomerase

Reaction: 2-trans, 6-trans-farnesol = 2-cis, 6-trans-farnesol

Other name(s): farnesol isomerase

Systematic name: 2-trans,6-trans-farnesol 2-cis-trans-isomerase

References: [10]

[EC 5.2.1.9 created 1989]

EC 5.2.1.10

Accepted name: 2-chloro-4-carboxymethylenebut-2-en-1,4-olide isomerase

Reaction: *cis*-2-chloro-4-carboxymethylenebut-2-en-1,4-olide = *trans*-2-chloro-4-carboxymethylenebut-2-en-

1,4-olide

Other name(s): 2-chlorocarboxymethylenebutenolide isomerase; chlorodienelactone isomerase

Systematic name: 2-chloro-4-carboxymethylenebut-2-en-1,4-olide *cis-trans*-isomerase

References: [249]

[EC 5.2.1.10 created 1992]

[5.2.1.11 Deleted entry. 4-hydroxyphenylacetaldehyde-oxime isomerase. The existence of this enzyme has been called into question by one of the authors of the reference cited]

[EC 5.2.1.11 created 1992, deleted 2005]

EC 5.3 Intramolecular oxidoreductases

These enzymes bring about the oxidation of one part of a molecule with a corresponding reduction of another part. They include the enzymes interconverting, in the sugar series, aldoses and ketoses, and related compounds (sugar isomerases, EC 5.3.1), enzymes catalysing a keto-enol equilibrium (tautomerases, EC 5.3.2), enzymes shifting a carbon-carbon double bond from one position to another (EC 5.3.3), enzymes transposing S-S bonds (EC 5.3.4), and a group of miscellaneous enzymes (EC 5.3.99).

EC 5.3.1 Interconverting aldoses and ketoses, and related compounds

EC 5.3.1.1

Accepted name: triose-phosphate isomerase

Reaction: D-glyceraldehyde 3-phosphate = glycerone phosphate

Other name(s): phosphotriose isomerase; triose phosphoisomerase; triose phosphate mutase; D-glyceraldehyde-3-

phosphate ketol-isomerase

Systematic name: D-glyceraldehyde-3-phosphate aldose-ketose-isomerase

References: [193, 194]

[EC 5.3.1.1 created 1961]

[5.3.1.2 Deleted entry. erythrose isomerase]

[EC 5.3.1.2 created 1961, deleted 1976]

EC 5.3.1.3

Accepted name: arabinose isomerase **Reaction:** D-arabinose = D-ribulose Other name(s): D-arabinose(L-fucose) isomerase; D-arabinose isomerase; L-fucose isomerase; D-arabinose ketol-

isomerase

Systematic name: D-arabinose aldose-ketose-isomerase

Comments: Also acts on L-fucose and, more slowly, on L-galactose and D-altrose.

References: [49, 97]

[EC 5.3.1.3 created 1961]

EC 5.3.1.4

Accepted name: L-arabinose isomerase
Reaction: L-arabinose = L-ribulose
Other name(s): L-arabinose ketol-isomerase

Systematic name: L-arabinose aldose-ketose-isomerase

References: [109, 205]

[EC 5.3.1.4 created 1961]

EC 5.3.1.5

Accepted name: xylose isomerase **Reaction:** D-xylose = D-xylulose

Other name(s): D-xylose isomerase; D-xylose ketol-isomerase

Systematic name: D-xylose aldose-ketose-isomerase

Comments: Some enzymes also convert D-glucose to D-fructose.

References: [114, 263, 330]

[EC 5.3.1.5 created 1961 (EC 5.3.1.18 created 1972, part incorporated 1978)]

EC 5.3.1.6

Accepted name: ribose-5-phosphate isomerase

Reaction: D-ribose 5-phosphate = D-ribulose 5-phosphate

Other name(s): phosphopentosisomerase; phosphoriboisomerase; ribose phosphate isomerase; 5-phosphoribose iso-

merase; D-ribose 5-phosphate isomerase; D-ribose-5-phosphate ketol-isomerase

Systematic name: D-ribose-5-phosphate aldose-ketose-isomerase

Comments: Also acts on D-ribose 5-diphosphate and D-ribose 5-triphosphate.

References: [64, 115, 122]

[EC 5.3.1.6 created 1961]

EC 5.3.1.7

Accepted name: mannose isomerase **Reaction:** D-mannose = D-fructose

Other name(s): D-mannose isomerase; D-mannose ketol-isomerase

Systematic name: D-mannose aldose-ketose-isomerase **Comments:** Also acts on D-lyxose and D-rhamnose.

References: [219]

[EC 5.3.1.7 created 1961]

EC 5.3.1.8

Accepted name: mannose-6-phosphate isomerase

Reaction: D-mannose 6-phosphate = D-fructose 6-phosphate

Other name(s): phosphomannose isomerase; phosphohexomutase; phosphohexoisomerase; mannose phosphate iso-

merase; phosphomannoisomerase; D-mannose-6-phosphate ketol-isomerase

Systematic name: D-mannose-6-phosphate aldose-ketose-isomerase

Comments: A zinc protein. **References:** [41, 96, 262]

[EC 5.3.1.8 created 1961, modified 1976]

EC 5.3.1.9

Accepted name: glucose-6-phosphate isomerase

Reaction: D-glucose 6-phosphate = D-fructose 6-phosphate

Other name(s): phosphohexose isomerase; phosphohexomutase; oxoisomerase; hexosephosphate isomerase; phosphohexomerase; phosphoh

phosaccharomutase; phosphoglucoisomerase; phosphohexoisomerase; phosphoglucose isomerase; glucose phosphate isomerase; hexose phosphate isomerase; D-glucose-6-phosphate ketol-isomerase

Systematic name: D-glucose-6-phosphate aldose-ketose-isomerase

Comments: Also catalyses the anomerization of D-glucose 6-phosphate.

References: [18, 204, 209, 210, 231, 295]

[EC 5.3.1.9 created 1961, modified 1976 (EC 5.3.1.18 created part 1972, incorporated 1978)]

[5.3.1.10 Transferred entry, glucosamine-6-phosphate isomerase, Now EC 3.5.99.6, glucosamine-6-phosphate deaminase]

[EC 5.3.1.10 created 1961, deleted 2000]

[5.3.1.11 Deleted entry. acetylglucosaminephosphate isomerase]

[EC 5.3.1.11 created 1961, deleted 1978]

EC 5.3.1.12

Accepted name: glucuronate isomerase

Reaction: D-glucuronate = D-fructuronate

Other name(s): uronic isomerase; uronate isomerase; D-glucuronate isomerase; uronic acid isomerase; D-glucuronate

ketol-isomerase

Systematic name: D-glucuronate aldose-ketose-isomerase

Comments: Also converts D-galacturonate to D-tagaturonate.

References: [17, 143]

[EC 5.3.1.12 created 1961]

EC 5.3.1.13

Accepted name: arabinose-5-phosphate isomerase

Reaction: D-arabinose 5-phosphate = D-ribulose 5-phosphate

Other name(s): arabinose phosphate isomerase; phosphoarabinoisomerase; D-arabinose-5-phosphate ketol-isomerase

Systematic name: D-arabinose-5-phosphate aldose-ketose-isomerase

References: [305]

[EC 5.3.1.13 created 1965]

EC 5.3.1.14

Accepted name: L-rhamnose isomerase

Reaction: L-rhamnose = L-rhamnulose

Other name(s): rhamnose isomerase; L-rhamnose ketol-isomerase

Systematic name: L-rhamnose aldose-ketose-isomerase

References: [66]

[EC 5.3.1.14 created 1965]

EC 5.3.1.15

Accepted name: D-lyxose ketol-isomerase **Reaction:** D-lyxose = D-xylulose

Other name(s): D-lyxose isomerase; D-lyxose ketol-isomerase

Systematic name: D-lyxose aldose-ketose-isomerase

References: [11]

[EC 5.3.1.15 created 1972]

EC 5.3.1.16

Accepted name: 1-(5-phosphoribosyl)-5-[(5-phosphoribosylamino)methylideneamino]imidazole-4-carboxamide iso-

merase

Reaction: 1-(5-phosphoribosyl)-5-[(5-phosphoribosylamino)methylideneamino]imidazole-4-carboxamide =

5-[(5-phospho-1-deoxyribulos-1-ylamino)methylideneamino]-1-(5-phosphoribosyl)imidazole-4-

carboxamide

Other name(s): N-(5'-phospho-D-ribosylformimino)-5-amino-1-(5"-phosphoribosyl)-4-imidazolecarboxamide

isomerase; phosphoribosylformiminoaminophosphoribosylimidazolecarboxamide isomerase; *N*-(phosphoribosylformimino) aminophosphoribosylimidazolecarboxamide isomerase; 1-(5-phosphoribosyl)-5-[(5-phosphoribosylamino)methylideneamino]imidazole-4-carboxamide ketol-

isomerase

Systematic name: 1-(5-phosphoribosyl)-5-[(5-phosphoribosylamino)methylideneamino]imidazole-4-carboxamide

aldose-ketose-isomerase

References: [175]

[EC 5.3.1.16 created 1972, modified 2000]

EC 5.3.1.17

Accepted name: 4-deoxy-L-threo-5-hexosulose-uronate ketol-isomerase

Reaction: 4-deoxy-L-*threo*-5-hexosulose uronate = 3-deoxy-D-*glycero*-2,5-hexodiulosonate

Other name(s): 4-deoxy-L-*threo*-5-hexulose uronate isomerase

Systematic name: 4-deoxy-L-*threo*-5-hexosulose-uronate aldose-ketose-isomerase

References: [228]

[EC 5.3.1.17 created 1972]

[5.3.1.18 Deleted entry. glucose isomerase. Reaction is due to EC 5.3.1.9 glucose-6-phosphate isomerase, in the presence of arsenate, or EC 5.3.1.5 xylose isomerase]

[EC 5.3.1.18 created 1972, deleted 1978]

[5.3.1.19 Transferred entry. glucosaminephosphate isomerase. Now EC 2.6.1.16, glutamine—fructose-6-phosphate transaminase (isomerizing)]

[EC 5.3.1.19 created 1972, deleted 1984]

EC 5.3.1.20

Accepted name: ribose isomerase **Reaction:** D-ribose = D-ribulose

Other name(s): D-ribose isomerase; D-ribose ketol-isomerase

Systematic name: D-ribose aldose-ketose-isomerase

Comments: Also acts on L-lyxose and L-rhamnose.

References: [124]

[EC 5.3.1.20 created 1978]

EC 5.3.1.21

Accepted name: corticosteroid side-chain-isomerase

Reaction: 11-deoxycorticosterone = 20-hydroxy-3-oxopregn-4-en-21-al

Systematic name: 11-deoxycorticosterone aldose-ketose-isomerase

Comments: An epimerization at C-20 and C-21 is probably catalysed by the same enzyme.

References: [178, 197]

[EC 5.3.1.21 created 1983]

EC 5.3.1.22

Accepted name: hydroxypyruvate isomerase

Reaction: hydroxypyruvate = 2-hydroxy-3-oxopropanoate **Systematic name:** hydroxypyruvate aldose-ketose-isomerase

References: [316]

[EC 5.3.1.22 created 1983]

EC 5.3.1.23

Accepted name: S-methyl-5-thioribose-1-phosphate isomerase

Reaction: S-methyl-5-thio- α -D-ribose 1-phosphate = S-methyl-5-thio-D-ribulose 1-phosphate

Other name(s): methylthioribose 1-phosphate isomerase; 1-PMTR isomerase; 5-methylthio-5-deoxy-D-ribose-

1-phosphate ketol-isomerase; *S*-methyl-5-thio-5-deoxy-D-ribose-1-phosphate ketol-isomerase; *S*-methyl-5-thio-5-deoxy-D-ribose-1-phosphate aldose-ketose-isomerase; 1-phospho-5'-*S*-methylthioribose isomerase; *S*-methyl-5-thio-D-ribose-1-phosphate aldose-ketose-isomerase

Systematic name: S-methyl-5-thio-α-D-ribose-1-phosphate aldose-ketose-isomerase

References: [90, 293, 86]

[EC 5.3.1.23 created 1989]

EC 5.3.1.24

Accepted name: phosphoribosylanthranilate isomerase

Reaction: N-(5-phospho- β -D-ribosyl)anthranilate = 1-(2-carboxyphenylamino)-1-deoxy-D-ribulose 5-phosphate

Other name(s): PRA isomerase; PRAI; IGPS:PRAI (indole-3-glycerol-phosphate synthetase/N-5'-

phosphoribosylanthranilate isomerase complex); N-(5-phospho-β-D-ribosyl)anthranilate ketol-

isomerase

Systematic name: N-(5-phospho- β -D-ribosyl)anthranilate aldose-ketose-isomerase

Comments: In some organisms, this enzyme is part of a multifunctional protein, together with one or more other

components of the system for the biosynthesis of tryptophan [EC 2.4.2.18 (anthranilate phosphoribosyltransferase), EC 4.1.1.48 (indole-3-glycerol-phosphate synthase), EC 4.1.3.27 (anthranilate synthase)

thase) and EC 4.2.1.20 (tryptophan synthase)].

References: [36, 51, 123]

[EC 5.3.1.24 created 1990]

EC 5.3.1.25

Accepted name: L-fucose isomerase **Reaction:** L-fucose = L-fuculose

Systematic name: L-fucose aldose-ketose-isomerase

References: [171]

[EC 5.3.1.25 created 1999]

EC 5.3.1.26

Accepted name: galactose-6-phosphate isomerase

Reaction: D-galactose 6-phosphate = D-tagatose 6-phosphate **Systematic name:** D-galactose-6-phosphate aldose-ketose-isomerase

Comments: Involved in the tagatose 6-phosphate pathway of lactose catabolism in bacteria.

References: [306, 241]

[EC 5.3.1.26 created 1999]

EC 5.3.1.27

Accepted name: 6-phospho-3-hexuloisomerase

Reaction: D-arabino-hex-3-ulose 6-phosphate = D-fructose 6-phosphate

Other name(s): 3-hexulose-6-phosphate isomerase; phospho-3-hexuloisomerase; PHI; 6-phospho-3-hexulose iso-

merase; YckF

Systematic name: D-arabino-hex-3-ulose-6-phosphate isomerase

Comments: This enzyme, along with EC 4.1.2.43, 3-hexulose-6-phosphate synthase, plays a key role in the

ribulose-monophosphate cycle of formaldehyde fixation, which is present in many microorganisms that are capable of utilizing C1-compounds [75]. The hyperthermophilic and anaerobic archaeon *Pyrococcus horikoshii* OT3 constitutively produces a bifunctional enzyme that sequentially catalyses the

reactions of EC 4.1.2.43 (3-hexulose-6-phosphate synthase) and this enzyme [213].

References: [75, 339, 136, 213, 179, 283]

[EC 5.3.1.27 created 2008]

EC 5.3.1.28

Accepted name: D-sedoheptulose 7-phosphate isomerase

Reaction: D-sedoheptulose 7-phosphate = D-glycero-D-manno-heptose 7-phosphate

Other name(s): sedoheptulose-7-phosphate isomerase; phosphoheptose isomerase; gmhA (gene name); lpcA (gene

name)

Systematic name: D-glycero-D-manno-heptose 7-phosphate aldose-ketose-isomerase

Comments: In Gram-negative bacteria the enzyme is involved in biosynthesis of ADP-L-glycero-β-D-manno-

heptose, which is utilized for assembly of the lipopolysaccharide inner core. In Gram-positive bacteria the enzyme is involved in biosynthesis of GDP-D-glycero- α -D-manno-heptose, which is required

for assembly of S-layer glycoprotein.

References: [150, 149, 301, 144, 285]

[EC 5.3.1.28 created 2010]

EC 5.3.2 Interconverting keto- and enol-groups

EC 5.3.2.1

Accepted name: phenylpyruvate tautomerase

Reaction: keto-phenylpyruvate = enol-phenylpyruvate

Other name(s): phenylpyruvic keto-enol isomerase
Systematic name: phenylpyruvate *keto—enol*-isomerase
Comments: Also acts on other arylpyruvates.

References: [31, 151, 152]

[EC 5.3.2.1 created 1961]

EC 5.3.2.2

Accepted name: oxaloacetate tautomerase

Reaction: *keto*-oxaloacetate = *enol*-oxaloacetate **Other name(s):** oxalacetic keto-enol isomerase **Systematic name:** oxaloacetate *keto—enol*-isomerase

References: [13]

[EC 5.3.2.2 created 1972]

EC 5.3.3 Transposing C=C bonds

EC 5.3.3.1

Accepted name: steroid Δ -isomerase

Reaction: a 3-oxo- Δ^5 -steroid = a 3-oxo- Δ^4 -steroid

Other name(s): hydroxysteroid isomerase; steroid isomerase; Δ^5 -ketosteroid isomerase; Δ^5 (or Δ^4)-3-keto steroid iso-

merase; Δ^5 -steroid isomerase; 3-oxosteroid isomerase; Δ^5 -3-keto steroid isomerase; Δ^5 -3-oxosteroid

isomerase

Systematic name: 3-oxosteroid Δ^5 - Δ^4 -isomerase

Comments: May be at least three distinct enzymes.

References: [72, 137, 281]

[EC 5.3.3.1 created 1961]

EC 5.3.3.2

Accepted name: isopentenyl-diphosphate Δ -isomerase

Reaction: isopentenyl diphosphate = dimethylallyl diphosphate

Other name(s): isopentenylpyrophosphate Δ -isomerase; methylbutenylpyrophosphate isomerase; isopentenylpyrophosphate

rophosphate isomerase

Systematic name: isopentenyl-diphosphate Δ^3 - Δ^2 -isomerase

Comments: The enzyme from Streptomyces sp. strain CL190 requires FMN and NAD(P)H as cofactors. Activity

is reduced if FMN is replaced by FAD, but the enzyme becomes inactive when NAD(P)H is replaced

by NAD⁺ or NADP⁺. That enzyme also requires Mg²⁺, Mn²⁺ or Ca²⁺ for activity.

References: [134, 30, 3]

[EC 5.3.3.2 created 1961, modified 2002]

EC 5.3.3.3

Accepted name: vinylacetyl-CoA Δ -isomerase **Reaction:** vinylacetyl-CoA = crotonyl-CoA

Other name(s): vinylacetyl coenzyme A Δ -isomerase; vinylacetyl coenzyme A isomerase; Δ^3 -cis- Δ^2 -trans-enoyl-CoA

isomerase

Systematic name: vinylacetyl-CoA Δ^3 - Δ^2 -isomerase Comments: Also acts on 3-methyl-vinylacetyl-CoA.

References: [172, 239]

[EC 5.3.3.3 created 1961]

EC 5.3.3.4

Accepted name: muconolactone Δ -isomerase

Reaction: (*S*)-5-oxo-2,5-dihydrofuran-2-acetate = 5-oxo-4,5-dihydrofuran-2-acetate

Other name(s): muconolactone isomerase

Systematic name: 5-oxo-4,5-dihydrofuran-2-acetate Δ^3 - Δ^2 -isomerase

References: [214, 216]

[EC 5.3.3.4 created 1961 as EC 3.1.1.16, part transferred 1972 to EC 5.3.3.4 rest to EC 5.3.3.4]

EC 5.3.3.5

Accepted name: cholestenol Δ -isomerase

Reaction: 5α -cholest-7-en-3 β -ol = 5α -cholest-8-en-3 β -ol

Systematic name: Δ^7 -cholestenol Δ^7 - Δ^8 -isomerase

References: [315]

[EC 5.3.3.5 created 1972]

EC 5.3.3.6

Accepted name: methylitaconate Δ -isomerase

Reaction: methylitaconate = 2,3-dimethylmaleate

Other name(s): methylitaconate isomerase Systematic name: methylitaconate Δ^2 - Δ^3 -isomerase

References: [156]

[EC 5.3.3.6 created 1972]

EC 5.3.3.7

Accepted name: aconitate Δ -isomerase

Reaction: *trans*-aconitate = *cis*-aconitate

Other name(s): aconitate isomerase Systematic name: aconitate Δ^2 - Δ^3 -isomerase

Comments: cis-Aconitate is used to designate the isomer (Z)-prop-1-ene-1,2,3-tricarboxylate. This isomerization

could take place either in a direct cis-trans interconversion or by an allelic rearrangement; the enzyme

has been shown to catalyse the latter change.

References: [148, 147]

[EC 5.3.3.7 created 1972]

EC 5.3.3.8

Accepted name: dodecenoyl-CoA isomerase

Reaction: (3Z)-dodec-3-enoyl-CoA = (2E)-dodec-2-enoyl-CoA

Other name(s): dodecenoyl-CoA Δ -isomerase; Δ^3 -cis- Δ^2 -trans-enoyl-CoA isomerase; acetylene-allene isomerase;

dodecenoyl-CoA Δ -isomerase; dodecenoyl-CoA Δ^3 -cis- Δ^2 -trans-isomerase

Systematic name: dodecenoyl-CoA (3Z)-(2E)-isomerase

Comments: Also catalyses the interconversion of 3-acetylenic fatty acyl thioesters and (+)-2,3-dienoyl fatty acyl

thioesters, with fatty acid chain lengths C_6 to C_{12} .

References: [195, 273, 274, 275]

[EC 5.3.3.8 created 1978, modified 1980]

EC 5.3.3.9

Accepted name: prostaglandin- $A_1 \Delta$ -isomerase

Reaction: (13E)-(15S)-15-hydroxy-9-oxoprosta-10,13-dienoate = (13E)-(15S)-15-hydroxy-9-oxoprosta-11,13-

dienoate

Other name(s): prostaglandin A isomerase

Systematic name: (13E)-(15S)-15-hydroxy-9-oxoprosta-10,13-dienoate Δ^{10} - Δ^{11} -isomerase

Comments: Interconverts prostaglandin A_1 and prostaglandin C_1 .

References: [102]

[EC 5.3.3.9 created 1978]

EC 5.3.3.10

Accepted name: 5-carboxymethyl-2-hydroxymuconate Δ -isomerase

Reaction: 5-carboxymethyl-2-hydroxymuconate = 5-carboxy-2-oxohept-3-enedioate

Systematic name: 5-carboxymethyl-2-hydroxymuconate Δ^2 , Δ^4 -2-oxo, Δ^3 -isomerase

References: [87]

[EC 5.3.3.10 created 1984]

EC 5.3.3.11

Accepted name: isopiperitenone Δ -isomerase isopiperitenone = piperitenone **Systematic name:** isopiperitenone Δ^8 - Δ^4 -isomerase

Comments: Involved in the biosynthesis of menthol and related monoterpenes in peppermint (*Mentha piperita*)

leaves.

References: [146]

[EC 5.3.3.11 created 1989]

EC 5.3.3.12

Accepted name: L-dopachrome isomerase

Reaction: L-dopachrome = 5,6-dihydroxyindole-2-carboxylate

Other name(s): dopachrome tautomerase; tyrosinase-related protein 2; TRP-1; TRP2; TRP-2; tyrosinase-related

protein-2; dopachrome Δ^7 , Δ^2 -isomerase; dopachrome Δ -isomerase; dopachrome conversion factor; dopachrome isomerase; dopachrome oxidoreductase; dopachrome-rearranging enzyme; DCF; DCT;

dopachrome keto-enol isomerase; L-dopachrome-methyl ester tautomerase

Systematic name: L-dopachrome keto-enol isomerase

Comments: A zinc enzyme. Stereospecific for L-dopachrome. Dopachrome methyl ester is a substrate, but

dopaminochrome (2,3-dihydroindole-5,6-quinone) is not (see also EC 4.1.1.84, D-dopachrome de-

carboxylase).

References: [266, 220, 221]

[EC 5.3.3.12 created 1992, modified 1999, modified 2005]

EC 5.3.3.13

Accepted name: polyenoic fatty acid isomerase

Reaction: (5Z,8Z,11Z,14Z,17Z)-icosapentaenoate = (5Z,7E,9E,14Z,17Z)-icosapentaenoate

Other name(s): PFI; eicosapentaenoate $cis-\Delta^{5,8,11,14,17}$ -eicosapentaenoate $cis-\Delta^{5}$ -trans- $\Delta^{7,9}$ - $cis-\Delta^{14,17}$ isomerase;

(5Z,8Z,11Z,14Z,17Z)-eicosapentaenoate $\Delta^{8,11}$ - $\Delta^{7,8}$ -isomerase (incorrect); (5Z,8Z,11Z,14Z,17Z)-

eicosapentaenoate $\Delta^{8,11}$ - $\Delta^{7,9}$ -isomerase (*trans*-double-bond-forming)

Systematic name: (5Z,8Z,11Z,14Z,17Z)-icosapentaenoate $\Delta^{8,11}$ - $\Delta^{7,9}$ -isomerase (*trans*-double-bond-forming)

Comments: The enzyme from the red alga Ptilota filicina catalyses the isomerization of skip dienes (methylene-

interrupted double bonds) in a broad range of fatty acids and fatty-acid analogues, such as arachido-

nate and γ -linolenate, to yield a conjugated triene.

References: [317, 319, 318, 341]

[EC 5.3.3.13 created 2004]

EC 5.3.3.14

Accepted name: *trans*-2-decenoyl-[acyl-carrier protein] isomerase

Reaction: a *trans*-dec-2-enoyl-[acyl-carrier protein] = a *cis*-dec-3-enoyl-[acyl-carrier protein]

Other name(s): β-hydroxydecanoyl thioester dehydrase; *trans-2-cis-*3-decenoyl-ACP isomerase; *trans-2,cis-*3-

decenoyl-ACP isomerase; trans-2-decenoyl-ACP isomerase; FabM; decenoyl-[acyl-carrier-protein]

 Δ^2 -trans- Δ^3 -cis-isomerase

Systematic name: decenoyl-[acyl-carrier protein] Δ^2 -trans- Δ^3 -cis-isomerase

Comments: While the enzyme from *Escherichia coli* is highly specific for the 10-carbon enoyl-ACP, the enzyme

from *Streptococcus pneumoniae* can also use the 12-carbon enoyl-ACP as substrate in vitro but not 14- or 16-carbon enoyl-ACPs [177]. ACP can be replaced by either CoA or *N*-acetylcysteamine thioesters. The *cis*-3-enoyl product is required to form unsaturated fatty acids, such as palmitoleic

acid and cis-vaccenic acid, in dissociated (or type II) fatty-acid biosynthesis.

References: [39, 32, 177, 52]

[EC 5.3.3.14 created 2006]

EC 5.3.3.15

Accepted name: ascopyrone tautomerase

Reaction: 1,5-anhydro-4-deoxy-D-*glycero*-hex-3-en-2-ulose = 1,5-anhydro-4-deoxy-D-*glycero*-hex-1-en-3-ulose

Other name(s): ascopyrone isomerase; ascopyrone intramolecular oxidoreductase; 1,5-anhydro-D-glycero-hex-3-en-2-

ulose tautomerase; APM tautomerase; ascopyrone P tautomerase; APTM

Systematic name: 1,5-anhydro-4-deoxy-D-*glycero*-hex-3-en-2-ulose Δ^3 - Δ^1 -isomerase

Comments: This enzyme catalyses one of the steps in the anhydrofructose pathway, which leads to the degrada-

tion of glycogen and starch via 1,5-anhydro-D-fructose [338, 337]. The other enzymes involved in this pathway are EC 4.2.1.110 (aldos-2-ulose dehydratase), EC 4.2.1.111 (1,5-anhydro-D-fructose dehydratase) and EC 4.2.2.13 [exo- $(1\rightarrow 4)$ - α -D-glucan lyase]. Ascopyrone P is an anti-oxidant [337].

References: [338, 337]

[EC 5.3.3.15 created 2006]

EC 5.3.4 Transposing S-S bonds

EC 5.3.4.1

Accepted name: protein disulfide-isomerase

Reaction: Catalyses the rearrangement of -S-S- bonds in proteins

Other name(s): S-S rearrangase

Systematic name: protein disulfide-isomerase

Comments: Needs reducing agents or partly reduced enzyme; the reaction depends on sulfhydryl-disulfide inter-

change.

References: [170, 84]

[EC 5.3.4.1 created 1972]

EC 5.3.99 Other intramolecular oxidoreductases

[5.3.99.1 Deleted entry. hydroperoxide isomerase. Reaction due to combined action of EC 4.2.1.92 (hydroperoxide dehydratase) and EC 5.3.99.6 (allene-oxide cyclase)]

[EC 5.3.99.1 created 1972, deleted 1992]

EC 5.3.99.2

Accepted name: prostaglandin-D synthase

Reaction: $(5Z,13E,15S)-9\alpha,11\alpha$ -epidioxy-15-hydroxyprosta-5,13-dienoate = $(5Z,13E,15S)-9\alpha,15$ -dihydroxy-

11-oxoprosta-5,13-dienoate

Other name(s): prostaglandin-H₂ Δ-isomerase; prostaglandin-R-prostaglandin D isomerase; PGH-PGD

isomerase (5,13)-(15S)-9 α ,11 α -epidioxy-15-hydroxyprosta-5,13-dienoate Δ -isomerase (incorrect); (5,13)-(15S)-9 α ,11 α -epidioxy-15-hydroxyprosta-5,13-dienoate D-isomerase; prostaglandin endoper-

oxide Δ -isomerase; prostaglandin D synthetase

Systematic name: $(5Z,13E,15S)-9\alpha,11\alpha$ -epidioxy-15-hydroxyprosta-5,13-dienoate D-isomerase

Comments: Brings about the opening of the epidioxy bridge. Some enzymes require glutathione.

References: [48, 257]

[EC 5.3.99.2 created 1976, modified 1990]

EC 5.3.99.3

Accepted name: prostaglandin-E synthase

Reaction: (5Z,13E)-(15S)- 9α , 11α -epidioxy-15-hydroxyprosta-5, 13-dienoate = (5Z,13E)-(15S)- 11α , 15-

dihydroxy-9-oxoprosta-5,13-dienoate

Other name(s): prostaglandin-H₂ E-isomerase; endoperoxide isomerase; endoperoxide isomerase; prostaglandin R-

prostaglandin E isomerase; prostaglandin endoperoxide E isomerase; PGE isomerase; PGH-PGE isomerase; PGE₂ isomerase; prostaglandin endoperoxide E₂ isomerase; prostaglandin H-E isomerase

Systematic name: (5Z,13E)-(15S)- 9α , 11α -epidioxy-15-hydroxyprosta-5, 13-dienoate E-isomerase

Comments: Brings about the opening of the epidioxy bridge. Requires glutathione.

References: [211, 282]

[EC 5.3.99.3 created 1976, modified 1990]

EC 5.3.99.4

Accepted name: prostaglandin-I synthase

Reaction: (5Z,13E)-(15S)- 9α , 11α -epidioxy-15-hydroxyprosta-5,13-dienoate = (5Z,13E)-(15S)-6, 9α -epoxy-

11α,15-dihydroxyprosta-5,13-dienoate

Other name(s): prostacyclin synthase; prostacycline synthetase; prostagladin I2 synthetase; PGI₂ synthase; PGI₂ synthase;

thetase

Systematic name: (5Z,13E)-(15S)- 9α , 11α -epidioxy-15-hydroxyprosta-5, 13-dienoate 6-isomerase

Comments: Converts prostaglandin H₂ into prostaglandin I₂ (prostacyclin). A heme-thiolate protein.

References: [63, 297]

[EC 5.3.99.4 created 1984, modified 1990]

EC 5.3.99.5

Accepted name: thromboxane-A synthase

Reaction: (5Z,13E)-(15S)- 9α , 11α -epidioxy-15-hydroxyprosta-5, 13-dienoate = (5Z,13E)-(15S)- 9α , 11α -epoxy-

15-hydroxythromboxa-5,13-dienoate

Other name(s): thromboxane synthase; (5Z,13E)-(15S)- 9α , 11α -epidioxy-15-hydroxyprosta-5, 13-dienoate

thromboxane-A2-isomerase

Systematic name: (5Z,13E)-(15S)- 9α , 11α -epidioxy-15-hydroxyprosta-5,13-dienoate isomerase

Comments: Converts prostaglandin H₂ into thromboxane A₂. A heme-thiolate protein.

References: [253, 298]

[EC 5.3.99.5 created 1984, modified 1990]

EC 5.3.99.6

Accepted name: allene-oxide cyclase

Reaction: (9Z)-(13S)-12,13-epoxyoctadeca-9,11,15-trienoate = (15Z)-12-oxophyto-10,15-dienoate

Systematic name: (9Z)-(13S)-12,13-epoxyoctadeca-9,11,15-trienoate isomerase (cyclizing)

Comments: Allene oxides formed by the action of EC 4.2.1.92 hydroperoxide dehydratase, are converted into cy-

clopentenone derivatives.

References: [104]

[EC 5.3.99.6 created 1992]

EC 5.3.99.7

Accepted name: styrene-oxide isomerase

Reaction: styrene oxide = phenylacetaldehyde

Other name(s): SOI

Systematic name: styrene-oxide isomerase (epoxide-cleaving)

Comments: Highly specific.

References: [107]

[EC 5.3.99.7 created 1992]

EC 5.3.99.8

Accepted name: capsanthin/capsorubin synthase **Reaction:** (1) violaxanthin = capsorubin

(2) antheraxanthin = capsanthin

Other name(s): CCS; ketoxanthophyll synthase; capsanthin-capsorubin synthase

Systematic name: violaxanthin—capsorubin isomerase (ketone-forming)

Comments: This multifunctional enzyme is induced during chromoplast differentiation in plants [34]. Isomeriza-

tion of the epoxide ring of violaxanthin gives the cyclopentyl-ketone of capsorubin or capsanthin.

References: [34, 163, 327]

[EC 5.3.99.8 created 2005]

EC 5.3.99.9

Accepted name: neoxanthin synthase **Reaction:** violaxanthin = neoxanthin

Other name(s): NSY

Systematic name: violaxanthin—neoxanthin isomerase (epoxide-opening)

Comments: The opening of the epoxide ring of violaxanthin generates a chiral allene. Neoxanthin is a precursor

of the plant hormone abscisic acid and the last product of carotenoid synthesis in green plants [33].

References: [6, 33]

[EC 5.3.99.9 created 2005]

EC 5.4 Intramolecular transferases

This subclass contains enzymes that transfer a group from one position to another within a molecule. Sub-subclasses are based on the group transferred: acyl group (EC 5.4.1), phospho group (EC 5.4.2), amino group (EC 5.4.3), hydroxy group (EC 5.4.4), or some other group (EC 5.4.99).

EC 5.4.1 Transferring acyl groups

EC 5.4.1.1

Accepted name: lysolecithin acylmutase **Reaction:** 2-lysolecithin = 3-lysolecithin

Other name(s): lysolecithin migratase lysolecithin 2,3-acylmutase

References: [300]

EC 5.4.1.2

Accepted name: precorrin-8X methylmutase

Reaction: precorrin-8X = hydrogenobyrinate

Other name(s): precorrin isomerase; hydrogenobyrinic acid-binding protein

Systematic name: precorrin-8X 11,12-methylmutase

References: [287, 244, 240, 54]

[EC 5.4.1.2 created 1999]

EC 5.4.2 Phosphotransferases (phosphomutases)

Most of these enzymes were previously listed as sub-subclass EC 2.7.5, under the heading: 'Phosphotransferases with regeneration of donors, apparently catalysing intramolecular transfers'. The reaction for these enzymes was written in the form: pi

 $X-(P)2 + AP = BP + X-(P)_2.$

In fact, since phosphorylation of the acceptor produces a bisphosphate that is identical to the donor, the overall reaction is an isomerization of AP into BP, with the bisphosphate acting catalytically. It has been shown in some cases that the enzyme has a functional phosphate group, which can act as the donor. Phosphate is transferred to the substrate, forming the intermediate bisphosphate; the other phosphate group is subsequently transferred to the enzyme:¡p¿

 $E-P+AP=E+X-(P)_2$ ip; $X-(P)_2 + E = BP + E-P.$

The bisphosphate may be firmly attached to the enzyme during the catalytic cycle, or, in other cases, may be released so that free bisphosphate is required as an activator. Under these circumstances, it was agreed in 1983 that all of these enzymes should be listed together in this sub-subclass based on the overall isomerase reaction.

EC 5.4.2.1

Accepted name: phosphoglycerate mutase

Reaction: 2-phospho-D-glycerate = 3-phospho-D-glycerate

Other name(s): phosphoglycerate phosphomutase; phosphoglyceromutase; glycerate phosphomutase (diphosphoglyc-

 $erate\ cofactor);\ monophosphoglycerate\ mutase;\ monophosphoglyceromutase;\ diphosphoglycerate\ mutase;\ diphosphoglyceromutase;\ GriP\ mutase;\ MPGM;\ PGA\ mutase;\ PGAM-i;$

PGAM; PGAM-d; PGM

Systematic name: D-phosphoglycerate 2,3-phosphomutase

Comments: The enzymes from mammals and from yeast are phosphorylated by (2R)-2,3-bis-phosphoglycerate,

which is also an intermediate (see introduction to section EC 5.4.2). With the rabbit muscle enzyme, dissociation of bisphosphate from the enzyme is much slower than the overall isomerization. These enzymes also catalyse, slowly, the reactions of EC 5.4.2.4 bisphosphoglycerate mutase; they were formerly listed as EC 2.7.5.3. Enzymes from wheat, rice, insects and some fungi, however, have maximum activity in the absence of 2,3-bisphosphoglycerate, and were formerly listed under the present

number as phosphoglycerate phosphomutase.

References: [99, 234, 243]

[EC 5.4.2.1 created 1961 (EC 2.7.5.3 created 1961, incorporated 1984)]

EC 5.4.2.2

Accepted name: phosphoglucomutase

Reaction: α-D-glucose 1-phosphate = D-glucose 6-phosphate **Other name(s):** glucose phosphomutase; phosphoglucose mutase

Systematic name: α -D-glucose 1,6-phosphomutase

Comments: Maximum activity is only obtained in the presence of α-D-glucose 1,6-bisphosphate. This bisphos-

phate is an intermediate in the reaction, being formed by transfer of a phosphate residue from the enzyme to the substrate, but the dissociation of bisphosphate from the enzyme complex is much slower than the overall isomerization. The enzyme also catalyses (more slowly) the interconversion of 1-phosphate and 6-phosphate isomers of many other α -D-hexoses, and the interconversion of α -D-ribose

1-phosphate and 5-phosphate.

References: [130, 201, 235, 234, 278]

[EC 5.4.2.2 created 1961 as EC 2.7.5.1, transferred 1984 to EC 5.4.2.2]

EC 5.4.2.3

Accepted name: phosphoacetylglucosamine mutase

Reaction: N-acetyl- α -D-glucosamine 1-phosphate = N-acetyl-D-glucosamine 6-phosphate

Other name(s): acetylglucosamine phosphomutase; acetylglucosamine phosphomutase; acetylglucosamine phosphomutase

phosphomutase; phospho-N-acetylglucosamine mutase; N-acetyl-D-glucosamine 1,6-phosphomutase

Systematic name: N-acetyl- α -D-glucosamine 1,6-phosphomutase

Comments: The enzyme is activated by N-acetyl- α -D-glucosamine 1,6-bisphosphate.

References: [44, 165, 234, 237]

[EC 5.4.2.3 created 1961 as EC 2.7.5.2, transferred 1984 to EC 5.4.2.3]

EC 5.4.2.4

Accepted name: bisphosphoglycerate mutase

Reaction: 3-phospho-D-glyceroyl phosphate = 2,3-bisphospho-D-glycerate

Other name(s): diphosphoglycerate mutase; glycerate phosphomutase; bisphosphoglycerate synthase; bisphospho-

glyceromutase; biphosphoglycerate synthase; diphosphoglyceric mutase; 2,3-diphosphoglycerate mutase; phosphoglyceromutase; 2,3-diphosphoglycerate synthase; DPGM; 2,3-bisphosphoglycerate

mutase; BPGM; diphosphoglyceromutase; 2,3-diphosphoglyceromutase

Systematic name: 3-phospho-D-glycerate 1,2-phosphomutase

Comments: In the direction shown, this enzyme is phosphorylated by 3-phosphoglyceroyl phosphate, to give

phosphoenzyme and 3-phosphoglycerate. The latter is rephosphorylated by the enzyme to yield 2,3-bisphosphoglycerate, but this reaction is slowed by dissociation of 3-phosphoglycerate from the enzyme, which is therefore more active in the presence of added 3-phosphoglycerate. This enzyme also catalyses, slowly, the reactions of EC 3.1.3.13 (bisphosphoglycerate phosphatase) and EC 5.4.2.1

(phosphoglycerate mutase).

References: [234, 242, 243]

[EC 5.4.2.4 created 1961 as EC 2.7.5.4, transferred 1984 to EC 5.4.2.4]

EC 5.4.2.5

Accepted name: phosphoglucomutase (glucose-cofactor)

Reaction: α-D-glucose 1-phosphate = D-glucose 6-phosphate

Other name(s): glucose phosphomutase; glucose-1-phosphate phosphotransferase

Systematic name: α-D-glucose 1,6-phosphomutase (glucose-cofactor)

Comments: The enzyme is activated by D-glucose, which probably acts as an acceptor for a phosphate residue

from the substrate, thus being itself converted into the product.

References: [85, 234]

[EC 5.4.2.5 created 1972 as EC 2.7.5.5, transferred 1984 to EC 5.4.2.5]

EC 5.4.2.6

Accepted name: β-phosphoglucomutase

Reaction: β -D-glucose 1-phosphate = β -D-glucose 6-phosphate

Systematic name: β-D-glucose 1,6-phosphomutase

Comments: No cofactor requirement has been demonstrated.

References: [26, 234]

[EC 5.4.2.6 created 1984]

EC 5.4.2.7

Accepted name: phosphopentomutase

Reaction: α -D-ribose 1-phosphate = D-ribose 5-phosphate

Other name(s): phosphodeoxyribomutase; deoxyribose phosphomutase; deoxyribomutase; phosphoribomutase;

α-D-glucose-1,6-bisphosphate:deoxy-D-ribose-1-phosphate phosphotransferase; D-ribose 1,5-

phosphomutase

Systematic name: α-D-ribose 1,5-phosphomutase

Comments: Also converts 2-deoxy-α-D-ribose 1-phosphate into 2-deoxy-D-ribose 5-phosphate. α-D-Ribose 1,5-

bisphosphate, 2-deoxy-α-D-ribose 1,5-bisphosphate, or α-D-glucose 1,6-bisphosphate can act as co-

factor.

References: [105, 132, 234]

[EC 5.4.2.7 created 1972 as EC 2.7.5.6, transferred 1984 to EC 5.4.2.7]

EC 5.4.2.8

Accepted name: phosphomannomutase

Reaction: α -D-mannose 1-phosphate = D-mannose 6-phosphate

Other name(s): mannose phosphomutase; phosphomannose mutase; D-mannose 1,6-phosphomutase

Systematic name: α-D-mannose 1,6-phosphomutase

Comments: α-D-Mannose 1,6-bisphosphate or α-D-glucose 1,6-bisphosphate can act as cofactor.

References: [264]

[EC 5.4.2.8 created 1981 as EC 2.7.5.7, transferred 1984 to EC 5.4.2.8]

EC 5.4.2.9

Accepted name: phospho*enol*pyruvate mutase

Reaction: phospho*enol*pyruvate = 3-phosphonopyruvate

Other name(s): phospho*enol*pyruvate-phosphonopyruvate phosphomutase; PEP phosphomutase; phosphomutase;

phoenolpyruvate phosphomutase; PEPPM; PEP phosphomutase

Systematic name: phospho*enol*pyruvate 2,3-phosphonomutase

Comments: Involved in the biosynthesis of the C-P bond, although the equilibrium greatly favours phos-

phoenolpyruvate.

References: [35, 113, 251]

[EC 5.4.2.9 created 1990]

EC 5.4.2.10

Accepted name: phosphoglucosamine mutase

Reaction: α-D-glucosamine 1-phosphate = D-glucosamine 6-phosphate

Systematic name: α-D-glucosamine 1,6-phosphomutase

Comments: The enzyme is involved in the pathway for bacterial cell-wall peptidoglycan and lipopolysaccharide

biosyntheses, being an essential step in the pathway for UDP-*N*-acetylglucosamine biosynthesis. The enzyme from *Escherichia coli* is activated by phosphorylation and can be autophosphorylated in vitro by α -D-glucosamine 1,6-bisphosphate, which is an intermediate in the reaction, α -D-glucose 1,6-bisphosphate or ATP. It can also catalyse the interconversion of α -D-glucose 1-phosphate and glucose

6-phosphate, although at a much lower rate.

References: [190, 60, 129, 127, 128]

EC 5.4.3 Transferring amino groups

[5.4.3.1 Deleted entry. ornithine 4,5-aminomutase. This reaction was due to a mixture of EC 5.1.1.12 (ornithine racemase) and EC 5.4.3.5 (D-ornithine 4,5-aminomutase)]

[EC 5.4.3.1 created 1972, deleted 1976]

EC 5.4.3.2

Accepted name: lysine 2,3-aminomutase

Reaction: L-lysine = (3S)-3,6-diaminohexanoate

Systematic name: L-lysine 2,3-aminomutase

Comments: Activity is stimulated by S-adenosyl-L-methionine and pyridoxal phosphate.

References: [1, 340]

[EC 5.4.3.2 created 1972]

EC 5.4.3.3

Accepted name: β-lysine 5,6-aminomutase

Reaction: (3S)-3,6-diaminohexanoate = (3S,5S)-3,5-diaminohexanoate

Other name(s): β -lysine mutase; L- β -lysine 5,6-aminomutase Systematic name: (3S)-3,6-diaminohexanoate 5,6-aminomutase

Comments: Requires a cobamide coenzyme.

References: [238, 270]

[EC 5.4.3.3 created 1972]

EC 5.4.3.4

Accepted name: D-lysine 5,6-aminomutase

Reaction: D-lysine = 2,5-diaminohexanoate

Other name(s): D-α-lysine mutase; adenosylcobalamin-dependent D-lysine 5,6-aminomutase

Systematic name: D-2,6-diaminohexanoate 5,6-aminomutase

Comments: Requires a cobamide coenzyme.

References: [198, 271]

[EC 5.4.3.4 created 1972, modified 2003]

EC 5.4.3.5

Accepted name: D-ornithine 4,5-aminomutase

Reaction: D-ornithine = (2R,4S)-2,4-diaminopentanoate

Other name(s): D- α -ornithine 5,4-aminomutase; D-ornithine aminomutase

Systematic name: D-ornithine 4,5-aminomutase

Comments: A pyridoxal-phosphate protein that requires a cobamide coenzyme for activity.

References: [267]

[EC 5.4.3.5 created 1972 as EC 5.4.3.1, transferred 1976 to EC 5.4.3.5, modified 2003]

EC 5.4.3.6

Accepted name: tyrosine 2,3-aminomutase

Reaction: L-tyrosine = 3-amino-3-(4-hydroxyphenyl)propanoate

Other name(s): tyrosine α,β -mutase

Systematic name: L-tyrosine 2,3-aminomutase

Comments: Requires ATP.

References: [157]

[EC 5.4.3.6 created 1976]

EC 5.4.3.7

Accepted name: leucine 2,3-aminomutase

Reaction: (2S)-α-leucine = (3R)-β-leucine Systematic name: (2S)-α-leucine 2,3-aminomutase Comments: Requires a cobamide coenzyme.

References: [83, 227, 226]

[EC 5.4.3.7 created 1982]

EC 5.4.3.8

Accepted name: glutamate-1-semialdehyde 2,1-aminomutase
Reaction: L-glutamate 1-semialdehyde = 5-aminolevulinate
Other name(s): glutamate-1-semialdehyde aminotransferase
Systematic name: (S)-4-amino-5-oxopentanoate 4,5-aminomutase

Comments: Requires pyridoxal phosphate.

References: [95]

[EC 5.4.3.8 created 1983]

EC 5.4.4 Transferring hydroxy groups

EC 5.4.4.1

Accepted name: (hydroxyamino)benzene mutase

Reaction: (hydroxyamino)benzene = 2-aminophenol

Other name(s): HAB mutase; hydroxylaminobenzene hydroxymutase; hydroxylaminobenzene mutase

Systematic name: (hydroxyamino)benzene hydroxymutase

References: [108, 59]

[EC 5.4.4.1 created 2003]

EC 5.4.4.2

Accepted name: isochorismate synthase **Reaction:** chorismate = isochorismate

Other name(s): MenF

Systematic name: isochorismate hydroxymutase

Comments: Requires Mg^{2+} . The reaction is reversible.

References: [336, 303, 55, 58]

[EC 5.4.4.2 created 1972 as EC 5.4.99.6, transferred 2003 to EC 5.4.4.2]

EC 5.4.4.3

Accepted name: 3-(hydroxyamino)phenol mutase

Reaction: 3-hydroxyaminophenol = aminohydroquinone **Other name(s):** 3-hydroxylaminophenol mutase; 3HAP mutase **Systematic name:** 3-(hydroxyamino)phenol hydroxymutase

References: [246]

EC 5.4.99 Transferring other groups

EC 5.4.99.1

Accepted name: methylaspartate mutase

Reaction: L-*threo*-3-methylaspartate = L-glutamate

Other name(s): glutamate mutase; glutamic mutase; glutamic isomerase; glutamic acid mutase; glutamic acid iso-

merase; methylaspartic acid mutase; β-methylaspartate-glutamate mutase; glutamate isomerase

Systematic name: L-threo-3-methylaspartate carboxy-aminomethylmutase

Comments: Requires a cobamide coenzyme.

References: [21, 309]

[EC 5.4.99.1 created 1961]

EC 5.4.99.2

Accepted name: methylmalonyl-CoA mutase

Reaction: (R)-methylmalonyl-CoA = succinyl-CoA

Other name(s): methylmalonyl-CoA CoA-carbonyl mutase; methylmalonyl coenzyme A mutase; methylmalonyl

coenzyme A carbonylmutase; (S)-methylmalonyl-CoA mutase; (R)-2-methyl-3-oxopropanoyl-CoA

CoA-carbonylmutase [incorrect]

Systematic name: (*R*)-methylmalonyl-CoA CoA-carbonylmutase

Comments: Requires a cobamide coenzyme.

References: [20]

[EC 5.4.99.2 created 1961, modified 1983]

EC 5.4.99.3

Accepted name: 2-acetolactate mutase

Reaction: 2-acetolactate = 3-hydroxy-3-methyl-2-oxobutanoate **Other name(s):** acetolactate mutase; acetohydroxy acid isomerase

Systematic name: 2-acetolactate methylmutase

Comments: Requires ascorbic acid; also converts 2-aceto-2-hydroxybutanoate to 3-hydroxy-3-methyl-2-

oxopentanoate.

References: [7]

[EC 5.4.99.3 created 1972]

EC 5.4.99.4

Accepted name: 2-methyleneglutarate mutase

Reaction: 2-methyleneglutarate = 2-methylene-3-methylsuccinate

Other name(s): α -methyleneglutarate mutase

Systematic name: 2-methyleneglutarate carboxy-methylenemethylmutase

Comments: Requires a cobamide coenzyme.

References: [155, 156]

[EC 5.4.99.4 created 1972]

EC 5.4.99.5

Accepted name: chorismate mutase **Reaction:** chorismate = prephenate

Other name(s): hydroxyphenylpyruvate synthase Systematic name: chorismate pyruvatemutase

References: [50, 169, 268, 325]

[EC 5.4.99.5 created 1972]

[5.4.99.6 Transferred entry, isochorismate synthase, Now EC 5.4.4.2, isochorismate synthase]

[EC 5.4.99.6 created 1972, deleted 2003]

EC 5.4.99.7

Accepted name: lanosterol synthase

Reaction: (S)-2,3-epoxysqualene = lanosterol

Other name(s): 2,3-epoxysqualene lanosterol cyclase; squalene-2,3-oxide-lanosterol cyclase; lanosterol 2,3-

oxidosqualene cyclase; squalene 2,3-epoxide:lanosterol cyclase; 2,3-oxidosqualene sterol cyclase; oxidosqualene cyclase; 2,3-oxidosqualene-lanosterol cyclase;

oxidosqualene-lanosterol cyclase; squalene epoxidase-cyclase

Systematic name: (S)-2,3-epoxysqualene mutase (cyclizing, lanosterol-forming)

References: [61]

[EC 5.4.99.7 created 1961 as EC 1.99.1.13, transferred 1965 to EC 1.14.1.3, part transferred 1972 to EC 5.4.99.7 rest to EC 1.14.99.7]

EC 5.4.99.8

Accepted name: cycloartenol synthase

Reaction: (S)-2,3-epoxysqualene = cycloartenol

Other name(s): 2,3-epoxysqualene cycloartenol-cyclase; squalene-2,3-epoxide-cycloartenol cyclase; 2,3-

epoxysqualene cycloartenol-cyclase; 2,3-epoxysqualene-cycloartenol cyclase; 2,3-oxidosqualene-

cycloartenol cyclase

Systematic name: (S)-2,3-epoxysqualene mutase (cyclizing, cycloartenol-forming)

References: [236]

[EC 5.4.99.8 created 1972]

EC 5.4.99.9

Accepted name: UDP-galactopyranose mutase

Reaction: UDP-D-galactopyranose = UDP-D-galacto- $(1\rightarrow 4)$ -furanose

Systematic name: UDP-D-galactopyranose furanomutase

References: [294]

[EC 5.4.99.9 created 1984]

[5.4.99.10 Deleted entry. isomaltulose synthetase. Now included with EC 5.4.99.11, isomaltulose synthase]

[EC 5.4.99.10 created 1984, deleted 1992]

EC 5.4.99.11

Accepted name: isomaltulose synthase

Reaction: sucrose = $6-O-\alpha$ -D-glucopyranosyl-D-fructofuranose

Other name(s): isomaltulose synthetase; sucrose α -glucosyltransferase; trehalulose synthase

Systematic name: sucrose glucosylmutase

Comments: The enzyme simultaneously produces isomaltulose (6-O- α -D-glucopyranosyl-D-fructose) and smaller

amounts of trehalulose (1-O- α -D-glucopyranosyl- β -D-fructose) from sucrose.

References: [45, 46]

[EC 5.4.99.11 created 1989 (EC 5.4.99.10 created 1984, incorporated 1992)]

EC 5.4.99.12

Accepted name: tRNA-pseudouridine synthase I **Reaction:** tRNA uridine = tRNA pseudouridine

Other name(s): tRNA-uridine isomerase; tRNA pseudouridylate synthase I; transfer ribonucleate pseudouridine syn-

thetase; pseudouridine synthase; transfer RNA pseudouridine synthetase

Systematic name: tRNA-uridine uracilmutase

Comments: The uridylate residues at positions 38, 39 and 40 of nearly all tRNAs are isomerized to pseudouridine.

References: [15, 133]

[EC 5.4.99.12 created 1990]

EC 5.4.99.13

Accepted name: isobutyryl-CoA mutase

Reaction: 2-methylpropanoyl-CoA = butanoyl-CoA

Other name(s): isobutyryl coenzyme A mutase; butyryl-CoA:isobutyryl-CoA mutase

Systematic name: 2-methylpropanoyl-CoA CoA-carbonylmutase

Comments: Requires a cobamide coenzyme.

References: [37]

[EC 5.4.99.13 created 1992]

EC 5.4.99.14

Accepted name: 4-carboxymethyl-4-methylbutenolide mutase

Reaction: 4-carboxymethyl-4-methylbut-2-en-1,4-olide = 4-carboxymethyl-3-methylbut-2-en-1,4-olide

Other name(s): 4-methyl-2-enelactone isomerase; 4-methylmuconolactone methylisomerase; 4-methyl-3-enelactone

methyl isomerase

Systematic name: 4-carboxymethyl-4-methylbut-2-en-1,4-olide methylmutase

References: [40]

[EC 5.4.99.14 created 1992]

EC 5.4.99.15

Accepted name: $(1\rightarrow 4)$ - α -D-glucan 1- α -D-glucosylmutase

Reaction: $4-[(1\rightarrow 4)-\alpha-D-glucosyl]_{n-1}-D-glucose = 1-\alpha-D-[(1\rightarrow 4)-\alpha-D-glucosyl]_{n-1}-\alpha-D-glucopyranoside$

Other name(s): malto-oligosyltrehalose synthase; maltodextrin α -D-glucosyltransferase

Systematic name: $(1\rightarrow 4)$ - α -D-glucan 1- α -D-glucosylmutase

Comments: The enzyme from *Arthrobacter sp.*, *Sulfolobus acidocaldarius* acts on $(1\rightarrow 4)$ - α -D-glucans containing

three or more $(1\rightarrow 4)$ - α -linked D-glucose units. Not active towards maltose.

References: [183, 203, 202]

[EC 5.4.99.15 created 1999]

EC 5.4.99.16

Accepted name: maltose α-D-glucosyltransferase

Reaction: maltose = α , α -trehalose

Other name(s): trehalose synthase; maltose glucosylmutase

Systematic name: maltose α -D-glucosylmutase

References: [207, 208]

[EC 5.4.99.16 created 1999]

EC 5.4.99.17

Accepted name: squalene—hopene cyclase

Reaction: (1) squalene = hop-22(29)-ene

(2) squalene + H_2O = hopan-22-ol

Systematic name: squalene mutase (cyclizing)

Comments: The enzyme produces a constant ratio of about 5:1 hopene:hopanol.

References: [250, 117]

[EC 5.4.99.17 created 2002]

EC 5.4.99.18

Accepted name: 5-(carboxyamino)imidazole ribonucleotide mutase

Reaction: 5-carboxyamino-1-(5-phospho-D-ribosyl)imidazole = 5-amino-1-(5-phospho-D-ribosyl)imidazole-4-

carboxylate

Other name(s): N⁵-CAIR mutase; PurE; N⁵-carboxyaminoimidazole ribonucleotide mutase; class I PurE

Systematic name: 5-carboxyamino-1-(5-phospho-D-ribosyl)imidazole carboxymutase

Comments: In eubacteria, fungi and plants, this enzyme, along with EC 6.3.4.18, 5-(carboxyamino)imidazole ri-

bonucleotide synthase, is required to carry out the single reaction catalysed by EC 4.1.1.21, phosphoribosylaminoimidazole carboxylase, in vertebrates [76]. In the absence of EC 6.3.2.6, phosphoribosylaminoimidazolesuccinocarboxamide synthase, the reaction is reversible [191]. The substrate is readily converted into 5-amino-1-(5-phospho-D-ribosyl)imidazole by non-enzymic decarboxylation

[191].

References: [192, 200, 191, 184, 77, 76]

[EC 5.4.99.18 created 2006]

EC 5.5 Intramolecular lyases

This subclass contains a single sub-subclass for enzymes that catalyse reactions in which a group can be regarded as being eliminated from one part of a molecule, leaving a double bond, while remaining covalently attached to the molecule (intramolecular lyases; EC 5.5.1).

EC 5.5.1 Intramolecular lyases (only sub-subclass identified to date)

EC 5.5.1.1

Accepted name: muconate cycloisomerase

Reaction: 2,5-dihydro-5-oxofuran-2-acetate = cis,cis-hexadienedioate

Other name(s): muconate cycloisomerase I; *cis,cis*-muconate-lactonizing enzyme; *cis,cis*-muconate cycloisomerase;

muconate lactonizing enzyme; 4-carboxymethyl-4-hydroxyisocrotonolactone lyase (decyclizing);

CatB; MCI

Systematic name: 2,5-dihydro-5-oxofuran-2-acetate lyase (decyclizing)

Comments: Requires Mn²⁺. Also acts (in the reverse reaction) on 3-methyl-*cis*,*cis*-hexadienedioate and, very

slowly, on cis,trans-hexadienedioate. Not identical with EC 5.5.1.7 (chloromuconate cycloisomerase)

or EC 5.5.1.11 (dichloromuconate cycloisomerase).

References: [214, 216, 261]

[EC 5.5.1.1 created 1961]

EC 5.5.1.2

Accepted name: 3-carboxy-cis,cis-muconate cycloisomerase

Reaction: 2-carboxy-2,5-dihydro-5-oxofuran-2-acetate = *cis*,*cis*-butadiene-1,2,4-tricarboxylate

Other name(s): β-carboxymuconate lactonizing enzyme; 3-carboxymuconolactone hydrolase

Systematic name: 2-carboxy-2,5-dihydro-5-oxofuran-2-acetate lyase (decyclizing)

References: [215, 216]

[EC 5.5.1.2 created 1972]

EC 5.5.1.3

Accepted name: tetrahydroxypteridine cycloisomerase

Reaction: tetrahydroxypteridine = xanthine-8-carboxylate **Systematic name:** tetrahydroxypteridine lyase (isomerizing)

References: [188]

[EC 5.5.1.3 created 1972]

EC 5.5.1.4

Accepted name: inositol-3-phosphate synthase

Reaction: D-glucose 6-phosphate = 1D-myo-inositol 3-phosphate

Other name(s): myo-inositol-1-phosphate synthase; D-glucose 6-phosphate cycloaldolase; inositol 1-phosphate syn-

thatase; glucose 6-phosphate cyclase; inositol 1-phosphate synthetase; glucose-6-phosphate inositol monophosphate cycloaldolase; glucocycloaldolase; 1L-myo-inositol-1-phosphate lyase (isomerizing)

Systematic name: 1D-myo-inositol-3-phosphate lyase (isomerizing)

Comments: Requires NAD⁺, which dehydrogenates the -CHOH- group to -CO- at C-5 of the glucose 6-

phosphate, making C-6 into an active methylene, able to condense with the -CHO at C-1. Finally, the

enzyme-bound NADH reconverts C-5 into the -CHOH- form.

References: [70, 254, 22, 23]

[EC 5.5.1.4 created 1972, modified 2001]

EC 5.5.1.5

Accepted name: carboxy-cis,cis-muconate cyclase

Reaction: 3-carboxy-2,5-dihydro-5-oxofuran-2-acetate = 3-carboxy-*cis*,*cis*-muconate

Other name(s): 3-carboxymuconate cyclase

Systematic name: 3-carboxy-2,5-dihydro-5-oxofuran-2-acetate lyase (decyclizing)

References: [100]

[EC 5.5.1.5 created 1972]

EC 5.5.1.6

Accepted name: chalcone isomerase
Reaction: a chalcone = a flavanone
Other name(s): chalcone-flavanone isomerase
Systematic name: flavanone lyase (decyclizing)

References: [199]

[EC 5.5.1.6 created 1972]

EC 5.5.1.7

Accepted name: chloromuconate cycloisomerase

Reaction: 2-chloro-2,5-dihydro-5-oxofuran-2-acetate = 3-chloro-*cis*,*cis*-muconate

Other name(s): muconate cycloisomerase II

Systematic name: 2-chloro-2,5-dihydro-5-oxofuran-2-acetate lyase (decyclizing)

Comments: Requires Mn²⁺. The product of cycloisomerization of 3-chloro-*cis*, *cis*-muconate spontaneously elim-

inates chloride to produce *cis*-4-carboxymethylenebut-2-en-4-olide. Also acts (in the reverse direction) on 2-chloro-*cis*, *cis*-muconate. Not identical with EC 5.5.1.1 (muconate cycloisomerase) or EC

5.5.1.11 (dichloromuconate cycloisomerase).

References: [247]

[EC 5.5.1.7 created 1983]

EC 5.5.1.8

Accepted name: bornyl diphosphate synthase

Reaction: geranyl diphosphate = (+)-bornyl diphosphate

Other name(s): bornyl pyrophosphate synthase; bornyl pyrophosphate synthetase; (+)-bornylpyrophosphate cyclase;

geranyl-diphosphate cyclase (ambiguous)

Systematic name: (+)-bornyl-diphosphate lyase (decyclizing)

References: [53]

[EC 5.5.1.8 created 1984]

EC 5.5.1.9

Accepted name: cycloeucalenol cycloisomerase **Reaction:** cycloeucalenol = obtusifoliol

Other name(s): cycloeucalenol—obtusifoliol isomerase

Systematic name: cycloeucalenol lyase (cyclopropane-decyclizing)

Comments: Opens the cyclopropane ring of a number of related 4α -methyl- 9β -19-cyclosterols, but not those with

a 4β-methyl group, with formation of an 8(9) double bond. Involved in the synthesis of plant sterols.

References: [111, 230]

[EC 5.5.1.9 created 1986]

EC 5.5.1.10

Accepted name: α-pinene-oxide decyclase

Reaction: α -pinene oxide = (Z)-2-methyl-5-isopropylhexa-2,5-dienal

Other name(s): α -pinene oxide lyase

Systematic name: α -pinene-oxide lyase (decyclizing)

Comments: Both rings of pinene are cleaved in the reaction.

References: [98]

[EC 5.5.1.10 created 1990]

EC 5.5.1.11

Accepted name: dichloromuconate cycloisomerase

Reaction: 2,4-dichloro-2,5-dihydro-5-oxofuran-2-acetate = 2,4-dichloro-*cis*,*cis*-muconate

Systematic name: 2,4-dichloro-2,5-dihydro-5-oxofuran-2-acetate lyase (decyclizing)

Comments: Requires Mn²⁺. The product of cycloisomerization of dichloro-*cis*,*cis*-muconate spontaneously elim-

inates chloride to produce *cis*-4-carboxymethylene-3-chlorobut-2-en-4-olide. Also acts, in the reverse direction, on *cis*,*cis*-muconate and its monochloro-derivatives, but with lower affinity. Not identical with EC 5.5.1.1 (muconate cycloisomerase) or EC 5.5.1.7 (chloromuconate cycloisomerase).

References: [154]

[EC 5.5.1.11 created 1992]

EC 5.5.1.12

Accepted name: copalyl diphosphate synthase

Reaction: geranylgeranyl diphosphate = (+)-copalyl diphosphate

Systematic name: (+)-copalyl-diphosphate lyase (decyclizing)

Comments: Part of a bifunctional enzyme involved in the biosynthesis of abietadiene. See also EC 4.2.3.18 (abi-

etadiene synthase)

References: [224, 225, 223, 233, 222]

[EC 5.5.1.12 created 2002]

EC 5.5.1.13

Accepted name: *ent-*copalyl diphosphate synthase

Reaction: geranylgeranyl diphosphate = *ent*-copalyl diphosphate

Other name(s): *ent*-kaurene synthase A; *ent*-kaurene synthetase A; *ent*-CDP synthase

Systematic name: *ent-*copalyl-diphosphate lyase (decyclizing)

Comments: Part of a bifunctional enzyme involved in the biosynthesis of kaurene. See also EC 4.2.3.19 (ent-

kaurene synthase)

References: [73, 277, 138, 292]

[EC 5.5.1.13 created 2002]

EC 5.5.1.14

Accepted name: *syn*-copalyl-diphosphate synthase

Reaction: geranyl diphosphate = 9α -copalyl diphosphate

Other name(s): OsCyc1; OsCPSsyn; syn-CPP synthase; syn-copalyl diphosphate synthase

Systematic name: 9α-copalyl-diphosphate lyase (decyclizing)

Comments: Requires a divalent metal ion, preferably Mg²⁺, for activity. This class II terpene synthase produces

syn-copalyl diphosphate, a precursor of several rice phytoalexins, including oryzalexin S and momilactones A and B. Phytoalexins are diterpenoid secondary metabolites that are involved in the defense mechanism of the plant, and are produced in response to pathogen attack through the perception of elicitor signal molecules such as chitin oligosaccharide, or after exposure to UV irradiation. The enzyme is constitutively expressed in the roots of plants where one of its products, momilactone B, acts as an allelochemical (a molecule released into the environment to suppress the growth of neighbouring plants). In other tissues the enzyme is upregulated by conditions that stimulate the biosynthesis of

phytoalexins.

References: [217, 328]

[EC 5.5.1.14 created 2008]

EC 5.5.1.15

Accepted name: terpentedienyl-diphosphate synthase

Reaction: geranylgeranyl diphosphate = terpentedienyl diphosphate

Other name(s): terpentedienol diphosphate synthase; Cyc1; clerodadienyl diphosphate synthase

Systematic name: terpentedienyl-diphosphate lyase (decyclizing)

Comments: Requires Mg²⁺. Contains a DXDD motif, which is a characteristic of diterpene cylases whose reac-

tions are initiated by protonation at the 14,15-double bond of geranylgeranyl diphosphate (GGDP) [103]. The triggering proton is lost at the end of the cyclization reaction [69]. The product of the reaction, terpentedienyl diphosphate, is the substrate for EC 4.2.3.36, terpentetriene synthase and is a

precursor of the diterpenoid antibiotic terpentecin.

References: [57, 103, 69]

[EC 5.5.1.15 created 2008]

EC 5.5.1.16

Accepted name: halimadienyl-diphosphate synthase

Reaction: geranylgeranyl diphosphate = halima-5(6),13-dien-15-yl diphosphate

Other name(s): Rv3377c; halimadienyl diphosphate synthase; tuberculosinol diphosphate synthase

Systematic name: halima-5(6),13-dien-15-yl-diphosphate lyase (cyclizing)

Comments: Requires Mg^{2+} for activity. This enzyme is found in pathogenic prokaryotes such as Mycobac-

terium tuberculosis but not in non-pathogens such as Mycobacterium smegmatis so may play a role in pathogenicity. The product of the reaction is subsequently dephosphorylated yielding tuberculosi-

nol [halima-5(6),13-dien-15-ol].

References: [206]

[EC 5.5.1.16 created 2008]

EC 5.99 Other isomerases

This subclass contains miscellaneous enzymes in a single sub-subclass (EC 5.99.1).

EC 5.99.1 Sole sub-subclass for isomerases that do not belong in the other subclasses

EC 5.99.1.1

Accepted name: thiocyanate isomerase

Reaction: benzyl isothiocyanate = benzyl thiocyanate

Other name(s): isothiocyanate isomerase

Systematic name: benzyl-thiocyanate isomerase

References: [304]

[EC 5.99.1.1 created 1965]

EC 5.99.1.2

Accepted name: DNA topoisomerase

Reaction: ATP-independent breakage of single-stranded DNA, followed by passage and rejoining

Other name(s): type I DNA topoisomerase; untwisting enzyme; relaxing enzyme; nicking-closing enzyme; swivelase;

ω-protein; deoxyribonucleate topoisomerase; topoisomerase; type I DNA topoisomerase

Systematic name: DNA topoisomerase

Comments: These enzymes bring about the conversion of one topological isomer of DNA into another, e.g., the

relaxation of superhelical turns in DNA, the interconversion of simple and knotted rings of single-stranded DNA, and the intertwisting of single-stranded rings of complementary sequences, *cf.* EC

5.99.1.3 DNA topoisomerase (ATP-hydrolysing).

References: [89]

[EC 5.99.1.2 created 1984]

EC 5.99.1.3

Accepted name: DNA topoisomerase (ATP-hydrolysing)

Reaction: ATP-dependent breakage, passage and rejoining of double-stranded DNA

Other name(s): type II DNA topoisomerase; DNA-gyrase; deoxyribonucleate topoisomerase; deoxyribonucleic topoi-

somerase; topoisomerase; DNA topoisomerase II;

Systematic name: DNA topoisomerase (ATP-hydrolysing)

Comments: The enzyme can introduce negative superhelical turns into double-stranded circular DNA. One unit

has nicking-closing activity, and another catalyses super-twisting and hydrolysis of ATP (cf. EC

5.99.1.2 DNA topoisomerase).

References: [89]

[EC 5.99.1.3 created 1984]

EC 5.99.1.4

Accepted name: 2-hydroxychromene-2-carboxylate isomerase

Reaction: 2-hydroxy-2*H*-chromene-2-carboxylate = (3*E*)-4-(2-hydroxyphenyl)-2-oxobut-3-enoate **Other name(s):** HCCA isomerase; 2HC2CA isomerase; 2-hydroxychromene-2-carboxylic acid isomerase

Systematic name: 2-hydroxy-2*H*-chromene-2-carboxylate—(3*E*)-4-(2-hydroxyphenyl)-2-oxobut-3-enoate isomerase

Comments: This enzyme is involved in naphthalene degradation.

References: [212, 139, 67, 290]

[EC 5.99.1.4 created 2010]

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